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of Central American Birds
III

FAMILIES COTINGIDAE, PIPRIDAE, FORMICARIIDAE,
FURNARIIDAE, DENDROCOLAPTIDAE, AND PICIDAE

By

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ILLUSTRATED WITH PHOTOGRAPHS BY THE AUTHOR AND
DRAWINGS BY DON R. ECKELBERRY



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Bicolored Antbird

To

JUAN SCHROEDER F.

whose friendly interest from my first
day in El General helped to prepare
the way for many of these studies

Edited by

JOHN DAVIS

and

GENE M. CHRISTMAN

at the

Museum of Vertebrate Zoology
University of California, Berkeley

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INTRODUCTION

This third volume of Life Histories contains accounts of representatives of five families of the Tyranni, that major division of the great order of passerine birds which is considered more primitive, because its members have vocal organs of simpler structure and accordingly produce less varied songs than we find in the larger branch of this order, the Oscines or true songbirds. The five families treated here are all confined to the Western Hemisphere, and their members are found largely in the tropical regions of the American continents. Only one of these families, the Furnariidae or ovenbirds, is well represented in the temperate regions of southern South America, and only a single representative of these five large families has extended its range as far northward as the southern boundary of the United States. The sixth family of the Tyranni that is represented north of the Isthmus of Panamá by more than one rare species, the Tyrannidae or American flycatchers, was, in order to keep these volumes fairly uniform in size, treated in Part II. For the same reason, the present volume has been extended beyond the passerines to include the nearly cosmopolitan woodpeckers.

The observations herein reported have been gathered over an interval of nearly forty years, mainly in the Central American localities that were described in the Introduction to the first volume of this series. Because so little had been published on the behavior of the five Neotropical families to which this book is chiefly devoted, I was from the first far more eager to discover their nests and to study their habits, than in the case of such widespread and comparatively well-known groups as the cosmopolitan finches, thrushes, jays, and swallows, and even the less widely distributed tanagers, wood warblers, vireos, wrens, and American flycatchers, the biographies of which form the bulk of the preceding volumes. But the finding of nests of representatives of these five families of sub-oscine passerines, and the accumulation of information about them, proceeded slowly.

For a variety of reasons, the majority of these birds are difficult to study. In Central America, scarcely any of them lives in such intimate association with man as do many songbirds and flycatchers, which often build their nests close to our dwellings and almost force themselves on our attention. The nests of the cotingas are almost invariably placed so high that they are difficult or impossible to reach; they are in holes in trees, or they are so bulky and well-enclosed that one cannot see what is happening in them, or they are so exceedingly slight that they escape detection. The nests of the abundant antbirds are mostly open and low, but they are hidden in the forest undergrowth or in scarcely penetrable second-growth thickets where they are hard to find. In addition, these nests are exposed to such heavy predation that few of the studies that one eagerly begins, when a nest has been found, can be carried to a successful conclusion. The ovenbirds breed in burrows in the earth and holes in trees or in elaborate nests so well enclosed that one cannot see their contents, even with the help of a mirror and an electric bulb, without opening them and seriously upsetting their attendants. The secretive woodcreepers or woodhewers prefer obscure natural crannies in trees to old woodpeckers' holes which have more obvious doorways; this group is among the most elusive and difficult to study of all the tropical American birds. The nests of manakins escape detection because of their slightness and the obscure coloration of their diminutive makers, but such nests are often low and abundant. In the case

of one species of manakin, alone of the birds treated in this volume, I have found nests in numbers corresponding to those of many of the songbirds and flycatchers. Finally, in Central America the woodpeckers usually carve their holes high in dead trees the uncertain stability of which discourages climbing. For all these reasons, few of the biographies included in this book are as complete and detailed as I wished them to be.

Of the 53 species of birds that have been given chapters in this book, 13 were the subjects of papers published earlier by me in ornithological journals. These fall into two groups: those for which I have, since the original accounts were written, accumulated a substantial amount of new information, and those for which I can add little or nothing to my previously published reports. For the first group of species, I have expanded and to a considerable extent rewritten my early accounts in order to present here the most complete biography that available information permits. The subjects of these amplified accounts are the Masked Tityra, Slaty Antshrike, Black-faced Antthrush, Buff-throated or Chestnut-tailed Automolus, Olivaceous Piculet, and Golden-naped Woodpecker. For the second group of species I have, in view of the high cost of printing, abridged my original papers for inclusion in the present volume. Without omitting any important observations, much condensation was possible when the original papers contained, for purposes of comparison, numerous references to related species. In the present book, this information is to be found in the chapters devoted to these other species, and comparisons are made in the general summary for each family. The subjects of these shortened accounts are the White-winged Becard, Yellow-thighed Manakin, Spotted Antbird, White-flanked Antwren, Spotted-crowned or Allied Woodcreeper, Golden-olive Woodpecker, and Hairy Woodpecker.

For whatever faulty observations, errors of fact, or wrong interpretations this volume and its predecessors may contain, I alone am responsible. For the faults and inconsistencies in presentation which the discerning reader may notice, I beg indulgence, for during the whole time that these books were being written and printed I have been some three thousand miles from the editors and publishers. The use of air mail for frequent exchanges of letters, and for transmitting proof sheets, greatly facilitated the preparation of these volumes for the press, but it has not been a wholly adequate substitute for personal consultations. Then, too, changes in nomenclature, especially those resulting from the recent great interest in providing adequate vernacular designations for the species of tropical American birds, have been numerous during the two decades since the writing of this series was begun, with resulting inconsistencies in the texts of the several volumes.

By far the greater part of the manuscript of this volume was completed late in 1960. Considerable additions were made in July of 1965, when Dr. Miller informed me that at last he was ready to prepare the work for the press. His untimely death has resulted in another long delay in publication. Some further observations made by me in the last two years have been incorporated in the text, and I have added references to some of the more important pertinent papers that have appeared since the general summaries of families were written more than seven years ago. Since there was never a definite plan to carry this series beyond this third part, I have published in ornithological journals my studies of non-passerines (other than woodpeckers) that might have filled additional volumes. For the convenience of those interested in the habits of Neotropical birds, I give in an appendix a list of my life history studies published elsewhere than in the present series.

In addition to those whose help was acknowledged in the introductions to Parts I and II of this work, I am grateful to the following: to the Cooper Ornithological Society, for supporting the publication of this series; to Alden H. Miller, for his painstaking editing of Parts I and II and for starting to edit the present volume, a task interrupted by his death; to John Davis and Gene M. Christman, for completing the editing of this volume and seeing it through the press; to Jane R. Durham, for preparing for the press, proofreading, and indexing Part II; to Gene M. Christman, for taking charge of the illustrations in Parts II and III; to C. V. Duff, for the large share that he took in financing and promoting the sales of this series, especially Parts I and II; to Darryl and María Cole, for hospitality on their farm "Loma Linda," near Cañas Gordas, where some of my later studies were made; to Leslie and Lydia Holdridge, for hospitality at "La Selva" in the Sarapiquí lowlands, where additional observations were made; to the Frank M. Chapman Memorial Fund of the American Museum of Natural History of New York, for supporting my field work in recent years; and finally to my wife, Pamela, and son, Edwin, for much assistance in the field.

Finca "Los Cusingos,"
San Isidro del General,
Costa Rica,
September 27, 1967.

FAMILY COTINGIDAE

BLACK-CROWNED TITYRA

Eratator inquisitor

The Black-crowned Tityra is a stocky bird about seven inches in length. The forehead, crown, and lores of the male are black, the back and rump pearl gray, the cheeks and nape and under plumage white or nearly so. His tail feathers are pale gray at the base and black on the terminal half, with white tips. His wings have gray coverts and black remiges, in the midst of which a small patch of white shows conspicuously in flight. The female is pale chestnut or whitish on the forehead, black on the crown, grayish brown on the hindhead, and bright chestnut on the sides of the head. Her back and rump are grayish brown. Her tail is brownish gray and dull black, and the wings are gray and black. Her under plumage is white, shading into pale gray on the chest and sides. In both sexes, the short, thick bill has a black upper mandible and a blue-gray lower mandible. The eyes are brown and the feet are gray.

In sea birds, white plumage is too common to attract attention, but among the birds of the tropical forest it is a mark of distinction. Of the passerine birds that I have seen in the Central American forests, only four, all members of the cotinga family, are predominantly white. Two are tityras and two are snowy cotingas (*Carpodectes*). Of these, the Masked Tityra is by far the most abundant and widespread. Although the Black-crowned Tityra has an extended range stretching from southern México to northern Argentina, it seems everywhere to be more rare. In all parts of Central America where I have worked, it has been far less abundant than its bare-cheeked relative, and from parts of the northern Pacific slope where the latter is not uncommon, the Black-crowned Tityra appears to be absent. In Costa Rica, it ranges from sea level up to nearly 4000 feet, at which altitude I saw a pair in the Cañas Gordas region near the Panamanian border, but above 2500 feet I have rarely found this species anywhere.

Wandering birds of the treetops, Black-crowned Tityras are found both in the highest levels of the forest and among the crowns of trees growing in neighboring cultivated areas. I have usually seen them in pairs or in family groups of three or four. Apparently they remain mated throughout the year.

FOOD

In November and December of 1943, a trio of these tityras came on sunny mornings to hunt in the tops of the low guava and other trees growing in my doorway and the surrounding pastures, which adjoin the high forest. There were an adult male and two individuals in the plumage of females, probably a pair with a young bird. One morning I followed them for nearly an hour as they foraged in close company from tree to tree through the riverside pasture and along its borders. I had an excellent opportunity to study their method of obtaining food. They flew in leisurely fashion from branch to branch through the treetops, pausing for a few moments here and there on a slender twig while they turned their heads from side to side, scrutinizing the foliage until they spied a tempting morsel, then darting out to snatch it up in their bills. Most of their prey was plucked from the leaves while

the birds were still in the air, after which the food was carried to a convenient perch. I saw them catch brown moths and green orthopterans, among the latter protectively colored forms which only keen eyes could descry amid the foliage they so closely matched. The tityras knocked their prey against the branch where they rested, not violently in the fashion of the Boat-billed Flycatcher, but in a quiet, restrained manner. Larger insects were subjected to this treatment for several minutes before they were swallowed. These birds were always sedate in manner and deliberate in their movements, save when they suddenly darted out to capture an insect. After making the circuit of the pasture, they returned to the woodland. Although insects form the bulk of the tityras' diet, they also eat berries and other fruits.

VOICE

All of the notes that I have heard from the Black-crowned Tityra were dry or nasal, insect-like, and usually low and weak. Those that I watched foraging through the trees in the pasture voiced only faint, dry notes, almost like the rustling sounds produced by the wings of some insect. A pair that I watched while the female built a nest frequently uttered a dry, nasal note with a somewhat rattling quality. At other times the male delivered a disyllable which sounded like *corre*, a thin note with a most peculiar intonation. Another utterance was higher and softer, more melodious, but very slight. At times this last was prolonged into a low, weak trill. Frequently the notes of these birds reminded me of some of the bizarre sounds made by the Acorn Woodpecker, but the tityra's voice is far less forceful than that of the woodpecker. The voice of the Black-crowned Tityra is sharper, thinner, and less grunty than that of the Masked Tityra.

NEST BUILDING

On the Pacific slope of southern Costa Rica, the Black-crowned Tityra nests in April, May, and June. The nest is built high above the ground in a cavity in a dead tree, usually a hole made by woodpeckers, and preferably one of the spacious chambers carved into fairly sound wood by species of *Tripurus*. These holes have a doorway just wide enough to permit the passage of the tityra. Five nests in southern Costa Rica were in holes of the Golden-naped Woodpecker, and a nest in eastern Perú was in a cavity carved by the Crimson-bellied Black Woodpecker. The hole occupied by a pair of tityras nesting on the Caribbean slope of Costa Rica was probably made by a pair of Black-cheeked Woodpeckers that was breeding close by. Often the tityras take possession of a hole still used by the woodpeckers as a dormitory, causing the woodpeckers to carve a new chamber for themselves. The eight nests of the Black-crowned Tityra that I have found were all in clearings near the forest's edge. In height they ranged from about 40 to more than 100 feet above the ground, and all were inaccessible to me.

For the tityra, nest building seems to consist merely in filling the bottom of the woodpecker's hole with a great litter of loose material, including dead or dying leaves, twigs, dry flower stalks, and the like. This work is done by the chestnut-cheeked female, while her mate as a rule follows her faithfully, or at least watches from a convenient perch, and often makes ineffectual gestures of helping. In June, 1939, I watched a tityra build a late nest, in a hole from which three fledgling Golden-naped Woodpeckers had recently departed. This was in a tall dead tree standing beside a roadway in El General. I found her working very actively be-

tween nine and ten o'clock on the morning of June 15. In this hour she brought twiglet after twiglet in rapid succession, working with a concentration of purpose rare in tityras of either this or the bare-cheeked species. On 33 trips to the nest, she came 29 times with fine sticks, flower-stalks, or the like, three times with small, yellowing leaves, and once with a brown leaf. All of this material was brought from the forest about 200 feet away, and most probably all was gathered high up in the trees, for I have seen tityras collect nest material only well above the ground. The doorway of the woodpeckers' hole was so narrow that the tityra had to squeeze through, but she was so skillful in passing in the sticks that only once did I see one knocked from her bill.

The male tityra behaved much as the male Masked Tityra does while his mate is filling the nest cavity. At the outset of the work, before I saw the female take anything into the hole, he brought a short, fine twig and clumsily managed to push it through the doorway while he clung in front, without entering. Then, when his mate flew off to fetch a twig, he followed, and on her return he accompanied her with a small, wilted leaf in his bill. While the female entered the hole with her burden, he rested in the tree with his leaf; and when she came out and flew away to seek another twig, he followed, still bearing the leaf. On ten consecutive visits of the female to the nest, he accompanied her with the leaf in his bill, always the same one, I believe. Once he actually went to the doorway with it; but as his mate at this point flew off to the forest, he hurried after her without having relinquished the leaf. Several times, while she was in the hole, he hovered in the air in front of it, as though desiring to take in the leaf. But he never found time to accomplish this, and in the end he dropped it to the ground. After this, he contented himself with following his mate faithfully back and forth, carrying nothing in his bill. Toward the end of the hour his zeal began to wane, and he sometimes rested in the dead tree while his more energetic mate went off to the forest to find more material.

Two days later, this male tityra came with a fine twig an inch or two in length, which he carried back and forth as he followed the female on three of her excursions to bring material from the forest. Four times he took the twiglet to the entrance of the nest and seemed to try to push inside with it, but he did not actually enter. Finally, still following the female, he carried away his trifling burden, and I saw it no more.

While the pair of tityras are still prospecting for a nest site, and before the female has begun in earnest the work of filling the chosen cavity, the male makes a great show of carrying leaves or twigs in his bill, as though to advertise the fact that he and his mate were house hunting. Most or all of this symbolic material soon reaches the ground. The following year, I watched another female tityra build in El General. This bird brought chiefly leaves, instead of twigs, to the woodpeckers' hole a hundred feet up in a dead tree at the edge of the forest. Some of the leaves were big and encountered enough air-resistance to cause her inconvenience as she flew. Her mate would sometimes bring a small yellow or brown leaf in his bill, hold it a while, then let it fall. Once he carried one of these leaves up to the doorway but dropped it outside.

On September 4, 1940, I spent a short time watching a Black-crowned Tityra build a nest in a hole belonging to a pair of Crimson-bellied Black Woodpeckers. The nest was high in an isolated tree standing in a clearing not far from the forest at Satipo in the eastern foothills of the Peruvian Andes. Here also the actual work of filling the cavity was done by the female. The male sometimes followed on her

visits to the nest, and once he carried a small leaf in his bill but failed to take it into the hole.

The tityras' habit of choosing for their nest a hole still used for sleeping by the woodpeckers who carved it often brings the two species into competition, but not, as far as I have seen, into physical conflict. The cavity into which the tityra carried so much material in June of 1939 was still occupied as a dormitory by a pair of Golden-naped Woodpeckers and the three young whom they had reared in it. About the time the tityras began to fill their chamber with dry trash, the parent woodpeckers started to carve a new nest hole in another branch of the same great tree. Although the woodpeckers saw the tityras going in and out of their dormitory, they seemed quite indifferent to this invasion of their home, and they calmly continued their carving. As a young male woodpecker went to rest in the evening of the day when the tityras had built so actively, he threw out a twig and a leaf. Only the three young birds slept in their usual dormitory that night. The male parent retired into an older hole in the same tree, and the female went to sleep with her mate after an ineffectual attempt to join her young in the reduced space of the chamber which had formerly accommodated all five of the woodpeckers.

Three evenings later, two of the woodpeckers retired to rest in the new hole, which was still not deep enough to accommodate more of the family, and the other three slept in the old hole that was serving as a temporary lodge pending the completion of the new one. They had quite abandoned the nest hole to the tityra. As far as I saw, the tityras never even threatened the woodpeckers, but the filling of the hole was enough to cause its abandonment. If the tityras had not interfered, these Golden-naped Woodpeckers would probably have continued for many months to lodge in the cavity where they had reared their young. Because of the lateness of the season, the tityras did not nest in the hole that they took from the woodpeckers.

Early in April of the following year, I saw a pair of tityras take another hole from a pair of Golden-naped Woodpeckers, with the difference that the woodpeckers were now preparing to breed and were not parents with full-grown young. The hole claimed by the tityras was an old one, in which the woodpeckers had apparently slept for many months. A little lower in the same trunk, the latter had already begun to carve the new chamber, which would be used for the eggs of the current season. While the tityras filled the old hole with leaves, the pair of woodpeckers went intently ahead with their chiselling, paying no attention at all to the birds passing and repassing so close above them.

Late one afternoon, I found the female woodpecker looking out of the new hole, which had been rapidly enlarged in the last few days. Soon she crawled out and climbed up to her old dormitory at the top of the tall dead trunk. Entering, she threw out in rapid succession about 36 pieces of leaf, which fluttered slowly downward, then several mouthfuls of wood dust from the bottom of the cavity. To all appearances, the tityra's nest building had been wholly undone! After cleaning out the old house, the female woodpecker descended to the new apartment to sleep with her mate. After this, the Golden-napes, comfortably installed in their new home, where they were soon engaged in rearing a family, took no heed of their neighbors in the upper story. Undaunted by the removal of all her furnishings, the tityra finished her nest and later in the month was incubating.

The hole into which I watched the tityra carry material in eastern Perú had been used on the preceding night as a dormitory by a pair of Crimson-bellied Black

Woodpeckers. While the tityras built, the woodpeckers worked at a new hole in a neighboring limb of the dead tree, ignoring the trespassers. But after the female tityra had taken many billfuls of material into their dormitory, one of the woodpeckers entered and started to throw it out. Meanwhile the tityras returned, the female with petioles in her bill, and quietly looked on while the woodpecker undid her work. They made no attack and voiced no protest. Over a great area, the relations of the Black-crowned Tityra with woodpeckers of the genus *Tripusurus* appear to follow the same pacific course. A similar relationship was noted between the Masked Tityra and the same species of woodpecker.

INCUBATION

I have never seen the eggs of the Black-crowned Tityra, and I have found no published description of them. Some sets consist of at least three eggs, for on the Caribbean slope of Costa Rica I watched a nest from which this number of young emerged.

Incubation is performed by the female alone. I spent seven hours watching the nest which the tityras rebuilt after the Golden-naped Woodpecker dropped all of the materials through the doorway. Four sessions which I timed lasted, respectively, 23, 57, 44, and 25 minutes. Six recesses were 11, 18, 30, 26, 16, and 30 minutes. Computed on the basis of the average session of 37.1 minutes and the average recess of 19.6 minutes, this tityra spent 65.4 per cent of the time on her eggs. But she began her night session early; on the afternoon when I watched, she entered her nest at 4:16 p.m. and remained continuously until nightfall, two hours later. If this interval were included among her sessions, it would substantially increase the percentage which expresses the constancy of incubation. However, this would be inconsistent with the practice adopted in these life histories.

When she returned to the nest after an outing, the female tityra often brought a dry leaf in her bill. The habit of bringing additional material to the nest while incubation is in progress is well developed in theotinga family, and I have witnessed it at nests of the Masked Tityra, the Rose-throated Becard, the White-winged Becard, and the Cinnamon Becard.

While his mate was absent, the male Black-crowned Tityra often guarded the nest, usually perching on the end of one of the truncate branches at the very top of the dead nest tree, over a hundred feet above the ground. What a splendid figure he made, standing sentinel-like so high in the air, his white plumage gleaming in the sunshine! Sometimes, becoming restless, he moved to one of the living trees that grew close by. From this vantage point he also had the nest in view, but he never remained long in these trees. In 131 minutes while his mate was away seeking food, the male was absent from the near vicinity of the nest only 6 minutes, and possibly even then he rested where he could see the nest but was invisible to me. During 294 minutes while the female incubated, the male was present on or near the nest tree only 66 minutes and absent 228 minutes.

Sometimes, when from a more distant tree the male tityra saw his mate fly from the nest, he came at once to stand atop the nest tree. While the female was absent, the male sometimes clung at the nest's doorway and looked in, but I did not once see him enter. Usually he would linger a short while on top of the nest tree after the female's return to her eggs. At other times he would come and perch there, doubtless expecting her to fly off a good while before she was ready to go. But the

male never delayed long by the nest except while the female was away. I saw him assert dominion over the nest tree only when some Masked Tityras rested on it and he drove them off, pulling feathers from the back of one. He never molested the Golden-naped Woodpeckers to whose industry he and his mate owed their nest chamber.

In the following year, I watched a tityra incubate at another nest, on the Caribbean slope of Costa Rica. In 3 hours the female took 3 sessions, lasting 16, 71, and 27 minutes, and 3 recesses, which lasted 18, 36, and 9 minutes. She spent 64.4 per cent of the 3 hours in the nest. At this nest, the male did not guard in the female's absence as consistently as did the male at the earlier nest.

THE NESTLINGS

On April 22 the parent tityras were bringing food to the nest on the Caribbean slope, indicating that the eggs had hatched. I was not able to see the nestlings until they were feathered and could look through their doorway, but when they flew out I counted three. At various times in the following 25 days, I spent a total of 8½ hours watching this nest. The female brought food 34 times and the male brought food 27 times. The food was mostly carried within the thick bills of the parents, where it was difficult or impossible to see. But at times, especially after the nestlings grew older and were served larger articles, I recognized through the binoculars the projecting legs or wings of insects. As far as I saw, these formed the entire diet of the nestlings. Once I recognized a brown moth, and a number of the insects were green. As the nestlings grew older, they were fed less often but received larger items.

These tityras often approached their nest by flying down the steep slope from the fringe of trees at its crest. They descended slowly with their wings widely spread and fluttering with a mincing motion, making a pleasing display. The male, which showed a conspicuous white patch in the center of each black wing, was especially attractive.

By April 27, the female was brooding very little by day. In 2½ hours of the morning, she remained within the hole, presumably brooding, only twice, once for 3 minutes and once for 2 minutes. Both parents rested for considerable periods on top of a stub a short distance in front of the doorway of the nest, guarding. This, however, was chiefly the office of the male, who, it will be remembered, had guarded irregularly before the eggs hatched. In 8½ hours, he occupied the position atop the stub for a total of 130 minutes, approximately one-quarter of the time. Once he stood there for 29 minutes, once for 22 minutes, and once for 17 minutes, but his other periods of guarding were shorter. Usually he began to stand guard after he had delivered food, but at times he came with empty bill to take his post on top of the stub. He was not called upon to defend the nest from anything more formidable than a pair of Masked Tityras, who came prospecting for a nest cavity. When they alighted on the stub in front of the nest, he darted at them again and again until they flew away.

The female Black-crowned Tityra rested on this stub far less than her mate, only 58 minutes in the 8½ hours, and her longest interval of continuous guarding was 13 minutes. Since, while I watched, she had devoted only 5 minutes to brooding, this would not account for her far less constant guarding. However, she compensated for her smaller participation in this duty by bringing food somewhat more often than the male.

On May 14, 22 days after I first saw the parents bring food, I glimpsed, for the first time, a nestling's head in the doorway. Two days later, two nestlings showed their heads together in the doorway, and for a while one stood in it. The following morning, May 17, the young tityras were more active. From time to time, one or another of them stood in the doorway, looking over the valley and sometimes preening its feathers, but after a while it went down into the cavity. Shortly before the departure of the first fledgling, I saw a young one standing in the doorway while both parents rested atop the tall dead stub a short distance in front. Now and again they called in their queer, dry voices. Twice the male started to fly toward the forest up the hillside, but after having gone fifty feet or so he circled around and rejoined his mate on the stub. This was unusual behavior. Both parents seemed to be excited and expectant.

Then, at 7:44 a.m., the young tityra that had been standing in the doorway suddenly flew forth. The nest faced down the steep slope of a field of maize in which the tall, dead tree stood. At first the fledgling flew toward the river, far below, while both parents followed it closely. But in this direction the ground beneath it fell away alarmingly, so the young bird turned in a great curve, swung inward—the parents still following—and came to rest on a tree at the edge of the woodland, southwest of the nest. The young tityra flew easily and covered possibly 400 feet on its first flight. For many minutes the fledgling rested in an exposed position at the tip of a long bough with dense foliage, where its whitish body was conspicuous from afar against the dark green background. Even the shower which soon began to fall did not at once cause the young one to move inward beneath the shelter of the leaves, and the parents brought food to it there.

Meanwhile, two more young tityras remained in the high hole, where they were not wholly forgotten by their parents. In the next two hours, the female brought them four meals, and the male fed them once. Both parents came a number of times without food, stood on the stub in front of the nest, and called. Sometimes the female went to cling beside the doorway. They seemed to be coaxing the remaining young birds to come into the open. Although for brief intervals one of the nestlings stood in the doorway, and once seemed on the verge of flying out, most of the time both remained out of sight in the chamber. They were not yet ready to forsake the sheltering nest. When I left, two hours after the departure of the first fledgling, the other two gave no indication of approaching flight.

When I returned to the nest at 6:35 a.m. the next day, May 18, a young tityra was standing in the doorway, but soon it went inside. At 7:03, both parents arrived without food and perched atop the stub in front of the nest, repeating their slight, dry notes. The female went to cling beside the doorway, where two heads were now visible. At 7:08, one of the young birds flew out. Both parents at once began to follow, but the male soon turned back to the stub. The female, however, continued to fly close above and slightly behind the fledgling until it alighted. This young tityra flew more weakly than the fledgling that had departed on the preceding day. Like the other, it started toward the river which the nest faced, but finding the trees farther and farther below as it continued on a slightly descending course, it gradually veered to the right, toward the forest. It lost altitude more rapidly than the first fledgling and did not reach the trees, but it came down into some bushes in the clearing a short distance from them.

The female tityra soon returned to the stub in front of the nest, which sheltered at least one more young bird. This one, probably the last to hatch, appeared less

vigorous than the others and did not often show itself in the doorway. Again and again, one parent or the other, and often both together, flew up to stand on top of the stub in front of the nest and call. Sometimes they clung in the doorway or beside it. Usually they came without food for the stay-at-home nestling, but three times they brought it something to eat. Then they would fly down into the bushes where the newly departed one had gone, or circle above it, then go back to the stub. They seemed to be dissatisfied with the continued presence of the third young tityra in the nest, and to all appearances they were urging it to join the others outside. But by 8:35 a.m. the young bird showed no inclination to venture forth, so I left.

On the following morning, I arrived in sight of the nest at 6:05, but the third fledgling did not appear in the doorway until 6:48. Before its departure, the female fed it twice and the male fed it once. Both parents came a number of times without food, stood on the stub in front of the nest, and called. The male also started to fly off several times, as though he expected the fledgling to follow. However, when he had gone a short distance and saw that he was alone, he circled around and came back to the stub.

At 7:48 a.m., the fledgling was standing in the doorway and the female was resting on the stub close by the hole. Suddenly the young bird launched out. It flew slowly and weakly, while the female followed closely; rapidly losing altitude, it came down in the cornfield scarcely fifty feet from the base of the stub where it was hatched. Thus the first fledgling to depart flew more strongly than the second, and the second flew very much better than the third. The male was out of sight at the moment of the third young tityra's departure, but soon he arrived and flew down among the maize plants to visit it.

In as much as the parents began to carry food to the nest on April 22, or perhaps a day or two earlier, and the first fledgling left on May 17, it remained in the nest at least 25 days, assuming that the young departed from the nest in the order in which they hatched. It is of no little interest that all three fledglings, in spite of the differences in their degree of development as indicated by their varying powers of flight, severed contact with the nest at very nearly the same hour of the morning: the first left the nest at 7:44 a.m., the second at 7:08, and the third at 7:48. Thus it seems that their departure was brought about largely by an inner urge that reached sufficient intensity at a certain time of day. Had the coaxing of the parents been itself sufficient to lure the young birds from the nest, independently of their state of development, the second and the third should have quit the nest soon after the first, for the parents then seemed quite eager to effect this.

Yet the fact that all three fledglings took flight while one or both of the parents were close by, although most of the time they were absent seeking food, suggests that the urgings of the adults were not entirely without influence on the movements of the fledglings. But their coaxing was effective only when the young birds were ready for departure. The inner readiness of the fledglings was the primary cause of their quitting the nest, the actions of the parents were a secondary influence that might have hastened this departure, somewhat. Most young birds that I have watched as they severed connection with the nest did so quite spontaneously, often in the absence of the parents.

Leaving my observation post, I found the newly departed tityra resting on a low perch in the hillside cornfield. In plumage it resembled the other two, but I had a

better opportunity to examine it, from a distance of only a few yards. Its head was largely chestnut, including the forehead, much of the crown, orbital and auricular regions, and cheeks. The center of its crown was dusky. The hindhead, hindneck, and upper back were whitish; the rest of the back, the rump, and the wing-coverts were gray; the remiges were black. The tail feathers, still very short, showed narrow white tips and a black subterminal region. Its under plumage was whitish, and its bill was black. There were a few lingering tufts of whitish natal down on the top of the young bird's head.

While I searched for the fledgling in the tall, tasseled maize, the female flew down and perched on a low stump only two yards from me. It is not often that one comes so close to a member of the cotinga family, for they are birds of the treetops. Full-grown young birds, with black feathers appearing on their chestnut crowns, follow their parents through the treetops, incessantly repeating a peculiar sharp, squeaky note, quite different from that of the adults. From time to time they receive an insect which a parent has caught amid the foliage and knocked against a branch to prepare it for the young bird. Sometimes the latter, impatient of the delay, tries to snatch the food prematurely from the adult's bill.

END OF THE BREEDING SEASON

In June, I have on several occasions watched Black-crowned Tityras carry material into holes used for sleeping by Golden-naped Woodpeckers, sometimes filling them with so much litter that, as already told, the woodpeckers found it preferable to carve a new dormitory for themselves. The male tityra may at this season show more interest in woodpeckers' holes than his mate, sometimes entering them while she looks on passively. But the tityras' great preoccupation with nest sites and nest building in June leads to nothing, for I have not known them to rear a late brood. Apparently, in the upper Terraba Valley, above 2000 feet, the Black-crowned Tityras do not rear a second brood. They seem merely to annoy the woodpeckers by carrying trash into their dormitories after their young of the first brood have become independent. In failing to produce a second brood, they differ from the Masked Tityra, which in the same locality may raise two broods in a season. Perhaps the superior fecundity of the latter species accounts for its greater abundance.

SUMMARY

Pairs of Black-crowned Tityras or family groups of three or four wander through the crests of the great trees of the rain forest and through neighboring clearings with scattered trees. In southern Costa Rica this species ranges upward to about 4000 feet above sea level. The adults appear to remain mated throughout the year.

Perching on a twig, these tityras scan the surrounding foliage until they sight an insect, which they catch while hovering on the wing and carry to a convenient perch, against which they beat it before swallowing it. Their largely insectivorous diet is varied with fruits.

The tityra's notes are low and weak, usually dry and nasal or insect-like, although at times it utters a slight trill.

In El General, Black-crowned Tityras breed in April, May, and June. The nest is placed in a woodpecker's hole, preferably in one made by a species of *Tripsurus*, at heights ranging from 40 to more than 100 feet above the ground. The

female fills the bottom of the cavity with a loose litter of dead or dying leaves, twigs, flower stalks, and the like, sometimes bringing as many as 33 billfuls in an hour. The male often follows his building mate, not infrequently carrying material, but only rarely is this added to the nest.

The tityras not infrequently choose for their nest a hole in which the woodpeckers sleep. Sometimes the woodpeckers throw out the litter carried in by the intruder, but usually they proceed to carve a new hole, abandoning their dormitory to the tityras. No aggressive behavior by either tityras or woodpeckers was ever witnessed.

Incubation is performed wholly by the female, who sometimes sits for more than an hour at a time. When returning from a recess, she often brings a leaf to the nest. Two females, each of whom was watched for several hours, kept their eggs covered about 65 per cent of the time. While the female is absent, the male guards the nest from a nearby perch, and sometimes he goes to look into the hole but he does not enter it.

The nestlings are brooded by the female and are fed by both parents. At one nest, the female brought slightly more food than did her mate, but he guarded the nestlings more than she did.

The departure of three fledglings of one brood was witnessed. They left early on consecutive mornings, at very nearly the same hour. Although, after the departure of the first fledgling, the parents seemed to try hard to coax forth the remaining two, their efforts were ineffective except at a time which was evidently determined by the young birds' internal state. The first fledgling to go flew more strongly than the second, and the second flew much better than the third. As the nestlings flew from the nest, each was closely followed by one or both parents. The nestling period was at least 25 days.

In June, tityras take great interest in woodpeckers' holes, and they may carry much material into them. This activity, however, never seems to result in the production of a late brood, at least in El General at altitudes above 2000 feet, where the species is near the upper limit of its altitudinal range.

MASKED TITYRA¹

Tityra semifasciata

In appearance, voice, and mannerisms, this medium-sized cotinga has a character all its own. At the first glimpse of a male Masked Tityra flying overhead, one is likely to exclaim, "A little white bird!" Closer scrutiny of the tityra reveals that his plumage is not so white as it first appears; a formal description of this stout, eight-inch bird fails to give an adequate notion of its whiteness when viewed in flight or as it rests in a treetop. His upper plumage is generally pale bluish gray, becoming almost white on the hindhead, and his under plumage approaches still more closely to white. His wings are largely black. The tail is pale gray with a broad, black subterminal band and a narrow whitish border across the end. His reddish eyes are surrounded by a broad area of bright red bare skin, which covers the lores. This naked patch is margined all around by black feathers, which form a narrow fringe across the chin and a broad band over the forehead. The short, stout bill, of which the upper mandible is terminated by a short, down-curved hook, is red basally and black at the tip. The female tityra is far less white than the male, for her plumage is grayish brown above and light gray below. The naked skin around her eyes is a paler red than that of the male. The legs and feet of both sexes are dark gray.

The species ranges from northern México to western Ecuador, Bolivia, Brazil, and the Guianas. Over much of this vast area, it is one of the first members of the cotinga family that a visiting naturalist is likely to meet. Tolerant of varied ecological conditions, it lives not only in the most humid rain forests but also in semi-arid regions with scattered trees. In Central America, it is widespread over the lowlands of both coasts, and it extends far upward into the mountains. On the Pacific side of the Cordillera de Talamanca, I found it in late February nearly 7000 feet above sea level, and on the Cordillera Central in May I saw a wandering male at about 7500 feet, but I doubt whether tityras nest so high. At Vara Blanca on the northern side of the Cordillera Central of Costa Rica, I found it nesting at an altitude of 5500 feet. But in this extremely wet region I failed to see a tityra between August and late February, whence I inferred that it performs a slight altitudinal migration, dropping down to lower levels after the close of the nesting season and ascending the mountains again as the following breeding season approaches.

Tityras are at home in the tops of the big forest trees, where one hears them far more often than he sees them. But they often make excursions, in pairs or small flocks, through clearings and plantations with scattered tall trees, and they often nest in dead trees standing isolated near the forest's edge. Almost always they fly and forage at a good height above the ground. Except while nesting, these restless, wandering birds seldom remain long in one locality. They appear to be mated throughout the year, for I have often seen pairs even in the autumn months. Yet at all seasons, including that in which they nest, one occasionally meets small, wandering flocks composed largely of males. The latter seem to be considerably more numerous than the females. After pairing, the male tityra is ever a faithful companion of his mate and seems subservient to her will. For example, late one cloudy afternoon in March, I noticed a pair of these birds resting in dead trees in a

¹This life history is an abridgement of Skutch (1946b), with the addition of later observations on roosting and nesting.

clearing beside the woodland, where they were preparing to nest. The male, which seemed eager to go to roost in the neighboring forest, flew twice across the clearing to a tree at its edge, where he called and waited for his partner to follow. Since she was not yet ready to go, he returned each time to await her pleasure. Soon, however, she yielded to his entreaties, and the two flew away over the forest together.

Like other cotingas, tityras, while perching, quietly turn their heads from side to side, scrutinizing the surrounding foliage until they detect an edible insect, which they snatch from the leaves by means of a sudden dart, without alighting beside it. The first tityra that I ever saw held in its bill a fleet-winged dragonfly, but I do not know whether this insect was captured while it was flying or at rest. Tityras also eat berries and other small fruits of trees.

ROOSTING

On the evening of September 13, 1947, I discovered a pair of tityras perching quietly in the top of a burío (*Heliocarpus*) tree beside our house. The birds rested, about a foot apart, on petioles of the large, cordate leaves, at a height of about 40 feet. Above them was a canopy of foliage, but their white underparts were plainly visible from the ground. They remained there through the night, and at daybreak I found them on the same petioles. The following evening I searched fruitlessly for them. A year later, almost to the day, I found a lone female tityra roosting in the top of the same burío tree, where she slept only two nights after I discovered her.

These tityras went to rest much earlier in the evening, and became active far later in the morning, than many of the surrounding birds. The pair had already become motionless when I first noticed them at about 5:30 p.m., and the following morning they remained inactive, save for a little preening, until they flew off at 5:45 a.m., a quarter of an hour before sunrise. A year later, I found the solitary female on her perch in the burío tree at 5:18 p.m. At this time the crown of the tree was in full sunshine, and it continued to be illuminated for the next quarter of an hour. Except for preening herself now and then in a desultory fashion, she sat motionless on the same twig until it grew dark, an hour after I first saw her there. Daybreak revealed her in the same spot, where she lingered, nibbling her plumage and voicing at long intervals a single thick note, until 6:13 a.m., when she at last bestirred herself, after about 13 hours of repose. As with the pair which had roosted in this tree in the preceding year, the first morning flight of this female took her from the isolated treetop to the forest, 40 yards away.

VOICE

The voice of the tityra is decidedly unbird-like, and resembles that of no other feathered creature that I know. To call its utterance a very low grunt conveys only an approximate notion of its quality. At times the tityra's notes are drier, more insect-like. To appreciate their oddness, one must hear them, after which he is not likely to confuse them with the calls of any other bird. Tityras have an extremely limited vocabulary, and if they possess any softer or more melodious notes I have failed to hear them.

NEST BUILDING

The Masked Tityra nearly always nests in cavities in dead or, more rarely, living trees, usually from 40 to 100 feet above the ground. Until quite recently,

the lowest hole into which I had seen a tityra carry material was 20 feet up in a slender stub standing in a clearing, but apparently she did not lay there. In 1964, however, a tityra built a nest in an old woodpecker hole only 13 feet up in the top of a small, dead avocado tree in a coffee plantation on our farm. I do not know whether she laid in this exceptionally low nest, as I left for field work elsewhere. On the same farm in the following year, a pair of tityras raised a brood in a hole carved by Red-crowned Woodpeckers only 11 feet up in a slender stub, decayed, riddled by insects, and partly consumed by fire, that stood in an area where second-growth woods had been recently felled and burned for planting maize. When the tityras took possession of this low nest site it was quite exposed, but by the time the eggs hatched it was barely above the tassels of the tall maize plants that surrounded it on all sides for 100 feet or more. Either cavities resulting from decay or those made by woodpeckers are acceptable to the tityras. The latter seem to be preferred, especially the chambers carved by species of *Centurus*, *Tripsurus*, and other medium-size woodpeckers, the doorways of which are barely wide enough to admit the tityra. Tityras not infrequently capture holes still used by the woodpeckers for sleeping, or even those newly completed for the accommodation of the woodpeckers' eggs and nestlings, evicting the hole-carvers by persistence rather than by violence, in a manner which we shall consider later. I have not known them to oust the woodpeckers from holes which held eggs or young.

In 1939, I was surprised to find tityras nesting in the crowns of three palms (*Attalea*, or some feather palm of similar aspect) standing not far apart in a cleared valley, with forest nearby. The three nests were placed in deep crannies between the crowded, massive, fiber-swathed bases of the great leaf stalks, at heights ranging from 40 to 75 feet above the ground. Two were among the living fronds in the spreading crowns of the stately palm trees; the third was among the stumps of fallen fronds at the base of the crown. That this sort of nest site was not unwelcome to the tityras was evident from the fact that each of the three palm trees, the only ones of the kind in sight, sheltered a nest. Each palm seemed to offer sites for a large number of nests, but the tityras' territorial habits prevented their fuller utilization. Except in this one spot in El General, I have never found the tityras nesting elsewhere than in holes in trees. All the nests that I have seen were in clearings near the forest.

Long before the approach of the breeding season, the tityras, roaming in pairs through the forest and adjacent clearings, begin to examine woodpeckers' holes and other cavities in trees which might later serve as nest sites. I have watched them pursue these investigations as early as November; indeed, at all times of the year, they display curiosity about the holes in trees that they encounter on their wanderings. The female goes to the doorway of the cavity and looks in, while her mate, who follows her like a shadow, clings to a neighboring part of the trunk, his black-and-white wings half-spread. The male often goes to the doorway, too, after his partner has completed her inspection. It is usually not until a later date that the birds enter the holes.

At times it appears that the examination of potential nest sites may be made before the pair has been formed, or at least before the rivals of the successful male have become discouraged and abandoned their suit. On February 20, 1938, I saw tityras at Vara Blanca for the first time in half a year. On the following morning, I found several of these birds in a narrow clearing in the forest 5300 feet above

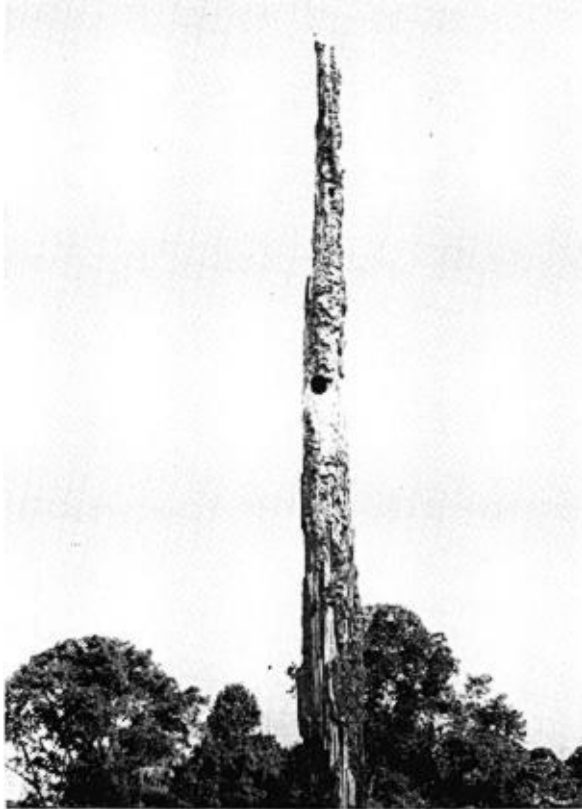


Fig. 1. Nest cavity of Masked Tityra, carved by Red-crowned Woodpeckers in a slender stub in a maize field. El General, Costa Rica, June, 1965.

sea level, where a pair had nested in the preceding July. While a female flew from one to another of the dead trunks standing in the pasture, looking into the many old holes that they contained, three males followed her, sometimes peering into the cavities, too. They voiced low notes, flitted their banded tails fanwise, and sometimes one flew toward another. But the individual so approached always retreated promptly, and there was no fighting, nor any suggestion thereof. After the female had made the rounds of the decaying trunks, she flew down the mountain, followed by her three suitors.

This observation suggests that the tityra's method of mating and establishing a breeding territory is very different from that of finches and many other songbirds, in which the male settles in an area, advertises his presence by singing, and awaits the arrival of a mate. The female tityra appeared to select the territory while the males followed her about, awaiting her decision. As late as March 6, there were three tityras in this clearing, but by the following day another of the males had been eliminated. The female's choice of a partner seemed to have been definitely made, but she was not seen building until April 3.

At lower altitudes of 2000 to 3000 feet in Costa Rica, I have known the tityra

to begin building as early as the end of February, at the height of the dry season. March and April are the months of greatest activity in nest building. Pairs seen nest building as late as May are probably preparing for second broods or replacing nests that have been destroyed. Like many other birds, the tityras, especially the female, may gather material some time before they actually begin to build, carry it in their bills awhile and then drop it to the ground. In 1937, a pair of tityras was much interested in the still-occupied dormitory of a pair of Golden-naped Woodpeckers. I first saw the female tityra with material in her bill on February 20, but it was March 2 before I witnessed her taking anything into the hole that she had chosen for her nest. Yet two days later she perched motionless near this cavity with a billful of leaves, which she dropped after 12 minutes.

While the female tityra was gradually working herself up to the point of beginning to build, her mate seemed impatient to have her proceed with the undertaking. Often, while she paused irresolutely in a neighboring tree, holding a twiglet or dead leaf in her bill, he went to cling at the doorway of the woodpeckers' hole, at times flying off a little way and then returning, as though to encourage her to take the stuff inside. Even when she was beyond sight, he might go to look into the prospective nest cavity, at times in the warmest hours of the afternoon.

For the tityra, nest building is a simple undertaking which requires no art. It consists merely of filling the bottom of the chosen cavity with a loose litter of small dead leaves, or pieces an inch or two long torn from larger ones, fine dry inflorescences of trees, thin twiglets, and rarely a small green leaf. This is done chiefly or wholly by the female, who gathers her material in the treetops, often at a distance from the hole, rather than from the ground, to which adult tityras never seem to descend unless drawn by a fledgling which rests there. As a rule, she works in a desultory fashion, taking a few billfuls into the hole, then flying off and remaining away until one grows tired of waiting for her return.

The male faithfully follows his building partner back and forth, often holding a leaf or twig, which after being carried on a number of trips is finally dropped somewhere, usually not into the nest. He sometimes takes material to the doorway, both while his mate is building and in her absence. He may do this repeatedly, seeming thereby to express his eagerness to have the female resume her task. The leaf or twig taken to the orifice by the male is often carried away again, and I have seen this happen four times in succession. Often the male drops his material while he clings in front of the doorway. Nearly always it flutters to the ground, but sometimes, one might say by accident, he pushes the leaf or twig far enough inside for it to remain when he releases it. His ineffectual efforts to help his mate in building are amusing to watch and remind one of the equally unproductive preoccupation with nest material of the male Black-crowned Tityra.

THE EGGS

The tityras' nests which are placed high in dead trees of uncertain stability cannot be reached without great difficulty and danger. For many years, the only one that I could examine was about 35 feet up in a massive trunk standing in Gatún Lake, about 100 yards from the shore. This tree had been killed about 20 years earlier, when in the construction of the Panamá Canal the lake was formed by impounding the waters of the Río Chagres, and the wood was far advanced in decay. Great chunks of the tree fell off as we threw a cord across the truncate

top in order to draw up a rope attached to a rope ladder. I should never have climbed such a trunk if it stood on solid ground, but a fall into the water seemed less dangerous. In the upper side of a short stub of an ascending thick branch, at the very top of the trunk, I found an irregular hollow, doubtless made by decay, a foot deep and wide enough to admit my hand. Although the cavity opened upward, it slanted down into the wood, so that it gave the tityra protection from both the sun and the direct impact of rain. When I peered in, I saw no eggs on the loose litter of leaves that filled the bottom of the cavity, but I could feel two eggs under the leaves. These eggs were dark buff or *café au lait* in color, heavily marbled, especially on the larger end, with brown. A few small, black spots were scattered over the surface. They measured 30.2 by 20.6 and 29.8 by 21.4 mm.

At the low nest to which I gave much attention in 1965, I could not see the eggs. This nest had an entrance too small to admit my hand, and to have made a larger opening would have endangered the contents. On 15 inspections with a mirror during incubation, I never glimpsed even part of an egg, as all were always completely covered by the leaf litter that filled the bottom of the cavity. It was the same whether the female had left the nest spontaneously or flew out when she heard me approaching. Apparently, however, this nest also contained only two eggs, for this was the number of nestlings present, and no unhatched egg remained in the litter after the young fledged. Incubation began in this nest in El General at the end of May, 1965. At the nest in the Canal Zone, incubation had already started by May 28, 1935. Both were probably second brood or replacement nests. I have no evidence of more than two broods per season in this species.

INCUBATION

Only the female incubates. Often a number of days elapse between the end of sustained building and the beginning of steady incubation, and in this interval the female brings occasional billfuls of dry leaves to the nest. Her vacillating behavior in this period is most confusing to the watcher who cannot learn by direct inspection what the hole contains. Sometimes the female is seen looking out of her high doorway, from which at times she darts forth as though to fly away, only to turn after she has gone a few inches and re-enter it. Her mate may remain perched in a neighboring tree, from time to time going to the doorway to look in at her. As the day ends, the female, often in company with her partner, lingers near the nest cavity, guarding it, but in the waning light both fly off together to sleep in the neighboring forest. After a few more days, the male departs first in the evening, leaving the female perching alone near the nest. As the twilight deepens, she may fly toward the doorway, only to turn back when in front of it, often repeating this move a number of times, but in the end losing courage or changing her mind, and winging away through the dusk in search of her mate. Such vacillation is especially likely to be noticed if, as often happens, a family of great-billed araçari toucans sleep in a neighboring hole. At daybreak, before woodpeckers have emerged from their dormitories, the male and female tityras often fly together from the adjoining forest to perch for a while near their nest.

From a cayuco moored to a neighboring stub, I watched the nest in Gatún Lake from 6:00 to 11:23 a.m. on May 29 and from 2:00 to 6:45 p.m. on the following day. In these ten hours, the female tityra took eight sessions on her eggs, ranging from 24 to 49 minutes and averaging 37.1 minutes. Her nine recesses

varied in length from 13 to 29 minutes and averaged 19.6 minutes. She was in her nest only 65.4 per cent of the observation periods, which is a poor record for so large a bird but is matched by that of the Black-crowned Tityra (p. 14).

When she left her eggs, the tityra would emerge from the cavity and hop along the broad top of the stump to its highest point, where she usually stood for several minutes, preening her feathers, stretching her wings, or idly looking around, before she flew toward the land. It was remarkable how often her mate, watching from the neighboring forest, saw her before she reached the shore. Sometimes he advanced a short distance over the water to meet her, then together they vanished over the treetops. On five of her ten returns to the nest, the male escorted his partner to the stub standing in the water. After resting for a minute or more atop the trunk near the doorway, he would fly back to the land, while his mate hopped down into the cavity.

Once, as she was returning alone to the nest, the female tityra was attacked above the water by one of the Streaked Flycatchers which was feeding nestlings in a hole lower in the same trunk. The flycatcher plucked at the tityra's feathers, causing her to cry out in alarm or pain. But as soon as she alighted on the stub, the flycatcher desisted from its attack. The tityra promptly returned to the shore, as though for consolation from her mate, who a minute later saw her safely back to her nest. On another occasion, one of the flycatchers darted at the male tityra while he rested on top of the stub near his mate's nest, causing him to retreat to the shore. But aside from these two incidents, the tityras, the Streaked Flycatchers, and the Palm Tanagers nesting in this stub dwelt in peace. The Blue-headed Parrots, whose two large but still naked nestlings rested in a large cavity below the tityras' nest, remained out of sight the whole time that I watched.

From time to time, the female tityra took a billful of leaves into the hole when she returned to resume incubation. I have seen other female tityras do the same. I climbed the rope ladder twice more, and each time I found the eggs completely buried in the litter. It was impossible to learn whether the tityra deliberately covered them as she departed or whether the leaves simply flowed over the eggs when she rose from the depression which she doubtless made in the loose mass while she sat. It is probable that the protectively colored eggs often escape predators by being covered with leaves in the bottom of a dark cavity.

In the middle of the afternoon, while the female tityra stood on the top of the trunk beside her nest, preening her feathers, her mate came bearing a big, green caterpillar and alighted close beside her. Without offering the food to her, he hopped to the rim of the nest cavity and looked down into it. Evidently he had brought the caterpillar in expectation of finding nestlings to receive it, and when he learned that the eggs were still unhatched, he swallowed it himself. The male tityra not infrequently brings food to the nest in this anticipatory fashion, finds that there are still no young mouths to take it, then eats it himself or carries it away. At another nest, I saw the male do this twice. Since, even while the two are attending nestlings, the male tityra does not pass food to his mate, these morsels are obviously not for her. Similar anticipatory food bringing has been witnessed at nests of a number of other passerine birds, especially those of wood warblers and tanagers. It serves to form in the male parent, when he does not incubate, the habit of bringing food to the nest in advance of the hatching of the nestlings, with the result that after the young are hatched he will promptly find and attend them.

Seated on a log amid the maize plants which partly screened me, I watched the low nest in the milpa from 5:20 to 11:36 a.m. on June 5, and from noon to 5:40 p.m. on June 7. In nearly 12 hours, this tityra took 14 sessions on her eggs, ranging from 4 to 81 minutes in length and averaging 21.6 minutes. An equal number of recesses varied from 10 to 26 minutes and averaged 17.1 minutes. She spent only 55.7 per cent of her active day on the nest, but this day was short. It began at 5:23 a.m. on June 5, when the tityra left her nest in the cloudy dawn. Until 2:23 p.m. on June 7, she had come and gone very frequently, taking no session longer than 26 minutes. After her return to the nest at 2:23, the sky became darkly overcast and intermittent sprinkles fell, hardly enough to wet the foliage. The tityra now stayed in her nest continuously for 81 minutes. When finally she emerged at 3:44 p.m., it was only to rest in a neighboring dead tree, preening, scratching, and stretching her wings, until her return to her eggs at 4:02. Then she remained within continuously, never even showing herself in the doorway, until I left when daylight was waning at 5:40 p.m. From 2:23 p.m. until nightfall, this tityra took no food. In comparing the incubation records of the two tityras, it should be noticed that the Canal Zone, where the first nested, is only about four degrees east of El General, where the second nested, yet the first locality uses standard time for the seventy-fifth meridian and the second that for the ninetieth meridian, and their clocks are accordingly an hour apart. Hence the sun rises and sets, by the clock, much earlier in Costa Rica than in Panamá.

The tityra in the cornfield could barely squeeze through the round doorway of her nest hole that the woodpeckers had made. She seemed to have little difficulty finding enough food in the neighboring forest where she foraged, for sometimes, even early in the morning, she would spend part or even the whole of her recess preening in a neighboring dead tree, often in company with her mate. He was attentive to her, and as she returned to her eggs he would often fly down with her, to rest atop the low stub while she entered the opening in its side. Once he clung before the doorway and pushed a piece of dead leaf through it. Sometimes the female carried pieces of dead leaf in her bill when she went to resume incubation.

This female was found in her nest late in the afternoon of May 29, and again on the following afternoon. Incubation had apparently begun by the former date. One of the unseen eggs had hatched by 7:20 a.m. on June 19, and the second egg no later than next morning, after an incubation period of about 21 days.

THE NESTLINGS

Hatching and the beginning of feeding.—Bracing the back of the rotten stub in the cornfield and setting my ladder almost upright against the front, I climbed up and looked into the nest hole with electric light and mirror, at 7:20 a.m. on June 19. Now for the first time I saw part of an egg—half of an empty shell. Its dark color made it difficult to distinguish from the leaves among which it rested. I heard *peeps* and from time to time saw the leaves move, but I could catch no glimpse of the newly hatched nestling(s) hidden beneath them.

Both parents were resting in a dead tree at the edge of the field. Presently the male flew away and his mate followed. At 8:01 she returned and entered the nest with a dead leaf in her bill, while the male rested on top of the stub. She brooded for 40 minutes, then left carrying a piece of eggshell. When she returned 11 minutes later, she again held fragments of leaf, which she dropped while standing on the

end of the stub, before she entered. Now she brooded for 18 minutes, was absent for 19 minutes, and on returning at 9:29 she held a small green object that was evidently an insect, the nestling's first meal. After another spell of brooding and another excursion, she again returned with a billful of leaf fragments which, before approaching the nest, she dropped while perching in a dead tree at the side of the field. Then she flew back to the forest, evidently for more food. Returning, she entered the hole so swiftly that I could not see whether she had brought anything. But apparently she fed the nestling, for she remained with her head downward and her tail sticking up in the top of the hole for about a minute.

At 10:54 the male and female returned together and clung side by side to the top of the nest stub. The female had food in her bill. While she delivered it with her tail pointing upward in the top of the nest cavity, her mate looked in through the doorway. He returned to the top of the stub, but a few minutes later he again went to peer inside while clinging in front. Thereupon the female left, but he remained clinging to the stub for about a minute more, before he followed her. He evidently had intimations that some important change had occurred in the nest, for now he spent more time on the stub than he had formerly done. Once more he looked in while his mate fed the nestling. Finally, at 11:42, he flew from the dead tree direct to the doorway with a small piece of food in his bill, entered, stayed in for about a minute, and emerged with empty bill. He first fed the nestling two hours and 13 minutes after the female did, and four hours and 22 minutes after I found the empty eggshell and heard the nestling peep. By noon, he had fed the newly hatched young twice; the female had brought food five or six times.

When I looked into the nest at 8:00 next morning, I could see parts of two nestlings. One promptly disappeared beneath the leaves, but most of the other, except its head, became visible when it shifted its position. The few tufts of fairly long, light gray down that it bore on its head, wings, and back were far too sparse to cover its pink skin. I could not induce it to gape. This was the most adequate view that I was to have of a nestling for many days. For the next two weeks, they were always beneath the leaves, with rarely a head exposed, whenever I looked into the nest.

Brooding.—Perhaps because they were embedded in dry leaves in a snug nursery, these nestlings were brooded little. During five hours of the morning of June 25, when they were about six days old, their mother brooded them only three times, for 28, 12, then 14 minutes. When 12 days old and still practically naked, the nestlings were not brooded at all during the first five hours of the morning.

Table 1

Age in days	5:35-6:35		6:35-7:35		7:35-8:35		8:35-9:35		9:35-10:35		Totals
	M	F	M	F	M	F	M	F	M	F	
6	0	1	3	2	0	0	2	1	0	1	10
12	0	1	1	1	1	3	2	3	0	0	12
18	0	2	0	2	1	0	0	2	0	3	10
24	1	0	3	1	1	2	1	0	1	1	11
26	2	3	2	2	1	2	3	4	1	4	24
27	9	2	0	2	1	3	2	1	2	4	26
Totals	12	9	9	10	5	10	10	11	4	13	
M + F	21		19		15		21		17		93

Feeding.—The number of meals delivered by both parents on six mornings is recorded in table 1. As far as seen, each meal consisted of a single item. Until the nestlings were over 24 days old, there was no significant increase in the rate of feeding, but after the first week the parents rather consistently brought articles that were noticeably larger than those which newly hatched nestlings had received. Rarely they offered the nestlings an insect so big that it was swallowed with difficulty, or not at all. This regimen of few but substantial meals was followed until a few days before the young left the nest, when feedings became twice as numerous as they had been through most of the nestling period but the articles of food were often small. In 30 hours of watching, the number of meals received by the two nestlings in a single hour varied from 0 to 11; they were fed a total of 93 times, or at the rate of about 1.5 meals per hour for each of them.

The nestlings' diet consisted chiefly of insects, especially orthopterans. The green color and massive bodies of many of these insects suggested that they had not been caught in the air but had been snatched from foliage, where their protective coloration had failed to conceal them from the tityras' sharp eyes. Sometimes a brown or dark-colored insect was brought, once a large orange-tawny butterfly, and twice I detected a large spider in the male's bill. Occasionally a small land snail was taken to the nestlings, as I learned when I found three small shells in the litter in the bottom of the nest after the young had flown. At other nests, I saw the parents bring caterpillars, and rarely a small lizard. No fruits were detected in the parents' bills when the nestlings in the cornfield were six days old, but when they were 12 days old they received a few. The rather large, green, olive-shaped fruit of a lauraceous tree was the kind most often brought. Each contained a single big seed surrounded by hard, thin flesh. After this had been digested away, the young birds regurgitated the seeds, of which I later found many among the leaves in the bottom of the nest. Each seed was from $\frac{3}{4}$ to $\frac{7}{8}$ inch long and about $\frac{3}{8}$ inch thick. During the nestlings' last days in the hole, they received an increasing number of bright red arils from the seeds of the "candela" (*Viola Koschnyi*), a large tree of the nutmeg family that was then beginning to ripen its fruits. Usually the big seed had been removed from the enclosing aril before the parents brought the latter to the nest. These brilliant arils could have come only from the forest 200 yards away, where the tityras seemed to find most of their food. They were never seen to forage in the cornfield in the midst of which their nest was situated.

At first the parent entered the hole and was completely hidden from me while it fed the nestlings, although sometimes I could detect its tail sticking up in the top of the cavity. When the young were 12 days old, the parent fed them while clinging upside-down in the doorway, its foreparts down in the hole and the tip of its tail projecting from the top of the aperture. Sometimes after delivering the meal it entered to turn around and perhaps collect a dropping, and sometimes it backed out. After the nestlings were 18 days old, the parent nearly always clung to the trunk and passed the food through the doorway; very exceptionally, if the young were sluggish in taking the meal, the adult would enter to deliver it. At first, the parent clung in front of the doorway, but later, when the nestlings stuck their heads out to receive their meals, it might cling around the side of the slender stub, somewhat above the level of the doorway, and reach down to place the food in the recipient's open mouth.

The parents took fairly equal shares in feeding the nestlings, but on most mornings the female fed them more often than did the male. In 30 hours of

watching, she brought food 53 times, he 40 times. At an inaccessible nest with at least two young that were no longer brooded by day, the male brought food nine times and the female ten times in three hours. If the male arrives with food while his partner is in the nest brooding recently hatched nestlings, he does not, like many male birds, give it to her to be passed to the little ones she covers, but he alights nearby and continues patiently to hold the morsel until, at her own good time, she departs, leaving the nestlings free to receive what he has brought for them. I have seen this inefficient behavior at several nests. Once I watched a male wait for a quarter of an hour, from time to time going to look into the hole, or voicing a slight grunt to proclaim his presence, until at last his brooding partner flew away and he could feed his offspring. At times, however, the male tityra grows tired of waiting for his mate to leave and carries away what he has brought. At one nest, the male somehow lost his tail, but despite this handicap he continued faithfully to feed the nestlings.

Sanitation.—During five hours of the sixth morning after the nestlings hatched, I saw only one dropping carried from the nest, by the male. Additional droppings had evidently been swallowed by the parents inside the hole. On the twelfth morning, the white fecal sacs were carried away although sometimes they were swallowed. By the eighteenth morning, the parents could reach inside to take the droppings while they clung before the doorway; less often, they entered to remove a dropping. On the twenty-seventh morning, the male entered the nest after delivering a lauraceous fruit, evidently to clean the interior. When he tried to come out, he stuck in the doorway. After a great struggle to squeeze through, he finally emerged upside down! Later the female also had a hard time getting out; yet both had entered without difficulty. Possibly while cleaning the nest they had swallowed enough of the large seeds regurgitated by the nestlings to increase their girth to an unusual degree. This explanation was suggested by the recollection of a Blue-throated Toucanet which had entered a nest hole with a lauraceous fruit that seemed too large for his nestlings to swallow. When he tried to pass outward through the doorway by which he had entered, he stuck so firmly that he could not move until he reduced his girth by regurgitating the fruit, which he held in his bill until he regained his freedom, then swallowed once more.

During the young tityras' last few days in the nest, the parents often swallowed the droppings instead of carrying them away in their bills. The young birds had remained beyond the time when their feces were enclosed in the gelatinous sacs that facilitate their disposal.

Taking leaves to the nest.—In earlier years, I had often seen tityras carry pieces of leaf to nests that held young. Sometimes the parents dropped these bits of leaf while they rested near the hole, and sometimes they did so while clinging in front of the doorway. At times the parents at this latest nest brought an odd billful of leaves, which they might drop or take into the hole, and at intervals they brought this material in a concentrated, purposeful manner. Thus, between 10:00 and 10:19 on the sixth morning after the nestlings hatched, the male entered the nest five times and the female four times. Sometimes they went in so swiftly that I could not see what they carried, but on four occasions I clearly saw that they held leaves, and I believe that on all of the nine visits they brought this material rather than food. In all the rest of the morning, up to 10:30, they fed the nestlings only ten times.

The parents are especially likely to bring leaves and drop them outside the nest in

moments of excitement, as when some critical event in the nesting cycle has just occurred or is about to occur, or when their nest has just been visited by a man. It will be recalled that the first two billfuls that the female brought to the nest after an egg hatched were leaves, not food. And two minutes before the first nestling flew from the nest, the female came with leaf fragments, which she dropped in front of the young bird's open mouth in the doorway. Another female tityra, whose three-week-old nestlings had apparently just been lost, gathered a billful of dead leaves in the top of a neighboring tree, then let them fall to earth.

The drive to gather leaves is strong in tityras apparently because leaves play an exceptionally large part in the birds' domestic economy. Not only are they the principal—sometimes the only—ingredient of the nest, but for some five weeks they serve to conceal the eggs and young from predators that might look into the hole. And at an earlier stage, tityras often gain possession of the holes in which woodpeckers or araçari toucans sleep or are preparing to nest by filling them with leaves and other materials with such persistence that the occupants finally abandon them, as told in more detail beyond.

Development and behavior of the nestlings.—My single reasonably adequate view of a newly hatched tityra revealed that it was blind, with pink skin that bore a few tufts of light-colored down. In the next few days, the glimpses I had of small portions of the nestlings that showed through the leaves revealed that their skin had become much darker, but it never became quite black. Once I heard a weak *peep peep peep* while I looked into the nest, and occasionally the leaves would move, but usually the nestlings lay in silent immobility. After a few days, I was more likely to see portions of their heads than of their bodies, and when they were ten days old, I found both nestlings lying with their heads completely free of the leaves which covered the rest of them. Three days later, they were also lying with exposed heads and concealed bodies. Then, when the elder was 15 days old, I discovered one of them resting wholly exposed, although only the head of the other nestling was visible. Thereafter, throughout their final two weeks in the nest, they were never again found beneath the leaves. They were always silent and immobile while I peered in at them.

When, after an interval of two weeks, I at last saw the nestlings entire, their dark skin was still nearly naked. The pins of the remiges were prominent, but those of the rectrices were much shorter. I could no longer detect any natal down on them; possibly much of it had been rubbed off by the leaves that covered them, but an odd tuft was still present when they left the nest. While I looked in, they kept their eyes tightly closed. They were silent; nothing that I could do, from the time they hatched until they left, would stimulate them to open their mouths.

Two days later, when the nestlings were 17 days old, their eyes were open, and both the contour and the flight feathers were expanding at the tips of their sheaths. At this age, the young could reach up so far that the parents fed them without entering the nest. Once, indeed, I glimpsed an open mouth in the doorway, and at last learned that the interior was orange-yellow. The flanges at the corners were whitish. When the nestlings were three weeks old, they were at last fairly well covered with plumage, but their flight feathers were still largely ensheathed. Now, if they were very hungry, their heads would often appear in the doorway when a parent arrived with food.

Aside from the weak *peep's* that I heard from the nestlings when newly hatched

and again a few days later, I heard no note from them until the fifteenth day after they hatched—the day on which I first saw one of them completely exposed. While I stood only about 25 feet from the nest, hardly concealed by the maize plants, the male flew to the top of the stub with food in his bill. Recognizing the arrival of the parent by the sound or vibration he made when he alighted, the nestlings repeated little sharp notes while he stood hesitating. They continued this chorus while, standing in the doorway, he fed them. Two days later I approached carefully, tapped the trunk and shook it slightly, trying to reproduce the sound and vibration made by a parent alighting there. The nestlings set up a chorus of the sharp notes that I had previously heard, but they fell silent as soon as I set the ladder against the stub. Soon they learned to distinguish my simulation of a parent's arrival from the real thing, and would no longer respond to it. Until they left the nest, I heard their peculiar, sharp notes with increasing frequency, especially when they were hungry. I can best describe them as "sucking" notes, such as one can make by suddenly opening his lips as he draws in his breath.

Departure.—On July 13, when the nestlings were 24 days old, the female from time to time alighted on the top of the nest stub and called. On the next day, this behavior was more frequent and pronounced. Without food, she would come to stand on the end of the stub, a few feet above the nestlings, repeating her sharp, dry notes and twitching her tail with a rapid movement that combined a slight fanwise opening and closing with a little vertical flick. Her calls consisted of one, two, three or, rarely, four notes. The monosyllable, a frequent call at all seasons, was the strongest. The more syllables that the phrase contained, the shorter and weaker each became; the insect-like notes of the tetrasyllable were so weak and rapidly delivered that it was difficult to distinguish all of them. These short, dry notes, uttered with twitching tail, suggested urgency and impatience. After standing atop the stub and behaving so for a few minutes, the female might fly off, only to return promptly and repeat the performance. She was obviously trying to call out her nestlings, now well feathered. The male never behaved in this fashion. From first to last, he seemed not to care whether they stayed in the nest or left, but continued faithfully to attend them wherever they were.

The female's excited notes were not without effect on the nestlings. At eight o'clock, while she stood calling on top of the stub, a young tityra pushed its foreparts through the doorway, farther than I had seen it emerge before. Then the male gave it a large green insect, and it went down inside. When the female repeated her performance half an hour later, a nestling stood on the doorsill, looking around and giving "sucking" notes that were audible to me 60 feet away. But soon it returned into the nest. Later in the morning, it again leaned so far out that I expected it to leave, but it did not.

On the following day, July 15, the female seemed less eager to bring her family into the open. Although she rested a good deal atop the stub, she did not, as on the preceding day, arrive there without food. While standing there, she called much less, and her voice sounded less urgent. Likewise, she twitched her tail much less. Apparently, the excitement caused by the nestlings' greater activity and the imminence of their departure was on July 14 expressed by impatience, at least on the part of the female, to have them make their exit, whereas on July 15 it was expressed by a greatly accelerated rate of feeding by both sexes. On this morning the parents fed the nestlings twice as often as on any previous morning that I

watched them (see table 1). On July 16, when the elder nestling was 27 days old, activities at the nest followed much the same pattern as on the preceding day, with occasional calling by the female from the top of the stub, responses by a nestling that brought it into the doorway but no farther, and an even higher rate of feeding.

Tityras of two species (see the preceding life history) have been more obviously eager to have their young leave the nest than any other birds that I have watched, most of which have seemed indifferent whether their offspring lingered in the nest or came out into the world. The fact that the tityras' attempts to induce their young to leave were associated with a greatly accelerated rate of feeding weighs heavily against the persistent belief that parent birds withhold food from their young to force them by hunger to leave the nest. Such behavior might defeat its own purpose, for unless the nestlings promptly gave the desired response, the longer it was continued the more debilitated and the less able to meet the demands of life in the open they would become.

On July 17, when one of the nestlings was just four weeks old, I arrived later, at 6:35 a.m. while the sun was shining brightly. Neither parent appeared until 6:53, when the female came with a billful of leaf fragments, which fluttered to the ground when she dropped them in front of the open orange-yellow mouth of the nestling in the doorway. Then she rose to the top of the stub and called with single, double, and triple notes. She flew off, but promptly returned and called as before. The young bird which had been standing in the doorway looking out now launched itself and flew down into the corn, with the female following from the top of the stub, at 6:55 a.m.

As soon as the first fledgling left the doorway free, the other one looked out. The female returned to the top of the stub and called briefly. During the next two hours, she tried hard to induce it to leave, in the manner already described. Often it stood in the doorway as though about to go, but it was not yet ready. In these two hours, it was offered food seven times by both parents, but once it refused because it was satiated. I could not see how many meals the fledgling down among the maize plants was receiving.

At nine o'clock, I went to look for the fledgling, which I promptly found on the ground in front of the nest. It tried to escape me by hopping over the ground and flitting from one charred branch or prostrate log to another, but despite these obstacles to my progress, I soon caught it. When I picked it up, it hardly resisted. The fledgling was well feathered, its plumage resembling that of the adult female. Its dusky remiges were well developed, ensheathed only at the base for a quarter of their length or less. Its blackish tail feathers were rather long but still about one-half ensheathed. A single tuft of natal down, long, loose, and light gray in color, adhered to the tip of a contour feather on the back but became detached and blew away. The fledgling's bill was blackish, slightly lighter at the base. The whole interior of its mouth was bright orange-yellow, and there were whitish flanges at the corners. Its eyes were deep brown, and the bare skin surrounding them was grayish, instead of red as in the adults of both sexes. Its legs and toes were plumbeous.

I set the fledgling on a stump near the nest, where it stayed. It seemed rather underdeveloped to have left its sheltering nest. Next morning, I found it 50 yards away, beneath a dead tree standing in the middle of the milpa, from which the parents had been dropping almost straight down with food in their bills. The

fledgling was perching as high as my head on a dead branch. Far more alert than the day before, it took wing as I approached and flew off competently to alight on a maize plant. It now seemed quite able to escape all but winged pursuers.

For two days after the departure of the first fledgling, the parents continued to feed the other young tityra in the nest. In this interval, the female tried again and again to persuade it to leave. Although her excited urging obviously stimulated it, it would look from the doorway, rapidly repeating "sucking" notes, only to lose courage and back down into the safety of the hole. It did this again and again. Once, indeed, while taking its meal, the nestling stretched out so far that one leg slipped outside. After a struggle, it pulled itself back into the cavity.

Finally, at 8:05 a.m. on July 19, the adult female alighted atop the stub and called, as she had done so many times before. The nestling alternately looked out and withdrew. But when, a minute later, its parent flew off, calling, it flew from the doorway in the same direction, to come down among the corn. Three minutes after this, the female returned with a large insect, which she took to the doorway of the empty nest. After looking in several times, she carried it down to the newly emerged fledgling. Both of the young tityras left the nest while their parent was calling for them to go, but apparently her urging was effective only after their own internal development had prepared them to respond to it. For tityras, it may be more important to leave the nest only in the presence of a parent than it is for most other land birds. Many of their nests are so situated that they must fly hundreds of feet before coming to rest, and they might be lost if no parent watched or accompanied them. Moreover, on this long flight the fledgling would be particularly vulnerable to a bird of prey, and their parents doubtless would not call them out if such an enemy were in sight.

Leaving my observation post, I found the second fledgling in a patch of bracken fern only three yards from the nest stub. When picked up, it bit my finger gently and struggled a little, but soon rested quietly in my hand. Its plumage was slightly less developed than that of its nestmate had been two days earlier. When I set it on a fallen branch amid the maize, the female alighted four yards from me and only about a foot above the ground—closer to me and to the earth than I had ever seen an adult tityra before. She called the fledgling with phrases of two and three syllables, as she had done while coaxing it to leave the nest. It hopped over the ground and fluttered toward her; it could fly only a few feet. Calling as before, she flew toward the dead tree in the center of the milpa and the fledgling fluttered after her. This was the last time that I saw either fledgling. Next day I could find neither them nor their parents in the cornfield. Doubtless, as is usually the way when a brood is raised in a clearing, as soon as the young birds could make the journey they were led to the neighboring high forest, whence I heard a tityra's call.

The first nestling had remained in the nest a full 28 days, the second, 29 or possibly 30 days. Probably they survived this long period in their low nest because I had wrapped an opened five-gallon tin around the stub to keep down climbing animals.

A slight push sufficed to overturn the rotten stub so that I could examine the contents of the nest. The doorway was 2 inches in diameter. The soft wood at the lower edge of the orifice had been worn down by the tityras' feet during the two months that they had been passing through and clinging to it. The cavity, which extended 9 inches below this edge, was 3 to 3½ inches in diameter. On the bottom

was a little dry moss. I do not know whether the tityras had carried this in; I have never seen them with such material. Above the moss was an accumulation, 2 or 3 inches thick, of pieces of brown dead leaves. The lower part of this litter was compacted into a coherent mass, but the upper part was loose. The largest piece was a nearly whole leaf $2\frac{1}{2}$ inches long by half as broad, but most of the leaf fragments were much smaller, ranging down to tiny bits. Mixed with the loose leaves were many regurgitated seeds, chiefly of the lauraceous fruit that I had so often seen the parents carry in, detached fragments of the legs and wings and other parts of large insects, and three small snail shells. There were also a few whole shrivelled fruits of the same lauraceous tree. The nest had been kept as clean as could be expected, given the tendency of waste to slip down among the loose leaves where it was difficult for the parents to find. Although the hole had a peculiar odor, I detected no vermin of any kind.

For 18 days after two young tityras left a high nest in a clearing, I could not find them. Doubtless they were being attended by their parents in the neighboring forest. At the end of this interval, they sometimes followed the adults into the clearing, where the female was incubating a second brood. After a few more days, they were no longer seen in the vicinity, having apparently become self-supporting about three weeks after quitting the nest, at the age of about seven weeks.

THE SECOND BROOD

In Costa Rica, the tityras frequently, if not regularly, attempt to rear a second brood when they have successfully brought forth their first brood at an early date. A female whose nestlings had departed on or shortly before April 29, 1936, was seen to enter and rest in the doorway of the nest hole on May 9 while she and her mate were still feeding two full-grown young birds. On May 11, she went into the cavity in the evening to pass the night. By May 17, she was certainly incubating again in the nest where her first brood had been reared, leaving her mate to attend the young birds, which seemed rapidly to be becoming self-supporting. By June 5, both parents were feeding the nestlings of the second brood, their older offspring having meanwhile gone their own way. By June 25 the nest was empty; and although the fledglings could not be found, the aggressive behavior of the usually mild parents suggested that their young were hiding nearby. In later years, additional evidence for second broods was gathered. Nestlings have been found as late as mid-July.

TERRITORIAL RELATIONS

The Masked Tityra is decidedly a "territorial" bird. Indeed, it is one of the relatively few tropical birds, especially among those of the treetops, which I have seen engage in disputes over territory, although these have been carried on with less violence than is often witnessed in similar contests by northern birds. A clearing by the forest, several acres in area, may contain a number of fire-killed trees, each of which has one or more holes that would be suitable nest sites for tityras; yet I have never known more than one pair to breed in such a clearing. The only tityras' nests that I have seen at all close together were those in the three palm trees already mentioned. Possibly the circumstance that the wide-spreading fronds of the palms screened the tityras from each other, enabled these three pairs to nest closer together than one would find them in the usual dead and naked trunks, where they are visible from afar.

While one pair of tityras nested in a tall dead trunk in a clearing beside the forest, a second pair came to investigate the woodpeckers' holes in another dead tree about a hundred yards distant. Presently the visiting female brought a piece of dead leaf, but as she carried it toward the hole that she had chosen, the resident pair discovered the intruders and, flying at them, drove them unresistingly away. Two days later, in a neighboring clearing, I watched a female, evidently the one which had been denied the use of a cavity, try again and again to force herself into woodpeckers' holes too small for her, while her mate looked on. This behavior suggested that there was a shortage of suitably isolated holes for the tityras.

At the end of February, when a pair of tityras established in a large clearing were preparing to nest, their territory was invaded by a small flock of their kind, consisting of four males and a female. The invaders and the resident pair rested not far apart, called in their thick, grunty voices, and twitched fanwise their short, black-and-white tails. Presently one would dart at another, who would quickly change his position to avoid a collision; and this might cause a general shifting around of the whole group. After a while, one would start to fly across the clearing, and some or all of the others would follow closely. They might all settle together in another tree in the clearing or at its edge, or else they would fly beyond sight over the neighboring forest. But soon they returned to grunt, dart at each other, and fly about in a loose flock as before.

In the ensuing days, the number of invaders dwindled, until the resident female was followed by only two males. When finally the number of males had been reduced to one, her mate, the female gathered a billful of leaves and took them into the hole—the first material that she carried inside in my presence. Weeks later, when the resident pair was feeding nestlings in this hole, two trespassing males followed the female as she took food to the nest. They perched nearby until the male parent of the nestlings arrived with food and, without even clearing his bill, drove them away simply by darting toward them. Unattached male tityras seem often to travel two or three together in search of a mate, and their presence at the height of the breeding season indicates that there are more males than females.

From May 24 to June 17 of 1939, two pairs of tityras contended for the possession of a tall, many-branched, dead tree that rose above a low second-growth thicket 200 yards from the forest, and which apparently they desired for rearing a second brood. This arboreal skeleton contained enough unoccupied holes to provide nest sites for several pairs of tityras, but each pair insisted on having exclusive possession of the tree and the surrounding area. The protracted dispute was carried on with characteristic mildness of temper, patience, and persistence. All four of the tityras would rest among the dead branches, often close together, apparently in perfect amity. Of a sudden, one would dart at a member of the other pair, causing it hastily to shift to a different perch. Then all would flit about confusedly for a few moments, apparently greatly excited, voicing their grunty notes and twitching their tails as they rested between movements. They rarely, if ever, struck each other, for the individual which saw itself the object of another's attack invariably retreated. When the flare-up ended without any participant having suffered the slightest injury, all rested from their nervous exertions quietly side by side as before. Soon becoming hungry, all four flew off to the forest, where doubtless they foraged in unruffled fellowship. After a brief absence, all four returned together to the dead tree, to resume the interrupted argument in the same intermittent fashion. Some-

times the dispute continued until evening, when the two pairs flew toward the woodland as though to roost together.

By June 25, a month after I found these two pairs quarreling over the tall dead tree, neither pair had begun to nest in it. The season was now so far advanced that further breeding was improbable. Were tityras fiercer and more decisive birds, doubtless the dispute would have been settled promptly, possibly by the maiming or death of one or more of the contestants, and the victorious pair would have proceeded to nest. But the two offspring which they might then have reared, if enemies of many kinds had not destroyed the eggs or young, would merely have sufficed to replace the casualties of their battle; the net increase of the local population would have been small or null. Since in this locality tityras were already so numerous that every clearing which provided a nest site had a breeding pair and there was a shortage of suitably isolated old woodpeckers' holes and other cavities, the failure of these two pairs to rear broods (probably second broods) was far from deplorable; for any increase in the population would have created more serious difficulties in the following years. We often wonder how tropical birds preserve their numbers at a fairly constant level from year to year, avoiding the great fluctuations in population which many birds and mammals of high latitudes exhibit. This episode of the tityras shows us one of the ways in which the regulation of numbers is accomplished.

While the Masked Tityras argued over the dead tree, a pair of Black-crowned Tityras built their nest in one of its cavities, undisturbed by them. Although rather similar in coloration, Black-crowned Tityras do not arouse the territorial jealousy of the Masked Tityras, as do others of their own species. The former may rest undisturbed close by a nest of the latter, and both at times breed in the same clearing.

Although tityras defend a nesting territory, they seem not to defend a feeding territory. Since the clearing where they often nest provides little or no food, it is strange that a breeding pair claims such a large area.

RELATIONS WITH OTHER BIRDS

As in many other birds which nest in holes which they do not make, the tityras' mode of life brings them into competition not only with wood-carving species but also with other hole-users in the same plight as themselves. In the first category are the woodpeckers whose holes they covet, often before the makers have abandoned them; in the second class are Southern House Wrens, Gray-breasted Martins, Black-crowned Tityras, and, above all, araçari toucans, which nest and sleep in holes carved by the larger woodpeckers.

In El General, a favorite nest site of the tityra is a deep, spacious cavity carved high in a fairly sound dead trunk by Golden-naped Woodpeckers. One great advantage of these holes is that the narrowness of the doorway keeps out Fiery-billed Araçaris, which easily enter chambers made by larger woodpeckers such as the Lineated and the Pale-billed. After a successful nesting, a pair of Golden-naped Woodpeckers sleep with their offspring, often in the hole in which the latter were reared, until the approach of the following nesting season, when the young disperse and the parents move into a newly carved hole in which the female soon lays. Tityras may carry litter into the woodpeckers' old dormitory before the new one is large enough for occupancy. When the woodpeckers arrive in the evening and find

the bottom of their usually clean chamber covered with trash, they may throw out many pieces, but at other times they sleep above it. If another old hole is available, the Golden-napes may roost in it rather than in that which the tityra is filling. In these circumstances they are often very unsettled, changing their lodgings a number of times until they are finally installed in the new hole, where they soon incubate.

I have seen a pair of tityras dispossess, without any fighting, a pair of Golden-napes of the lodging they had occupied for many months. If the woodpeckers were carving at their new hole lower in the trunk when the tityras arrived, they appeared uneasy and sometimes flew away. Rarely a tityra darted toward a woodpecker while it was at work and caused its prompt retreat. But the tityras also seemed to be slightly afraid of the woodpeckers, so that encounters were carefully avoided by both parties. Similar relations between Golden-naped Woodpeckers and Black-crowned Tityras are described in the chapter on the latter.

Although tityras are usually mild, peaceable birds, occasionally one finds an individual with a fiery temper. While a pair of tityras and a pair of Golden-naped Woodpeckers reared their early broods in the same dead tree, I noticed no enmity between them. But while the female tityra was preparing to rear a second brood in the same hole as the first, her attitude toward her picarian neighbors changed. One evening she perched at the top of the tall dead tree and darted at the woodpeckers as they approached their hole, which had now become the dormitory of the parents and two male offspring. Swooping down, with an audible *snap* she came so close that they fled to other trees, and she repeated this threat whenever one of them returned. She kept the woodpeckers out until long past their usual hour for retiring, but as it was growing dark she stood quietly atop the trunk and watched them cautiously slip into their chamber below her. Next morning, she twice flew menacingly at a Golden-nape which rested inoffensively in a treetop 50 yards from her nest. But after this she calmed down and incubated her eggs without, as far as I saw, again molesting her near neighbors the woodpeckers.

On the Caribbean slope of Costa Rica, I watched a pair of tityras gain possession of a freshly carved hole in which Black-cheeked Woodpeckers seemed to be preparing to nest. When the female tityra carried leaves into their hole, the woodpeckers promptly began a new cavity lower in the same trunk, where, as soon as it was large enough, they slept and later nested. Here, as with the Golden-naped Woodpeckers, the change in possession of the hole was effected, as far as I could tell, without any fighting. I have not known tityras to try to capture a woodpecker's hole that held eggs or nestlings.

High in the mountains, a male Golden-olive Woodpecker proceeded to throw out the material which a tityra had carried into an old cavity, in which he had not recently been sleeping and which, apparently, he did not desire for nesting. Although the woodpecker continued on two days to clean out this chamber, I noticed no fighting between the two kinds of birds. When the woodpecker looked into the hole and found a tityra within, he promptly flew away as though alarmed.

The tityra's relations with the brilliant Fiery-billed Araçaris are more complex than those with the woodpeckers. Not only do the two species compete for the possession of the big holes abandoned by the early-nesting Pale-billed and Lineated woodpeckers, but the tityras fear these great-billed nest-robbers for the injury they may inflict on themselves or their offspring. Sometimes the tityras choose as a

nest site a cavity in which several araçaris roost. At first, perhaps, they are unaware that the hole has prior claimants, for the toucans may be absent in the daytime while the female tityra carries leaves into their dormitory. Soon, however, the tityras discover that they have to contend with these birds to which all the smaller feathered creatures have a great antipathy. Then, as the day ends, the tityras take commanding positions near the hole, from which they harass the araçaris when they come to enter their dormitory, darting back and forth above their heads while they perch, pursuing them closely in flight, and swooping close by them while they cling before the doorway to inspect the interior of their cavity before they enter. Yet, for all their zeal, the tityras hardly touch the larger birds, and the latter pay little attention to their persecutors.

More effective in driving away the toucans than the tityras' feints of attack is the female's work in filling up the cavity and reducing the space available to the sleepers. Rarely an araçari removes a billful of litter when it arrives in the evening. As the accumulation grows, the toucans accommodate themselves with increasing difficulty, and the last to enter sometimes turns around and squeezes in rump-foremost, while it folds its long tail over its back to economize space. One and then another of the company deserts this shrinking chamber and flies off in the waning light, doubtless to seek another hole that it has kept in view for just such an emergency. Finally, the mildly persistent tityras remain in undisputed possession of the cavity.

Thus, in the course of two weeks, a pair of tityras wrested a hole in a dead tree from the three Fiery-billed Araçaris which had slept there. In this interval, the female tityra apparently laid in the cavity, in the morning when the dreaded toucans were absent, only to have her eggs broken when the big birds rested on them in the evening. But a fortnight after the araçaris abandoned their dormitory, the tityra was incubating another set of eggs in it. Mild-mannered though they be, the tityras often come off victorious by virtue of their great persistence, even in conflicts with birds far larger and more powerful than themselves. Probably their need to adopt a Fabian policy, in disputes with stronger rivals, accounts for the dilatory, indecisive character that is so evident to anyone who watches them closely.

Another pair of tityras nested in a very high hole in a trunk where, in a lower and larger cavity, from one to five Fiery-billed Araçaris slept. When she began to incubate, the female tityra hesitated to pass the night so near the araçaris. In the waning light, she rested at the top of a neighboring tall trunk, whence she started again and again toward her doorway, only to lose courage at the last moment and turn aside. As I watched her small figure silhouetted against the darkening sky, I could hardly doubt that she was in the throes of a severe inner conflict. Finally, after half a dozen false starts toward her nest, she flew off through the dusk to the forest, whither her mate had preceded her. On the following evening, she twice entered her nest, only to emerge again; then, after several fruitless attempts to return, she flew off in the twilight to seek her partner. Eventually, however, her maternal feeling grew strong enough to hold her on her eggs so close to the roosting toucans. Soon the number of araçaris that lodged there was reduced to one, whose mate incubated her eggs in another trunk in the same clearing. Every evening for a fortnight, the tityra left her nest when the larger bird flew against the dead trunk to enter its dormitory. As it slipped into the hole, she darted at it with a

little scolding grunt; then she resolutely returned to her nest a few feet above the araçari.

The tityra hatched her eggs, and as her nestlings acquired feathers she exhibited at nightfall the same wavering behavior that I had witnessed earlier as she started to incubate. At first, after turning back several times, she entered the nest in the deepening dusk to brood her offspring through the night. As the days passed and the nestlings outgrew their need of the female's warmth, the balance of forces tilted to the opposite side; now, after similar vacillation, the tityra flew off to roost in the darkening forest. There was no danger that the diurnal araçari would attack the nestlings in the night; but every day, in the early dawn before the toucan became active, the pair of tityras returned from the woodland to resume their guard and chase the great-billed bird when it emerged from its dormitory. Despite their dread of the araçaris, or perhaps because of the vigilance that this fear prompted, the tityras successfully reared their brood of two. Later they brought forth a second brood from the same hole, while the pair of araçaris, whose nest had been destroyed, continued to lodge near them. In another locality, both a pair of tityras and a pair of Fiery-billed Araçaris successfully reared families in the same dead trunk.

After the tityras' second brood had taken wing in late June, I found the parents guarding the fledglings in the trees at the edge of the clearing. When a long-tailed, brown Squirrel Cuckoo passed heedlessly by, they darted at the big, harmless wayfarer and knocked several feathers from its wing, so aggressive had they become in defense of their offspring. The cuckoo was probably as surprised by this rude behavior as I was, for I cannot recall another occasion when a tityra so mistreated another bird either of its own or of a different kind.

SUMMARY

The Masked Tityra wanders through the upper levels of the forest and over cultivated country with scattered trees. Tolerant of varied ecological conditions, it inhabits not only the wettest parts of Central America but also semi-arid regions. Most abundant at lower altitudes, it has been found occasionally as high as 7500 feet and it nests up to at least 5500 feet.

It lives in pairs throughout the year, but even in the nesting season one finds small, wandering flocks containing more males than females. Two or three of these unmated males may follow a female while she seeks a nest site, and at times they invade the territory of a breeding pair.

These tityras subsist mainly on insects, especially orthopterans, which they locate while perching well up in a tree, then capture by a sudden dart against the foliage. Occasionally they take a dragonfly, a butterfly, a land snail, or a small lizard. Their diet includes many fruits and arillate seeds.

They roost, singly or in pairs, in rather exposed situations in the treetops. They become active rather late in the morning and retire early in the evening.

The most frequent call is best described as a low grunt. Drier, more insect-like notes are also uttered, especially at times of excitement and to call the young from the nest.

The Masked Tityra nearly always nests in a cavity in a dead or, more rarely, a living tree, from 40 to 100 feet above the ground. Exceptionally, a hole as low as 11 feet may be occupied. Holes carved by the smaller woodpeckers are preferred,

but sometimes the tityras select a hole formed by decay, even one that opens upward so that rain can enter. Rarely this tityra nests in crannies between the broad bases of the petioles of palm trees. Potential nest sites are examined by the mated pair many months in advance of the breeding season.

The bottom of the nest cavity is filled with a loose litter of pieces of dead leaves, sometimes with an admixture of fine twiglets and pieces of dry inflorescences, all gathered among the treetops, largely by the female. The male often carries material and may take it to the doorway of the nest, but usually he lets it drop to the ground or carries it away again.

One accessible nest contained two eggs, and in another two young were hatched; evidence for larger broods is lacking. The eggs are dark buff or *café au lait* in color, heavily mottled, especially on the thicker end, with brown.

Only the female incubates, taking sessions which rarely exceed three-quarters of an hour. One female incubated with a constancy of 65 per cent; another, whose constancy was only 56 per cent, had a short active day. Her eggs were invariably hidden beneath the litter of leaves while she was absent. This made it difficult to learn the length of the incubation period, but it was about 21 days.

Always attentive to his mate, the male often escorts her when she returns to her eggs. Occasionally he looks into the nest, and he may bring food in anticipation of the hatching of the nestlings, but he had not been seen to feed the female.

Newly hatched nestlings have closed eyes, pink skin, and sparse natal down. The interior of the mouth is orange-yellow. For the first ten days, they remain so constantly beneath the litter of leaves that one rarely glimpses them. Then one finds them with only their heads exposed; and from the age of about two weeks onward, they rest above rather than beneath the leaves. They develop slowly and are about three weeks old before they are feathered. Older nestlings make sharp "sucking" sounds when hungry. One nestling remained in the nest 28 days, its nestmate, 29 or 30 days.

Only the female broods, and she does so little after the nestlings are a few days old, doubtless because they are well covered with leaves in their snug chamber. Both parents feed the nestlings, the female usually slightly more often than the male. The latter never passes food to his mate for delivery to the nestlings; if he finds her brooding when he arrives with a morsel, he either awaits her departure or carries it away undelivered. The nestlings' diet at first consists of insects, but later fruits and the arils of seeds are included. Meals tend to be infrequent but substantial. During 30 hours of observation, the average rate of feeding was about 1.5 times per capita per hour.

The parents continue to bring pieces of leaf to the nest during incubation, and even while attending the nestlings. The excitement caused by hatching, the imminence of the nestlings' departure, or the observer's visit to the nest, stimulates leaf-bringing.

At one nest, the female, but not the male, tried hard to call the nestlings into the open, beginning when the elder was 24 days of age. The young resisted her urging for several days, during which they were fed twice as often as previously. Each finally left while its mother was calling to it. Although at first they flew very weakly, they rapidly increased in skill.

In Costa Rica, the breeding season extends from late February or early March to June or July. A second brood is frequently reared, at times in the same hole

as the first. Incubation may be resumed about two weeks after the departure of the first brood.

The tityra defends a nesting territory, but probably not a feeding territory. Even when holes are available, two pairs do not nest in the same small clearing. Intruding tityras are gently but firmly repelled. For more than three weeks, two pairs disputed the possession of a tree that had several available holes. Although they made many feints of attack, the threatened individual always retreated in time to avoid contact. Fighting has not been seen.

Tityras sometimes capture holes used for sleeping, or newly completed and intended for nesting, made by Golden-naped and Black-cheeked woodpeckers. They continue to fill the holes with litter until the woodpeckers grow tired of cleaning them out and carve new holes nearby. No actual fighting between tityras and woodpeckers has been witnessed, nor have tityras been known to capture holes that contained the woodpeckers' eggs or young.

Tityras may dispossess Fiery-billed Araçaris of old holes made by the larger woodpeckers and used as dormitories by these toucans. They employ the same expedient of filling the cavities with nest material in the absence of the bigger birds. It may be several weeks before the araçaris relinquish their dormitory to the tityras.

When nesting near the araçaris, tityras at all times keep close watch over these toucans. The female tityra sometimes exhibits strange, vacillating behavior at night-fall as she begins to incubate near the araçaris, and again when she ceases to brood the nestlings.

In three instances, tityras successfully reared broods in the same trees where nest-robbing araçaris bred or slept in neighboring holes.

WHITE-WINGED BECARD¹

Pachyramphus polychopterus

The White-winged Becard is a small cotinga slightly over five inches in length, with a stout body and relatively large head. As in many members of this family, the sexes differ greatly in appearance. The prevailing color of the male's upper plumage is black, which fades to gray on the rump and upper tail-coverts. The top of his head is glossy blue-black. The black wings bear two conspicuous white bars, and many of the remiges have white margins. Along either side of his back is a prominent, elongated white patch, formed by the outer webs of the scapulars. His tail feathers are black with white tips that are most extensive on the outermost ones. These white markings on the dark dorsal plumage are conspicuous from afar and aid in the recognition of this becard. The sides of the head and under plumage are dark gray, becoming paler on the abdomen. The bill is blue-gray, tipped with black; the eyes are brown and the legs and feet are dark. The female is greenish-olive above, sometimes tinged with cinnamon on the back. The feathers of her dusky wings are margined and tipped with buff and dull white. The rectrices are dusky with buffy tips. Her ventral plumage is light olive and pale yellow, and her under wing-coverts are pale yellow. Although the colors of her plumage lack brilliance and are difficult to describe, they are so delicately blended that she is exceedingly attractive in her modest attire.

The White-winged Becard ranges across the mainland of tropical America from Guatemala to northern Argentina. At its northern limit it is rare and appears to be confined to the humid lowlands and foothills on the Caribbean side. Farther south, in Costa Rica, it is found on both coasts. It seems to occur in greater abundance on the Pacific side, where it is fairly common in the Térraba Valley. In the Cañas Gordas region on the Pacific slope of southern Costa Rica, I found this becard nesting as high as 4000 feet above sea level.

Like most cotingas, the White-winged Becard lives well up in the trees. I have found it chiefly among scattered trees growing in pastures or rising above low thickets, in the shade trees of coffee plantations, in light and open woodland, and at the edge of the primary forest. Contrary to the experience of Carriker (1910: 668), I have never met these becards in small flocks. They are found singly or in pairs, sometimes associating loosely with mixed companies of other small birds. I am not certain that the male and female stay together in the seasons when they do not nest; in these months I have seen the becards singly more often than in pairs. These birds subsist chiefly on insects which they capture among the foliage, usually flying up to snatch their prey from the leaves while hovering on wing, in the usual way of cotingas. At a nest which I watched with care, I saw the parents bring only winged insects and larvae, never fruit. But Cherrie (1916:252) reported that in the Orinoco region the food of the White-winged Becard "consists apparently of about equal parts of insects and small fruits."

For several years, a lone male becard roosted in a burío tree (*Heliocarpus*) close by my home in El General. His nightly perch was a slender twig at the very top of the tree, 35 or 40 feet above the ground. There he was screened above

¹ This life history is an abridgement of Skutch (1954*b*), with the addition of a few new observations.

by the large, cordate leaves, but from below he was often readily visible.

The White-winged Becard has a variety of utterances, among which are the softest and sweetest notes that I have heard from any bird. One of the most common songs of the male is a rapid sequence of about six soft, dulcet notes, each higher in pitch and weaker than its predecessor. On other occasions, he repeats six or seven times, more deliberately and with slight change in pitch, a full, melodious note like that which introduces the ascending series. The female voices similar but weaker notes, and while attending her nest she warbles a soft, liquid, long-drawn murmur.

In the nesting season, the male becard delivers at daybreak a beautiful song which in form resembles the more common song but differs from it subtly in tone-quality. It is a series of sweet notes delivered too rapidly to be counted accurately; often there seem to be about eight of them. All the notes are of about the same pitch, although at times they descend a little as the utterance proceeds with slightly decreasing tempo. The first syllable is accentuated, and the last may be given a minor emphasis. This beautiful utterance is a true dawn song, repeated tirelessly over and over for many minutes at daybreak but seldom given later in the day, except in moments of great excitement. Although many flycatchers sing dawn songs, the White-winged Becard is the only member of the *Cotinga* family from which I have heard such a performance.

In El General, I have heard the dawn song of this bird as early as March 1, although in some years I have not noticed it until late March or even April. Thenceforth, the becard performs every morning for the next five or six months. Toward the end of August or in early September, regular dawn singing ceases; yet occasionally I have heard, after an interval of silence, long-continued chanting on a few mornings in October and even in early November. The becard may begin to sing by moonlight in the tree where he has roosted, and after performing there for a while he may, as daylight increases, fly to neighboring treetops to continue his singing. When chanting steadily, he repeats his mellifluous phrase about eight or nine times per minute, and once I counted 307 songs in 36 minutes. Often the songster continues for nearly an hour, with perhaps interruptions of a minute or two toward the end of the long performance. He may sing three or four hundred songs before flying off to feed.

Usually the becard ceases his dawn song around sunrise, and through the remainder of the day he delivers only notes of a different character, but exceptions to this rule sometimes occur. On darkly cloudy or drizzly mornings, the becard may continue, or resume, the dawn song after the unseen sun is well above the horizon. He may even sing freely as he goes to roost on a rainy evening. Dawn singing is rarely heard in bright morning sunshine. In June and again in September, I heard a becard in female plumage, probably a young male, repeat the dawn song for an hour or more in the middle of the afternoon. On one of these occasions, another becard in the distance answered with similar songs. Presently, two or possibly three of these birds appeared in the trees, and there was much spirited chasing with intermittent singing of the dawn song, although I saw no actual fighting. In this instance, the delivery of the dawn song late in the day was definitely associated with emotional stress, apparently resulting from either a dispute over territory or the formation of pairs.

Early in the morning of April 5, 1960, I watched two male White-winged

Becards disputing in the top of a guava tree. Flitting from twig to twig, they uttered a variety of sweet, soft notes. From time to time, they slightly raised the glossy blue-black feathers of their crowns, drooped their wings, and fanned out their tails, displaying the white areas on both. After a while, I noticed a single female in the top of the guava tree; if there was a second female, the abundant foliage screened her from my view. As the altercation proceeded, one male flew more aggressively toward the other, but I did not see them come into contact. This vocal conflict continued for about 20 minutes, after which the becards flew toward the neighboring forest.

NESTING

In El General, building may begin in late March, but I have found few becards starting their nests before April, when the dry season has passed and showers are becoming frequent. The bulky nest is placed in the top of a tree standing somewhat apart from others in a pasture or coffee plantation, or rising above a low thicket. Twenty-six nests were from 14 to about 125 feet above the ground. Sixteen of these nests were at heights of 25 feet or more. The lowest nests, only 14 or 15 feet up, were placed amid dense foliage, one in the rounded, spreading crown of *Cassia spectabilis*, the other in a heavy tangle of the parasitic vine *Struthanthus*. The nests are usually far out on long, slender branches, and only two that I have seen were accessible to me. Three of the nests were close to large nests of wasps, which might have kept prowling animals away.

I watched the construction of one nest in the Motagua Valley in Guatemala, and, for longer or shorter intervals, I followed the construction of about 14 nests in Costa Rica. In each instance, the female built with no help from the male, which, however, attended her while she worked. When beginning the nest, the female usually brings long strands of inner bark or other fibrous material and gives each a complete turn around one of the arms of the supporting crotch, thereby assuring a firm attachment. After a good foundation has been accumulated, she builds the walls upward and then inward, until the cavity of the nest is completely roofed over. Then she alternately takes material inside for the lining and adds it to the top to make the roof thicker. Usually she works at a leisurely pace, bringing only 8 to 12 billfuls in an hour; but one becard building a late nest at the end of June brought 17 loads of material in an hour, and another came 10 times in half an hour of the early morning. While the female works, her mate usually prefers to rest close by the nest, voicing from time to time his sweet notes, rather than follow on her excursions to gather material, in the manner of the male tityra. The male becard drives away intruders with a loud clacking of his short, thick bill.

A nest found shortly after construction had begun on June 20 was still not completely roofed over on July 1. But by July 6, after a little more than two weeks of work, it appeared to be finished.

A fairly typical nest was a top-shaped mass, broadest above and tapering to a rounded bottom. It measured 7 inches in height by 7 to 7½ inches in diameter. The internal cavity was 3 inches high, 2½ inches from side to side, and 3 inches from front to back. The doorway in the side, overhung by the projecting roof, was 1½ inches high by 1¾ inches wide. This nest was composed chiefly of long skeins of bast fibers, more or less shredded. Apparently the fibers were obtained mostly from the burío, a rapidly growing tree with very light wood which is abundant on

abandoned fields. Other material was found only in the innermost layer of the nest's wall, surrounding the chamber. Here were many dead leaves, chiefly monocotyledonous, including bamboo leaves, strips of banana or plantain leaf that were often quite broad, fragments of palm fronds, and grass blades up to 13 inches in length. The very top of the nest was a loose, spreading mass of bast fibers, but beneath this stratum the body was strongly and compactly built of fibers and dry leaves. On top of all the becard had placed a number of large feathers from the wings and tails of domestic chickens. Other materials that I have found in fallen, partly destroyed nests, or seen in the bills of building females, were fibers from the leaf-sheaths of the banana; long, thread-like, dry, pistillate inflorescences of the small tree *Myriocarpa*; and, in regions where it grows, much "Spanish moss" (*Tillandsia usneoides*). The latter is absent from El General.

All species of *Pachyramphus* appear to build bulky nests of much the same form, supported below rather than swinging from a pendent bough like those of the Rose-throated Becard. In addition to nests of the present species, and a few of the Cinnamon Becard that are described in the following chapter, I have found in Central America a nest of the Barred Becard. This was about 50 feet above the ground in the top of a slender, isolated tree in the gorge of the Río Sarapiquí, at an altitude of about 5000 feet above sea level in the Cordillera Central of Costa Rica. The roughly globular structure, which I judged to be about a foot in diameter, was placed between four branches that diverged from the end of a slender, upright bough. On the outside its chief ingredients were green moss and lengths of thin, dead, herbaceous vines. The doorway was on the under side, well concealed by dangling tufts of moss.

One of my accessible nests of the White-winged Becard contained four eggs on May 29, and the other held three eggs on June 12. Others have reported sets of three from Nicaragua, Panamá, Colombia, and Trinidad. The interval between the laying of successive eggs may be one or two days, even in the same set. Because it was difficult to extract eggs from a closed nest while I hung precariously in a treetop, only two eggs were removed for closer examination. They were pale gray, mottled all over with brown, most heavily in a wreath around the thicker end. They measured 20.2 by 15.1 and 19.8 by 14.3 mm.

Only the female incubates. On June 4 and 5, 1937, I devoted a total of nine hours to watching an inaccessible nest in the top of a tall avocado tree. On the afternoon of the first day, the female brought fibrous material and a tuft of spider cocoon, but by the following morning she was taking in small particles of food. It was evident that the eggs had hatched before I completed my study of incubation. In the nine hours, I timed 20 sessions in the nest, which ranged from 3 to more than 38 minutes. This longest session had begun before I started to watch at 2:30 p.m. and was exceptional; the next longest session lasted only 18 minutes. Twenty absences varied from 2 to 36 minutes in length, but both extremes were recorded on June 5, after the eggs hatched. Before the female began to bring food to the nestlings, the shortest recess that I timed was 11 minutes, the longest 29 minutes. Excluding parts of her night session covered by my record, the female becard spent a total of 223 minutes in her nest and was away from it 291 minutes.

The nest most favorably situated for study of all those of the becards that I have found was 14 feet up among the wiry green stems of a great tangle of *Struthanthus* which smothered the crown of a small tree of the custard-apple family

on the steep hillside behind our house. To reach the nest, we firmly planted a 12-foot post in the slope beneath it, against which we set a ladder on each visit of inspection. The becard evidently slept in her nest during the period of laying, for she flew out as I passed beneath it on the evenings of June 9 and 10, although her set of three eggs was not completed until June 12, 1949. By June 13, if not earlier, diurnal incubation had begun. In more than ten hours of watching while incubation was in progress, I timed 17 sessions, ranging from 6 to 38 minutes and averaging 15.2 minutes, and 16 recesses, ranging from 8 to 35 minutes and averaging 18.9 minutes. The female was in the nest only 45 per cent of the observation periods. Like other becards, she was a restless sitter, apparently depending on the thick enclosing walls to retain the heat of the eggs, which sometimes I found partly covered with loose material of the lining in her absence. Both her sessions and recesses were longest in the afternoon, and the longest period in the nest of all that I timed came late in the afternoon. Between 8:56 and 11:08 a.m. on June 20, she brought material for the nest on each of her seven returns to resume incubation. Usually she came with a blade of grass or the like, but once she carried a feather. One load was deposited on top of the nest, but all the others were taken inside as she entered to attend her eggs. These additions to the nest involved no special trips, but once she came to lay a chicken feather on the roof, then flew off to continue her recess. In the afternoons, I did not see her add anything to her bulky structure. Thus, in becards, building continues until the eggs hatch.

Both of these incubating becards entered and left their nests in much the same fashion. Approaching her nest in the treetop, the female would alight on a perch close by it and turn her big head from side to side, looking carefully around. Often she flitted from twig to twig while continuing to scrutinize her surroundings. Then she advanced to perch close in front of her doorway, and from this point she hopped or flew into the nest, sometimes audibly striking the foliage in front of it. To leave, she nearly always darted through the narrow orifice headfirst and flew away without pausing in the nest tree. Rarely, she altered her procedure and hopped to a perch in front of the doorway before she flew. As she passed overhead, it was easy to see that her tail feathers were all bent to one side from long sitting in the confined space of the nest. This was a permanent curvature, equally prominent when she returned at the end of her outing.

In the early morning, the male becard was most attentive to his partner. Frequently he came to rest close beside the nest while she was within, to sing in his dulcet voice, or merely to be near her while he preened his feathers. At other times he sang in the tops of neighboring trees, where his mate could hear as she sat in the nest. At times he seemed to call her forth, then followed as she flew away to search for food. On her return, he escorted her to the nest. But later in the day he remained for long intervals out of sight and hearing, seeming to forget that he had a mate and a nest. During these long absences, which sometimes continued more than an hour, the female left and returned alone and did not hear her mate's soft voice while she sat in the dim, stuffy interior of her great nest.

When her mate's song reached her within the nest, the female becard often replied with a similar song, which was much fainter, because her voice, ordinarily weaker than his, was muffled by the thick walls that surrounded her. At other times when she heard him while sitting in the nest, she warbled low, sweet notes.

Sometimes she voiced these soft and contented twitters while perching in front of the doorway, on the point of entering.

At one nest the period of incubation was 18 or 19 days and at another it was about 18 days.

At the nest in the *Struthanthus*, all the shells had been removed before I saw the nestlings, less than 24 hours after they hatched. The nestlings had pink skin quite devoid of down and their eyes were tightly closed. When they were a week old, their pinfeathers began to push through the skin and their eyelids opened. The feathers did not begin to unsheathe until the nestlings were 11 days old, but at 15 days the young birds were fairly well clothed with plumage. They remained in the nest for another week.

Although the male helps to feed the nestlings, he may not begin to do so immediately after they hatch. While incubation is in progress, I have not seen a male becard make a visit of inspection to the nest, and certainly no casual glance could reveal to him what the well-enclosed structure contains. Hence his cue for bringing food must be either the sight of his mate bringing food or the sound of the nestlings' voices; but which of these stimuli is actually effective in starting him off, I have not been able to learn. On July 2, two days after the nestlings hatched in my lowest nest, I watched it for two hours in the morning. Soon after I arrived, the male came with food, but he delayed near the nest while his mate twice passed him, taking meals to the nestlings. After he had procrastinated for 12 minutes, he finally reached a point among the vines in front of the doorway, where he delayed for another half-minute, only to dart away with his food undelivered. After a few minutes more, he returned and seemed to feed a nestling. On his third visit, he delayed for four minutes before taking the food to the nest. On his fourth visit, he procrastinated 11 minutes, while his mate fed and brooded the nestlings. On his fifth visit he fed the nestlings fairly promptly, but on the following visit he waited among the vines for nine minutes before he took his food to the nest. His great hesitancy in going to the doorway suggested that now, about two days after the nestlings hatched, he was just beginning to feed them, and this activity was still strange to him.

In the two hours from 7:08 to 9:08 a.m., the male went to the doorway and apparently fed the three, two-day-old nestlings 5 times, and the female fed them 8 times. After each feeding, she brooded, for intervals ranging from 2 to 11 minutes and totalling 47 minutes.

When these three nestlings were eight days old, and again when they were 16 days old, I watched their nest from daybreak until 11:00 a.m. The female had

Table 2
Rates of Feeding Three Nestling White-winged Becards

Hour a.m.	Eight days old Number of feedings			Sixteen days old Number of feedings		
	Male	Female	Total	Male	Female	Total
6:00- 7:00	2	2	4	2	3	5
7:00- 8:00	4	5	9	2	4	6
8:00- 9:00	4	2	6	2	1	3
9:00-10:00	1	6	7	1	5	6
10:00-11:00	5	3	8	6	6	12
	—	—	—	—	—	—
Totals	16	18	34	13	19	32

already ceased to brood on bright mornings when the nestlings were eight days old and naked except for their sprouting pinfeathers. Doubtless the snug nest afforded them sufficient protection. The rates of feeding by both parents on these two mornings are given in table 2. The parents began to bring food rather late. On July 8, the female gave the eight-day-old nestlings their first meal at 6:00 a.m., and the male, who continued his dawn song until 6:07, first came with food at 6:20. On July 16, the male, after singing his long dawn song, brought the first meal at 6:23, an hour after daybreak, and the female first came with food a minute later. As far as I could distinguish, on both mornings the nestlings' nourishment consisted wholly of winged insects and larvae, usually green but sometimes brown in color, and nearly always of substantial size. Some of the insects resembled grasshoppers. I looked in vain for fruit in the parents' bills.

The male now approached the nest with scarcely more hesitation than his mate; but each on arriving alighted in the vine tangle some feet from it and paused to look around before advancing to the doorway. To deliver food to the eight-day-old nestlings, both clung in the orifice with back outward and somewhat downward, never entering. This position was apparently not easy for them to maintain. If the food was not promptly taken by the nestlings, the parent dropped down to perch on the vines below the doorway; after a pause it returned to the entrance, then perhaps after a few seconds there dropped down a second time with food still held in the bill; if necessary it repeated this three or four times until the insect vanished. Eight days later, the meals were delivered more rapidly while the parent clung upright at the entrance for a few seconds. It was rarely necessary for the parent to offer a morsel twice. After each feeding, the parent flew rapidly away. When eight days old, the nestlings were fed at the rate of 2.3 times per capita per hour; when 16 days old, they were fed at the rate of 2.1 times per capita per hour. The great acceleration in the rate of feeding after 10:00 a.m. on the nestlings' sixteenth day was apparently caused by a change in the weather. In the early morning, which was misty and almost uncomfortably cool, I noticed few insects flying. At about ten o'clock, the sun began to beat hotly through the clouds; little, black, biting flies and sweat bees became abundant. The parent becards then brought food more often, so that the nestlings soon became full and took their meals less promptly. At a nest of the Barred Becard, both parents also fed the nestlings.

After feeding, the female White-winged Becard sometimes carried away a dropping and more rarely I saw her swallow one. But I did not see the male take a share in cleaning the nest, which he never at any time entered while I watched. The insufficient attention to sanitation explained why the doorway and the ground below were well splashed with white droppings—a usual feature of becards' nests containing older young.

The male defended the nest and once drove away a Bellicose Elaenia.

When the nestlings were only eight days old and still naked, I heard a little song as I passed beneath their nest. When 16 days old, they gave a fair imitation of the day song of their parents, sometimes answering the male singing in the distance. When a parent bringing food shook the vine that supported the nest, the nestlings set up a little chorus of high-pitched notes of a different character. In non-oscine birds it is not unusual for young still in the nest to give fair, if weak-voiced, imitations of the calls and songs of their elders. In the true songbirds, with their

more complex songs and usually shorter period in the nest, such singing in the nest is rare.

All three becard nestlings flew from the nest in the vine tangle between the evening of July 20 and noon of the following day, at the age of approximately 21 days. All resembled the female in coloration. As they roamed with their parents through the treetops, the fledgling constantly repeated sweet notes and little songs, which often resembled the male's dawn song and sometimes the day song. These melodious but somewhat plaintive sounds floated down from the trees for many minutes together. But the young becards kept themselves so well concealed amid the foliage, and moved so seldom, that it was most difficult to glimpse them. I last saw the family together on August 5, two weeks after the young left the nest, when they passed through the trees by the house at the day's end. After their first flight, they never returned to sleep in their snug nest but roosted in the foliage, exposed to the heavy rains of this season.

In El General, at an altitude of about 2500 feet above sea level, I have found two nests which the young left in early September, and I have seen several other nests that held nestlings in August. On July 11, in the Motagua Valley of Guatemala, I watched a becard build a nest which, if successful, would have sheltered nestlings until about the end of August. Hence the becards' breeding season extends over about five months, from late March or April to early September. I do not know how many broods may be reared. Many nests are destroyed, and very late ones probably belong to pairs whose earlier nestings were unsuccessful.

The big nests of the White-winged Becard, conspicuously placed in the treetops, fall prey to numerous enemies, although doubtless they are above the reach, and escape the notice, of many of the more terrestrial nest robbers. One of the chief enemies of the becard is the Piratic Flycatcher, which I have twice found rearing its family in a nest stolen from these cotingas (Skutch, 1960a:451-464). One nest, about which a pair of the flycatchers loitered as though only waiting for the becard to complete it before claiming it as their own, was occupied by a swarm of small, black melipone bees, which put an end to the dispute between the two kinds of birds. The insects proceeded to close up the nest's doorway with wax or some kindred substance, leaving only a small, spout-like opening for their passage in and out. I have often found nests of the becard torn apart in the treetops where they had been built. This was apparently the work of toucans, probably the big Chestnut-mandibled Toucan, which in the breeding season roams through the trees, in clearings not far from the forest, pillaging nests.

Like the Rose-throated Becard, the White-winged Becard shows an amazingly strong attachment to its chosen nest site. Toward the end of March of 1937, a becard began to build in the top of an avocado tree growing in a small coffee plantation. On April 5, I found the nest, still unfinished, lying on the ground. Two days later, I noticed another nest, well begun, in the top of a neighboring avocado tree; but the following day this was also pulled out of the tree. By May 10, this becard was completing a third nest in the top of still another avocado tree. The two most widely separated of her three nest sites were only 40 feet apart. For a wide-ranging bird of the treetops, not confined by competition for territories to a narrow breeding area, this was unexpected loyalty to a chosen spot. In the third nest she at last hatched her eggs, only to lose her nestlings a few days later.

In four consecutive years, there were nests of the White-winged Becard in the

top of the same tall targuá tree (*Croton draco*) in the pasture in front of our house. The targuá is common in the vicinity and this tree was like many another; yet it had a peculiar attraction for the becard, despite the fact that most of the nests started there were unsuccessful. In 1945, the female was building in this tree at the beginning of May. In the following days, this nest grew smaller instead of larger, and on May 10 the becard started a second nest in a neighboring fork of the same treetop. By May 14, both nests had vanished. Yet, a few days later, a third structure was begun near the site of the first, but apparently it never contained eggs. On July 12, I found the becard working at still another nest in this same treetop. In this fourth nest she at last succeeded in rearing nestlings, which took wing in early September.

CINNAMON BECARD

Pachyramphus cinnamomeus

This small brown becard is five and a half inches in length and the sexes are alike in appearance. The upper plumage is plain rufous-tawny, darkest on the crown. The under parts are buff or tawny-buff, with paler throat and abdomen. The bill is dark; the eyes are brown; and the legs and toes are bluish gray.

The Cinnamon Becard ranges from western Ecuador and Venezuela to southern México. North of Panamá, it is largely confined to the Caribbean rain forests, although there are a few records from the Pacific side of Costa Rica. It has been found only from sea level up to slightly more than 2500 feet. Most observers (for example, Carriker, 1910:666) have reported that it lives in the heavy rain forest and is rarely seen anywhere except high in the trees. Until 1965, my experience with this little-known bird was limited to a single pair, whose activities in the breeding season centered in the shade trees surrounding a farmhouse which stood on a narrow ridge between the Río Pejivalle and its small affluent, the Río Humo, on the Caribbean slope of Costa Rica at an altitude of about 2100 feet. Large expanses of forest covered the surrounding hills, but several hundred yards of pasture with scattered trees separated the becards' nest from the nearest woodland.

These becards subsist largely on insects, which they sight while they perch on the leafy boughs of trees, then capture at the end of a swift dart, snatching them from the foliage without alighting. Once I saw the male of the nesting pair drop from his perch in a guava tree to the grassy slope on which it grew. Here he caught a small green grasshopper, which he carried up to the tree before he devoured it. A large proportion of the insects which the becards eat are green.

When I first arrived in this locality in early April of 1941, I heard, each morning at daybreak, an unfamiliar and most peculiar bird voice, weak, plaintive, and slightly whining. As it floated up to me from the distant songster, it had the thin, dreamy, unsubstantial quality of the song of the Black-throated Green Warbler. At other times it reminded me of the shrinking dawn song of the Paltry Tyranniscus. When the bird came closer to me, his song took more definite form, and I recognized a number of variations. A version frequently uttered consisted of about six slight, plaintive notes, ascending in pitch: *dee dee dee dee dee de*. In form, this song resembled that of the White-winged Becard; but the thin, weak notes of the Cinnamon Becard contrasted sharply with the dulcet, liquid voice of its more familiar relative. The utterances of the female Cinnamon Becard resembled those of the male, but her notes were weaker and delivered in shorter sequences.

NESTING

On April 12, I discovered that the Cinnamon Becards frequenting the trees around the farmhouse had begun a nest in a small guava tree that grew on the very steep, grassy slope which dropped from the dooryard to the shore of the Río Humo. The site of the nest was a wide, horizontal fork at the end of a long, horizontal branch, about 15 feet above the ground on the downhill side of the tree. It was about two feet from a small wasps' nest. The material already accumulated by the builder was chiefly green moss, which was bound together by cobweb and

formed a mass about the size of an orange. This mass was suspended between the arms of the fork and was apparently concave on its upper side.

On the morning of April 12, I watched this nest from 7:30 to 9:30 a.m. Apparently only the female worked, and her visits were infrequent. In the two-hour period, she brought only 15 contributions to the structure, including green moss, spider cocoons, and short pieces of fibrous material. Whenever she brought something to the nest, she stood on one of the supporting twigs and dropped her contribution into the concave top of the mass. Then, still standing beside it, she arranged the material with her bill, pulling it up here and poking it in there, often spending considerable time at this work. She flitted from side to side to reach different parts of the mass. Sometimes she started to leave, then returned with empty bill to continue the work of arrangement. But she never sat in or on the mass of material while she gave it shape, as birds which build cup-shaped nests usually do; she always stood beside it as she worked.

Once she flew up against the trunk of the guava tree that supported the nest and plucked off a tuft of spider's cocoon. But most of her material came from a greater distance. The moss was probably taken from the moss-laden limbs of neighboring trees.

The male often followed his mate while she gathered material; but sometimes he rested in the guava tree while she went back and forth, and at other times he stayed out of sight while she worked. One of the becards drove from the nest tree a Sulphur-bellied Flycatcher almost twice its own size. Although I could not distinguish the sexes, my failure ever to see both of the becards bringing material or shaping the nest at the same time led me to conclude that the male did not build.

Two days later, the female sometimes stood in the concavity of the nest while she arranged its constituents, but she still preferred to work on the nest while resting on one of the arms of the fork. On the morning of April 18, I found her building more actively. In the hour and a half from 6:42 to 8:12 a.m., she brought 23 billfuls of material. The nest was now so deep that she was all but hidden from view when she stood in the bottom arranging the materials. On the side which faced out from the supporting tree, she had left a gap in the wall which was destined to become the doorway of the completed nest. She rarely entered or left by way of this opening; more often she went in and out through the still-uncovered top. Sometimes, when she arrived with a contribution, she stood on the edge of the nest and dropped the material into the hollow, then she went off without arranging it. At other times she remained for a minute or more in the nest, giving it shape.

By April 21, the chamber had been covered over, chiefly with long, brown fibers. The female becard now went in and out through the round doorway in the side of the nest that faced out from the tree. Into the chamber she carried a variety of materials, some flat, some downy, others fibrous. Occasionally she placed a tuft of green moss on the roof. Although when the nest was first begun its predominant color was green due to the green moss, now it had faded to brown. By April 24, it appeared to be completed, after about two weeks of work. It was a bulky, roughly globular structure, with a lateral opening.

Because of the inaccessibility of the nest, placed above the steep declivity, I could not learn when the eggs were laid, nor how many there were. While incubation was in progress in May, I watched the nest for nearly six hours, divided between three mornings. As far as I could tell, only the female attended the eggs, and she

sat most impatiently. Her 13 completed sessions ranged from 2 to 28 minutes and averaged 10.5 minutes. Her 11 completed recesses ranged from 4 to 26 minutes and averaged 14.8 minutes. She was away from the nest more than she was present, and her constancy in incubation, computed from these averages, was only 41.5 per cent. During her absences, she found additional material for her already bulky nest. For the roof she brought dry bamboo leaves, fibrous materials, and down, including a whole dry milkweed pod from which the plumed seeds were escaping. Other dry bamboo leaves were taken into the chamber. During some recesses she brought three, four, or even five billfuls of material; the last billful was brought as she returned to resume incubation. In neglecting her eggs while she made her bulky nest still bulkier, this Cinnamon Becard resembled the White-winged and the Rose-throated becards. Her mate spent much time in the guava tree that supported the nest and drove away trespassing small birds.

Probably the female sat on her eggs more constantly in the afternoons, which at this season were usually rainy. One afternoon she returned to her nest at 2:52 p.m., and shortly afterward a drizzle began to fall. She was still within when, at 3:30, I left as the shower became hard. She had already incubated for 38 minutes, which was substantially longer than any morning session that I had recorded.

By May 24, the female had begun to take food into the nest. From 6:20 to 7:40 a.m. on this day, she brought insects four times. Yet even after her nestlings hatched, she continued to add material to her nest. From 6:45 to 8:35 a.m. on May 26, she took eight billfuls to the top of her nest. Seven of these billfuls, consisting largely of dry flowers of the sotacaballo (*Pithecolobium*) that grew along the neighboring river, were brought in a single interval between broodings. In the hour and 50 minutes that I watched, she brought food only three times and she brooded four times. One member of the pair, doubtless the male, came with a green insect in its bill, voiced low, musical notes while it hesitated in front of the doorway, and finally carried the insect off and ate it.

Male becards are often slow in beginning to feed their offspring in the well-enclosed nests, which they apparently never enter during the periods of construction and incubation. As late as May 29, five days after I had first seen the female take food into the nest, and three days after the male had brought food to the doorway without knowing what to do with it, I found no indication that he was feeding the nestlings. Eventually, however, he shared the work of nourishing them; and on June 9 I had no doubt that both parents were bringing food. Green insects, evidently plucked from foliage, formed the bulk of the nestlings' diet.

On June 12, the parents were still taking food into the nest, but by the following day they had ceased to do so, whence I inferred that the fledglings had flown. Since I first saw the female carry in food on May 24, and she may have done so a day or two earlier, the young remained in the nest at least 20 days, and possibly as long as 22 days.

In the Sarapiquí lowlands of northeastern Costa Rica, where the Cinnamon Becard was abundant, I found two additional nests in 1967. Each was situated about 50 feet up, near the end of a drooping, leafy branch in a tall tree, where it hung clear of the surrounding foliage. One of the nest trees was in a cacao plantation and the other in a pasture, but both were near heavy forest. In form these nests resembled the one already described. The first was found at the end of April, when construction was well advanced. I saw only the female build but she was

attended by a mate. Between 7:05 and 8:05 a.m. on April 30 she came with material 21 times, the most concentrated building that I witnessed. She brought pieces of fibrous material, papery pieces that were apparently old leaves or leaf sheaths, and great billfuls of seed down. By early June both parents were feeding nestlings, chiefly with small, green insects. At this date, incubation appeared to be still in progress at the second nest.

SUMMARY

The Cinnamon Becard lives high in the trees of the lowland rain forest, from sea level to somewhat above 2500 feet in Costa Rica. Frequently, however, it enters neighboring clearings with scattered trees in order to nest. It subsists on insects which it sights while it perches, making a swift dart to pluck them from the foliage without landing beside them.

Its voice is thin and weak. One song consists of about six slight, plaintive notes, ascending in pitch.

Three nests were situated at heights ranging from 15 to 50 feet, in trees growing in pastures and a cacao plantation. Each nest was a bulky, roughly globular structure with a doorway in the side. One was composed of green moss, long brown fibers, dry bamboo leaves, and downy materials. It was built in about two weeks by the female alone. Her mate often accompanied her or rested close by while she worked, but he was not seen to help.

The eggs, which were not seen, were incubated by the female alone. She sat most inconstantly and often neglected her eggs while she brought additional material to the nest. In nearly six hours of observation, she covered her eggs only 41.5 per cent of the time. The incubation period is unknown.

Both parents fed the nestlings, chiefly green insects, but some days passed before the male started to feed them. Even while attending nestlings which still required brooding, the female found time to bring additional material to the nest.

The nestling period was between 20 and 22 days.

ROSE-THROATED BECARD

Platypsaris aglaiae

The Rose-throated Becard is a cotinga about six and a half inches in length, with a large head and a short, broad bill. As in many members of this family, the sexes differ greatly in appearance. The upper plumage of the male is slate-color or black. His ventral surface is gray, and there is a conspicuous patch of purplish red on his throat. The top of the female's head is dark gray or blackish and the rest of her dorsal plumage is russet-brown or rufous-chestnut, becoming brighter on the tail. Her under parts are buff or tawny-buff. She lacks the conspicuous rose-colored patch which adorns the male, or has at most a faint trace of this color on her throat. The feathers of the crown are in both sexes erectile, and the male has white shoulder patches that are revealed only on special occasions. The foregoing description refers to the race *Platypsaris aglaiae sumichrasti* of southern México and northern Central America, with which this account chiefly deals. In other races of this variable species, the plumage is paler and the male lacks the bright gorget.

The Rose-throated Becard ranges from the southern border of the United States, in Texas and Arizona, to northern Costa Rica. In Central America, it extends from the lowlands of both coasts far into the highlands, reaching in western Guatemala an altitude of about 8500 feet. In its several races, this species tolerates a wide variety of ecological conditions. In Guatemala, I found it among the taller trees of the hot, arid portion of the Motagua Valley, where thorny shrubs and cacti abound, and likewise in the cool forests of oaks, alders, and other broad-leaved trees mixed with pines in the high mountains. It occurs also in the Caribbean rain forests, where it appears to be rare.

In the mountains of Guatemala, above 8000 feet, Rose-throated Becards were present not only in the breeding season but even in the months of the northern winter, when heavy frosts whitened the open spaces after every still, cloudless night. At this time, they roamed through the woodland in the mixed flocks of resident and migratory wood warblers and other small birds. On the few occasions when I saw them, there was in each flock a single becard, usually a female or perhaps a young male in brown plumage, more rarely a male in adult plumage. In November and December, the becards seemed not to associate in pairs.

Rose-throated Becards subsist chiefly on adult and larval insects, which they capture in the manner characteristic of the cotinga family: they perch on a branch until they sight their prey, then they either make a rapid dart to pluck it from the foliage where it rests, without alighting beside it, or they seize it in the air. They vary their diet with berries.

VOICE

The only notes which I heard from the Rose-throated Becards in the Guatemalan highlands were thin, high-pitched, often squeaky whistles. These notes were delivered with a number of variations, sometimes with a rising inflection that suggested a question. The becard's call resembled the note of its neighbor the Spotted-crowned Woodcreeper but it was shorter. Although not melodious, it was an agreeable sound, one of the minor notes in the great symphony of bird voices.

Other races of the Rose-throated Becard seem to have similarly weak notes. At the northern limit of the range of this species in Arizona, Phillips (1949:139) found the usual call to be "a high-pitched squealing *keeer* which is rather long drawn out and descending in pitch. . . . When excited, the male utters another thin, high-pitched call, *chrrr-chrrr-chrrr—quit—quit—quit*." In Tamaulipas, México, Sutton (Sutton and Pettingill, 1942:20) heard a male Rose-throated Becard sing uninterruptedly for over half an hour. "The song was a conversational *chi-zoo, wheez-oo, chi-zoo, kee-zoo*, repeated over and over, with pauses of a second or more after each group of four syllables." Other variations of this becard's song are given by Bent (1942:10-11). Most observers agree that its notes are thin and lack melody.

NEST BUILDING

When I lived on the Sierra de Tecpán in western Guatemala in 1933, one of my favorite walks was along a road that wound through the pastures, skirting the base of the mountain which rose sharply behind the house, then crossed a wooded ridge to the Indians' lands on the north. About a mile from the house, the road passed through an opening in the woods, where subterranean waters welled up diffusely through the surface and produced an open, sedgy marsh, through the center of which flowed a little rill. Beside the rivulet, in the middle of the marsh, four alder trees grew in a clump. Hanging from the end of one of the finer twigs of an alder, about 50 feet above the ground and quite unapproachable, was a large, globular bird's nest, perhaps a foot in diameter. When I first noticed it, in February, it was old and weathered and seemed to have been constructed the year before. No bird took an interest in the structure, and I could not imagine what kind of bird had built it, for I had so far seen on the Sierra de Tecpán no species which I thought likely to construct a nest of that type.

More than a month later, while I loitered in some bushy woodland about a thousand feet from the little marsh where the alder trees grew, I found a small blackish bird with a patch of rose on his throat. After giving me a fleeting glimpse of himself, he vanished among the trees and eluded all my efforts to find him again. But I had seen enough to recognize the stranger as my first Rose-throated Becard and, remembering the descriptions that I had read of the bulky hanging nests of some other kinds of becards, I began to associate the puzzling nest with the hastily glimpsed bird.

Another month passed before my association of nest and bird received confirmation. As I passed by the marshy opening on the morning of April 20, something falling from the old nest caught my eye, and looking up I saw a male becard clinging to the structure and attempting to pull a fragment from it. He detached some shreds of material and took them to a recently begun nest, a sprawling web of varied constituents attached to several of the fine twiglets at the tip of a slender branch, a few yards from the old structure and slightly lower. Working with him was another bird of the same size which was without doubt his mate, for she was brown, without rose on her throat. This brown bird brought to the new nest several billfuls of cobweb, a material which apparently was needed in considerable quantity. Both members of the pair made efforts to shape the growing structure, which was still irregular and formless.

A week later, I returned to watch the becards continue their task. The new

nest was now nearly the size of the old one when I first saw it. A roughly globular structure, higher than wide, it was provided with two entrances, one facing east and the other south. Since my last visit, the becards had pulled at the old nest until every trace had fallen or been incorporated in the new one. In the remnants of the old structure on the ground, I found fibrous plant stems, much gray lichen, spider cocoons, thistle down, and sheep's wool.

The blackish male and his brown mate again worked together at the nest, but now it was easy to see that the latter was the guiding spirit, the male only her assistant. She brought material more often than he, although he usually followed when she flew up to the nest, whether he carried anything or not. Once, when the two returned together with material in their bills, the female quickly added her lichen to the structure and was ready to leave before her mate, delaying on a nearby twig, had reached the nest. When she flew off to the woods to seek more building material, he followed still carrying his intended contribution. Yet sometimes he came alone to the nest with a lichen or some fibers. He was usually content to add his material to the top or sides of the nest, and I saw him enter only twice, whereas his brown partner went inside many times, shaped the structure, and pulled dangling fibers and loose down inward through the entrance. On both of the occasions when the male was inside his mate entered with him, evidence that the chamber was large enough to contain the two of them.

They were alert birds, very quick on the wing. Once as the male alighted on the nest he accidentally knocked off a large tuft of down, which floated slowly earthward. Immediately he darted down in pursuit of it with the stuff he had just brought still in his bill, caught it well above the ground, and returned to the nest with a double load. Sometimes the becards descended to levy further contributions from the remains of the fallen nest, but most of the material that they now brought was new. At times they flew to the new nest with a long fiber that trailed far behind them, and among other things the female brought a large piece of dry fern frond.

On May 3, two weeks or a little more after they had started to build, I found the becards putting the finishing touches on their commodious nest. They had closed the aperture on the southern side, leaving only the opening which faced the rising sun as their permanent entrance. The blackish bird and the brown bird continued to bring material as from the beginning, but their methods of placing it were now very different. In an hour and a quarter, the female came 24 times with materials, including pine needles, long fibers, and tufts of down. Twenty times she went directly into her nest with her burden, flying skillfully through the entrance without clinging first to the exterior. Three times she deposited long fibers on the top of the nest, and once she placed part of her load on the roof, then took the remainder inside.

The male brought material only 13 times, and everything he carried, whether fibrous or downy, was added to the roof of the nest. I did not see him enter even once. His eagerness to be near his mate was far stronger than his desire to advance their undertaking, and he followed her to and from the nest more often than he brought anything in his bill. If she were ready to fly off while he still waited to place his billful on the nest, he turned about and followed her into the woods, foolishly bearing his burden in the wrong direction. Sometimes, as he approached the female, he spread his white epaulets, which became very fluffy and conspicuous, standing above his shoulders and contrasting with his deep gray back. These downy

white feathers on his shoulders seemed intended for her eyes alone; except when in her presence, he kept them laid flat, so completely covered by the blackish plumage of his back that one would never have suspected their presence.

The becards worked rather silently, but at intervals one of them called its mate with a thin, high-pitched whistle, which was delivered in a number of different tones.

When I returned to the becards' nest two days later, I was dismayed to find that some vandal had cut down the alder tree from which the structure hung. After more than two weeks of work, the nest was hardly completed, for the entrance was still without a sill, and eggs would certainly have rolled out if deposited in the structure as it then was. It measured a foot in height and 9 inches in transverse diameter. The most conspicuous constituent throughout was a kind of long, slender, much-branched, gray lichen, which accounted for three-quarters of the nest's bulk. There were many pieces of fibrous bark of various kinds, dry and partly disintegrated; a wiry piece of orange-colored dodder vine, still living and 13 inches in length; many long, dead pine needles, in their original bundles; many yellow spider cocoons and tufts of silk derived from them; many small tufts of sheep's wool; a few downy feathers; some thistle down; a few pieces of green moss; some slender, dry vine stems; a coiled tendril; a piece of a bush-tits' nest, probably of the preceding year. Hanging from the outside was a thick piece of blackberry cane, 5 inches long, which had probably been brought for the sheep's wool that had caught on its thorns. The thickness of the nest's walls varied from 1½ to 2½ inches, and the interior cavity, as large as my fist, was lined chiefly with thistle down and fibrous bark.

Three days later, or on May 8, I found that the becards, nowise discouraged by their disaster, had begun a new nest in another alder tree of the same clump, only 20 feet distant from the site of their first ill-fated attempt. I thought them most imprudent to persist in building in the same spot; but since they seemed determined to nest in the place where they had apparently been successful in the preceding year, I decided to help them. I tied up the fallen nest as near the foundation of the new one as I could climb. This gave them an abundance of material close at hand and made the task of reconstruction much easier. They promptly took advantage of it, and in three busy days they transferred most of the constituents of the fallen nest to their new structure, which at the end of this interval had reached its full size.

Again disaster overtook the unfortunate becards. Their second nest followed the first to the ground. Their relentless enemy, if he was indeed the same, had climber the alder tree and cut off the supporting limb. Then the nest was covered with mud and used to dam a runnel which flowed through the marshy opening. This time even its materials were ruined. When I reached the clump of alders on May 12, the birds were in the vicinity, giving their high-pitched whistles, which in the circumstances sounded most melancholy. It was now the middle of May, the rainy season was threatening to break, and the becards had nothing to show for nearly a month of work.

But the dauntless birds, undiscouraged by two failures, promptly set about building a third nest in the very tree where the second had met disaster. This time they picked a location directly below the site of the last nest and about 30 feet above the ground. The new nest, instead of being suspended from a single slender branch in the manner of the earlier structures, was attached to two branches, with the result that the top, between the points of attachment, was concave like a saddle.

By May 20, this latest structure had reached its full size. This time the becards had better luck and succeeded in completing their nest and laying in it.

Two years later, on July 18, 1935, I found a pair of Rose-throated Becards building in a shade tree in a coffee plantation near Colomba on the Pacific slope of Guatemala, at an altitude of about 2600 feet above sea level. The nest was attached to a slender, drooping twig, about 50 feet above the ground, and both male and female were bringing material to it. Four days later, the growing mass had been spread apart to form the chamber, and the female was taking pieces into it.

These few nests, swinging from slender, drooping twigs, at heights ranging from about 30 to 50 feet above the ground, are the only nests of the Rose-throated Becard that I have seen, but others have found this bird building in similar situations. A. W. Anthony (*vide* Griscom, 1932:281) saw a nest hanging about 40 feet above the ground at the end of a slender limb, in the Pacific lowlands of Guatemala, and in El Salvador, Dickey and van Rossem (1938:345) found nests attached to the spray of foliage at the end of long, drooping branches, 20 or 30 feet above the ground and usually inaccessible. In Tamaulipas, México, Sutton and Pettingill (1942:20) saw nests at the ends of long, swaying branches, from 40 to 70 feet above the ground or water. At the northern limit of this species' range, in the lower Río Grande Valley of Texas, Davis (1945) discovered three nests at heights of about 20 feet; and in southern Arizona, Phillips (1949) found nests attached to drooping branches at heights of 30 to 60 feet.

In Arizona, as in Guatemala, these becards are strongly attached to their chosen nest site, building their new nest either in the very spot which they had occupied in the preceding year or only a few feet away from it. As at the nests that I watched in Guatemala, both sexes were seen to share the work of construction by Sutton and Pettingill in México and by Davis in Texas. The last-mentioned author (1945) stated that the female brought material to the nest about twice as often as the male, and that she alone did the work on the interior, much as at the nests that I watched in Guatemala. Sutton and Pettingill (*loc. cit.*) reported that in México five to nine days were spent in building a nest.

Others have found becards' nests even bulkier than those that I saw. In Arizona, Phillips (*op. cit.*:137) measured nests that were from 12 to 25 or 30 inches high and from 10 to 12 inches in general diameter. These nests were spherical to rather pear-shaped in outline, and they were "composed mainly of long strips of inner bark taken from dead cottonwood limbs, interwoven with quantities of grass, leaves, patches of insect webs, rootlets, and other miscellaneous materials." The nests found by Sutton and Pettingill in Tamaulipas were made largely of "Spanish moss" (*Tillandsia usneoides*); they measured roughly 15½ inches in height by 12½ inches in width, and they had an aperture in the side that was 2½ inches in diameter. Most unusual in site and pattern was the exceedingly bulky nest discovered in Nuevo León, México, by Eaton and Edwards (1947). This amazing structure was only four feet above the ground in an orange tree, where it rested on a main horizontal branch, with one end against the trunk. Composed of dead leaves, grasses, and even a few strands of small hemp rope, this nest measured approximately two feet horizontally across the front, one foot in height, and one foot from front to rear. The entrance was a hole near the center of the long side of the nest, and within were nestlings beginning to be feathered. Another bulky nest was discovered in Arizona by Levy (1958).

At Jalapa, México, Frank M. Chapman (*vide* Bent, 1942:7) found a becard's nest which was covered in part with fresh green mosses and had the internal cavity lined with mud. These materials, especially the lining of mud, seem not to be typical. Most nests are lined with softer materials, including shredded bark, seed down, feathers, and the like.

THE EGGS

In the nest which the becards finally completed on the Sierra de Tecpán, eggs were laid about the end of May. I did not try to reach these eggs, far out from the trunk of the brittle alder tree; but in June, when the parents were feeding nestlings, one of the eggs which had failed to hatch was found, unbroken, in the grass beneath the nest. This egg was grayish brown, irregularly mottled, especially at one end, with darker brown. It measured 25.4 by 17.5 mm.

Even in the tropical portion of its range, in El Salvador, the Rose-throated Becard may lay five eggs, an unusually large set for a passerine in Central America (Dickey and van Rossem, 1938). Farther north, in México and Arizona, a few sets of six eggs have been reported (Bent, 1942:8; Phillips, 1949:137). So few records of the contents of becards' nests are available that we do not know what size of set is most frequent, nor do we know the range of variation. The eggs vary considerably in coloration and have been described in detail by Bent.

INCUBATION

Only the female incubates. I watched the nest in the alder tree from 6:55 a.m. to 12:09 p.m. on June 6, from 11:57 a.m. to 6:55 p.m. on June 7, from 5:25 to 11:54 a.m. on June 8, and from 1:32 to 2:37 p.m. on June 13. Much of my watching was in the cold rain and chilling mists which were frequent in the wet season at this high altitude. On the rainy afternoon of June 7, the female returned to her nest at 5:13 p.m. and remained there until I left in the waning light at 6:55. On the following morning I resumed my vigil as the wet day broke at 5:25 a.m., but the female stayed within the nest, despite the repeated calls of her mate which she answered, until 6:17, when she at last came forth to break her long fast. Thus her nocturnal session had lasted 13 hours and 4 minutes.

In about 17 hours of watching which fell within the female's active periods, I timed 49 sessions, which ranged from 3 to 38 minutes and averaged 11.6 minutes. The becard was very irregular in her movements, and sometimes a long session came between two others that were only half as long. For instance, once she sat for 6 minutes, then 23, then 8 minutes. Her longest diurnal session, 38 minutes, was taken on a rainy afternoon, but on a clear, cold morning she sat continuously for 30 minutes. Her longest recess, 19 minutes, followed her longest session and was taken while rain fell hard. I timed 50 recesses, which ranged from 2 to 19 minutes and averaged 9 minutes. The female covered her eggs only 56.3 per cent of the 17 hours. This becard incubating in the cold, wet highlands covered her eggs only slightly more constantly than becards of other species that I have watched in lower and milder regions. It may be that the thick roof and walls of her nest kept her eggs warm during her frequent short absences. Toward the end of the incubation period, she sat no more constantly than at the beginning.

The entrance to the nest was at the bottom, a little to one side of the center. Just how the aperture communicated with the interior, and what arrangement

prevented the eggs' rolling out when the bough swayed in the wind, I could not learn without taking down the structure. When she returned from her foraging expeditions in the neighboring woods, the female becard almost always paused for a few moments on a branch of the nest tree, from which point she turned her head rapidly from side to side as she surveyed her surroundings before darting into the nest. If anything excited her suspicion, she raised the gray feathers of her crown in an attitude of inquiry and flew back and forth among the boughs until finally assured that she could safely go in. To enter the downward-facing doorway, with no perch or point of support below it, was not easy, but the bird accomplished the feat with admirable skill. Sometimes she started from a perch below and to one side of the nest, inclined her course sharply upward until it became vertical as she neared her goal, hit with an audible slap the alder leaves which draped below her doorway, and disappeared into the interior. At other times she would take off from a perch above the level of the nest, fall almost straight downward, turn sharply upward in mid-air and rise directly to the entrance, describing a narrow "U." Whichever mode of approach she chose, her course was so well calculated from the start that it followed a perfectly smooth curve. Only once in about 50 times was her approach to the doorway faulty. At such times she rose a little to the side of the aperture, wavered, then turned sharply in order to reach it. On leaving the nest, she darted forth head downward and described a long, smooth curve that generally terminated in the neighboring trees.

It is characteristic of birds which build large and elaborate nests, or those that require an unusual amount of labor because of the quantity of material which must be gathered, that they continue to add to the structure even while they incubate. This is true of the Rufous-breasted Castlebuilders, which construct great castles of sticks; of the Black-eared Bush-tits, which build elaborate pouches of down and lichens; of hummingbirds, whose nests are simple in form but laborious to build because of the great amount of fine downy material they contain. Birds which build simple, cup-shaped nests, including finches, tanagers, wood warblers, thrushes, and related families, rarely bring any material to them after the eggs have been laid. These remarks apply especially to the passerines; less advanced types of birds may continue to carry material to their nests while incubation is in progress, regardless of the size or complexity of the structures.

The construction of the great globular nest of the becards was a very large undertaking for birds no bigger than a sparrow, and as is usual in such cases as just noted, they continued to be preoccupied with it until their eggs hatched. Almost every time that the female returned to her eggs after a brief absence in rainless weather, she carried a piece of material to add to her already bulky structure. She brought long pieces of slender dry vines, leaves, tufts of cobweb, and an occasional small twig, which she attached to the top, and she took inside small dead leaves, pine needles, and fibers. Sometimes, on leaving her eggs, she found something suitable and brought it back to the nest before she flew out of sight to seek food. Not infrequently, she brought material twice or even three times in the course of a single recess. Like the castlebuilders, she occasionally emerged from the nest holding in her bill a fragment of material, usually a piece of dead leaf, and attached it to the top of the structure before she went off to forage. In 17 hours while the female followed her usual rhythm of sessions and recesses, she brought

26 billfuls of material to the nest. In the same period, the male brought seven billfuls.

When I saw that, as the nest neared completion, the male becard placed all his contributions on the outside, I surmised that he would not help to keep the eggs warm. This prediction proved correct; I did not once see him enter the nest during the incubation period. He remained close by and sometimes brought material, usually a piece of lichen, which was the easiest thing to find, since the trunks and limbs of the neighboring trees were covered with them. Once, to do him justice, I saw him come with a tuft of cobweb, and once with some fibrous stuff. All of his contributions were placed on the roof, where they were not wasted, since they helped to shed the hard rain which fell almost every day in early June.

Frequently the male called to his mate while she sat in the nest, and her reply came softened and subdued by the thick walls through which it filtered. If she did not respond immediately, the male persisted in his calls until she answered him. In the early morning he came to call her from the nest, and frequently through the day she seemed to leave in response to his invitations to come forth and join him. He was certainly in part responsible for the short periods which the female devoted to warming her eggs, but many times she emerged spontaneously after a brief session. Often he accompanied her on her foraging excursions, then returned with her and stayed near the nest while she sat within. At times he went off into the woods and remained out of sight for an hour or more. Often he displayed his white epaulets when he approached the female after a separation. Altogether, he was a devoted partner, and his attention to his mate was pleasant to watch.

THE NESTLINGS

Although I could not climb up to the nest to see when the eggs hatched, I went every other day to watch for an hour and learn whether the parents had begun to carry in food for the nestlings. By June 15, the becards no longer brought leaves and lengths of vine to the nest but appeared to approach it with empty bills. By looking carefully through the binoculars, I could now and then detect a portion of some small insect projecting from their mandibles. Doubtless at other times they brought insects so small that they were carried wholly inside the bill and therefore passed unseen. Now, at last, the male began to enter the nest. At first, he seemed to prefer to deliver his offerings while his mate was inside with the nestlings. On arriving with something in his bill, he called to learn whether she was within and delayed his entry for several minutes when he received no confirmatory reply. When the nestlings were very young, the female sometimes, from force of habit, brought inedible building material to the nest; but feeding the young birds soon occupied all her time.

As the nestlings grew older, their parents brought them portions that were larger and more readily seen. Small green larvae were the articles that I most often recognized, and there were a number of small moths and butterflies, which were given with their bright wings still attached to their bodies. The male and female were about equally assiduous in feeding the nestlings. From 8:00 to 10:00 a.m. on June 21, the young, about a week old but of unknown number, were fed 11 times by the male and 9 times by the female. From 4:00 to 5:00 p.m. on June 24, the male brought food 10 times, the female 7 times. After the nestlings were no longer brooded by day, the female fed them slightly more often than did the male.

In a total of six hours of watching divided between as many days from June 27 to July 3, the male brought 58 meals and the female brought 68. The greatest number of feedings that I counted in a single hour was 28, which were delivered by both parents between 7:20 and 8:20 a.m. on June 28, when the nestlings were about two weeks old. The parents now stayed in the nest only a few seconds at each visit, then darted away so rapidly that my eyes could hardly follow them.

Only the female brooded the nestlings. At first she covered them somewhat more constantly than she incubated the eggs. Between 8:25 and 10:31 a.m. on June 15, the day I first saw the parents take food into the nest, she was within the nest a total of 65 minutes and absent 41 minutes. This excludes one session and one recess which I could not time, because I failed to see her dart from the nest. From 8:00 to 10:00 a.m. on June 21, the female brooded seven times, for periods ranging from 2 to 9 minutes. On subsequent days, she left the nest after each feeding, and I recorded no more brooding by day. By June 27, when the young were about 13 days old, nocturnal brooding had also ceased, and the female no longer emerged from the nest at daybreak.

When the nestlings were about ten days old, I began to hear their faint notes issuing from their high cradle. Soon they could utter the typical calls of the adults, with all their varied inflections, but in a weaker voice—at least, coming from inside the nest, it sounded weaker. They answered the calls of their parents, and at meal time they uttered peculiar undulatory notes that suggested laughter. On the whole, they were noisy nestlings, and despite their apparent security, so high above the ground, I began to be apprehensive, fearing that their calls would draw the attention of the people who at long intervals passed along the road by the side of the marsh.

I thought that perhaps the male becard, after he began to enter the nest with food, would discover that it afforded a snug refuge from the cold rain of those June nights and take to sleeping in it, just as the male Black-eared Bush-tits slept in the nests that they attended. But as evening fell, he always delivered his last offering to the nestlings and flew off into the woods where I could not follow him, and before long the female did likewise. Neither parent used the nest as a dormitory.

For small birds, the young becards remained long in their swinging nursery. I last saw the parents take food to them on July 3, when they were 18 or 19 days old. When I reached the alder trees two days later, there was a gaping hole in the side of the nest, and the piece which had been torn from it was lying on the ground beneath. A short, heavy stick, stuck upright in the sod told the story. Some vandal, unable to climb to the nest, had thrown sticks until he succeeded in knocking it apart. Doubtless the oft-repeated cries of the nestlings had betrayed them to him. Possibly they were old enough to fly away when their nest was attacked, if they had not been injured by the impact of the sticks. Although I searched the vicinity, I could find neither parents nor fledglings.

SUMMARY

The Rose-throated Becard is exceedingly variable in both coloration and habitat. In Central America, it lives in lowland rain forest, in the light woods of hot and arid regions, and in the cool forests of the altitudinal Temperate Zone, its range extending from sea level up to about 8500 feet. In the highlands, single individuals

attach themselves to the mixed flocks of small birds in the winter months.

This becard flies out from its perch to pluck an insect from the foliage without alighting beside it, or it captures insects in the air. Fruits are also included in its diet.

The usual notes of the Rose-throated Becard are thin, high-pitched, often squeaky whistles.

The nest is a very bulky, roughly globular or pyriform structure that hangs at the end of a slender, drooping branch, or several such branches, in a clear space from about 20 to 70 feet above the ground, rarely lower. It is entered through a round orifice in the bottom or lower part of the side. The nest is composed of fibrous bark and stems, lichens, sheep's wool, spiders' cocoons, thistle down, pine needles, feathers, and the like, according to what the locality affords. Both sexes build, but the female takes the leading part, and as the nest nears completion, she alone enters it to line the chamber. More than two weeks may be devoted to the construction of early nests, but replacement nests may reach their full size in a few days.

These becards are strongly attached to a nest site. They build close to the remains of their nest of the preceding year, or in the very spot where it had hung. One pair, whose first and second nests were maliciously cut down, built their third nest in the same small clump of alder trees.

The Rose-throated Becard may lay five eggs in a set in Central America and six farther north, but very few records of sets are available. An egg found in Guatemala was grayish brown, irregularly mottled with darker brown.

Only the female incubates, sitting very inconstantly. Forty-nine sessions of one female ranged from 3 to 38 minutes and averaged 11.6 minutes. Her 50 recesses varied from 2 to 19 minutes and averaged 9 minutes. In 17 hours of observation, she covered her eggs only 56.3 per cent of the time. Throughout the incubation period, she continued to add much material to both the outside and inside of her nest, and her mate brought a smaller number of contributions to the outside. She showed great skill in shooting into her narrow doorway by means of an upwardly directed darting flight.

Both parents nourished the young with green caterpillars, small moths and butterflies, and other insects. At first, the male brought more meals than the female; but after she ceased to brood, the female fed the nestlings slightly more often than the male. The maximum rate that was observed was 28 feedings in an hour by both parents, for an unknown number of nestlings. Only the female brooded. After the young were about 13 days old, neither parent slept in the nest.

The nestlings were noisy, continually uttering weaker versions of their parents' calls. They remained in the nest until they were 18 or 19 days old, and they might have stayed longer if their nest had not been destroyed.

RUFOUS PIHA

Lipaugus unirufus

In the lowland rain forests of Central America, a sudden noise, such as a shout or the sharp crack of a dry stick breaking beneath one's foot, is sometimes answered by a loud, clear whistle. If one is exceptionally fortunate, he will glimpse, far above him in the trees, a bright brown bird between nine and ten inches in length, which in size and carriage suggests a thrush of the genus *Turdus*. As the specific name *unirufus* suggests, the Rufous Piha is almost uniformly reddish brown, but the cinnamon-rufous of the upper plumage is brighter than the tawny-ochraceous of the under parts. The sexes are alike in appearance.

The Rufous Piha is found from southern México to Ecuador. An inhabitant of heavy rain forest, through most of Central America it is confined to the Caribbean side, but in southern Costa Rica it occurs also on the Pacific slope. Here it is abundant in the tall primeval forests from sea level up to about 4000 feet, and I have found no record of its occurrence anywhere above this. It lives high up in the great trees, never flocking, but appearing always to be solitary. Rarely I have seen a piha in the shade trees around my house, at times as much as fifty yards from the forest.

FOOD

The piha subsists on a mixture of animal and vegetable foods. Small creatures, including winged and larval insects, spiders, and an occasional small scorpion, are captured in the manner characteristic of cotingas, by hovering beside the foliage and plucking them off, without alighting. This bird also eats berries, hard green fruits, apparently from lauraceous trees, and small palm fruits. Once, in my garden, I saw a piha descend to the ground, apparently to pick up an insect.

VOICE

As one wanders through the forests of southwestern Costa Rica, he hears from time to time a clear whistle, so sharp and loud that, if a newcomer in this region, he may look around for the man who is trying to attract his attention. These notes are heard through most of the year, both in the rainless season, when the dry, insistent *chirilin chirilin* of innumerable cicadas and the rustling and crackling of fallen leaves underfoot are the chief sounds of the woodland, and in the more profound silence that prevails in the months of heavy rains, when one moves almost noiselessly over the sodden ground litter. Even if the silence is so prolonged that one may doubt that any bird is within hearing, a sudden loud sound, such as a sneeze, a shout, a handclap, may elicit the clear whistle. When a Great Tinamou, alarmed where it forages unseen amid the ferny ground cover, rises abruptly with loudly whirring wings, the piha often calls out far above, as though exclaiming at the occurrence. This sequence of sounds was characteristic of the unspoiled forests in the valley of El General. The author of these arresting whistles remains so high and perches so quietly in the massed foliage, that he is most difficult to detect. I spent hours peering into the treetops until my neck ached before, a year after my arrival in El General, I satisfied myself that they are the utterance of the Rufous Piha.

Sometimes the piha's whistle consists of a single note, loud, shrill, and far-carrying: *peer*. At other times the whistle consists of two softer, less insistent notes: *wheer-weet*. (One might also paraphrase this as *pee-ha*, the bird's name.) More seldom the whistle consists of three notes, of which the first is long, the second short and contrasting in tone: *whee-er-wit*. Again, the whistle may be prolonged into a short, loud trill, or a longer, very musical trill, both of which are difficult to paraphrase. Each bird seems to have its particular part of the forest, where it is heard day after day over a long period. Early in April, I watched a piha which for over half an hour remained unusually low, from 20 to 30 feet up, in the same small area on a forested ridge. The bird rested quietly for many seconds on a slender branch; then it suddenly flew to another perch. Sometimes it whistled twice in the course of a minute, but more often only once. At times the utterances were still more widely spaced. If I made a noise, as by calling out or breaking a dry twig, the bird answered immediately. But even with this stimulation, I could not greatly increase the rate of calling; for the repetition after a few seconds of the sound to which the piha responded failed to elicit a second response. Only if I waited a good while before repeating the noise could I cause the bird to whistle again.

Since, as with a number of other cotingas, the male piha apparently takes no part in the nesting and pairs are not formed, these periodic whistles seem to be a method of advertising his presence to the females. Observations on courtship are unfortunately lacking. Females, and even feathered nestlings, sometimes utter similar but weaker whistles.

THE NEST

I was standing with a companion in a little-used woodland roadway, trying to glimpse a Pale-billed Woodpecker whose hammering revealed its presence far above, when I suddenly became aware of a Rufous Piha, motionless on a low branch. Only when I trained my field glasses on the bird did I notice that it rested on something which might have been a nest. Despite its closeness and the scrutiny to which it was subjected, the piha remained motionless, so we proceeded along the roadway leaving it undisturbed. When I returned nearly an hour later, the bird was in the same spot and posture, and I continued to watch for another hour until, after giving increasing signs of restlessness, it flew up into the treetops.

As long as the piha sat, I could see little of the small, roundish mat which it covered. The bird's departure revealed a structure the slightness of which amazed me. Looking upward through the bottom, I could clearly see the single egg which it held. A month later, after the termination of the nesting, I took down the nest for closer examination. It had been built 20 feet above the ground, in a small tree growing in high second-growth woodland that adjoined a large tract of primary forest. Support was provided by two, slender, parallel, horizontal twigs, each about a quarter of an inch in diameter. Between these twigs the piha had built a nearly flat pad about three inches in diameter and somewhat less than an inch in thickness. It was composed almost wholly of wiry tendrils, many of which were coiled. A few twigs and petioles had been built into the nest along with the tendrils that were attached to them. There was a single strand of decaying fibrous material. The whole fabric was light brown in color and so loose and open that I could read a

printed page through the middle of it. Green foliage had formed a canopy close above it.

The most meager arboreal nest that I had seen, this unbelievably slight structure seemed to contain the irreducible minimum of material that would suffice to support an egg in the air. It is hardly possible to imagine a scantier bird's nest. What a contrast with the bulky structures built by the becards, which are currently placed in the same heterogeneous family!

This nest was discovered on our farm in the valley of El General, at about 2500 feet above sea level, on May 31, 1950. My search for a second nest went unrewarded until February 26, 1965, when I found a piha building within 50 yards of the site of the first nest, in a situation in all respects similar. Unfortunately, I was unable to stay to watch this nest but my wife kept a record of events. As late as March 3, no egg could be seen on the slight, open structure. Incubation evidently began on March 4, when the piha sat on the nest for over an hour in the late afternoon. On nine visits during the following days, the bird was sitting and what she covered could not be seen. Finally, on March 10, my wife found the nest uncovered and could distinguish one egg. The parent evidently incubated quite constantly, for she was absent on only one of nine visits during the next week. On March 17 she was not seen and the egg had vanished.

On July 15, 1967, I found a third nest near the sites of the first two. It was about 35 feet up in a slender tree, far out on a thin ascending branch, where three small sprouts and one sturdier twig diverged from its broken-off end, providing a seemingly precarious support for the diminutive structure. My attention was drawn to this nest by the activity of a piha, who was tearing it apart and scattering its materials. Half an hour later, after the structure had been quite demolished, I saw a piha feed a stubby-tailed fledgling who had evidently left this nest at most a few days earlier. Then she rested for several minutes close to the young bird.

On July 25, as I followed a path along a forested ridge about 500 feet from the area where the three preceding nests were found, I noticed a piha arranging a long, curled tendril 17 feet up in a slender young tree, at a point where five twigs, of which the stoutest was hardly thicker than my middle finger, sprang from a short secondary branch. When the bird left, I noticed that the site held only the single tendril at which she had been tugging; I had had the good fortune to witness the very beginning of a nest. This piha had chosen an exposed situation, where she could be seen from a considerable distance on all sides. Probably she was the mother of the fledgling that I had seen near the demolished nest, for once as she approached the incipient nest she was accompanied by a juvenile with a half-grown tail.

As I came in view of the new nest at 7:20 a.m. on July 27, the piha was approaching it with a tendril in her bill, followed by the juvenile. The young bird remained behind and soon vanished, while the adult proceeded to the nest site. To the single tendril that had been present two days earlier perhaps a dozen had been added. The piha placed her latest contribution on her incipient nest, then remained sitting on it, pulling up the projecting ends or loops of the tendrils and tucking them into the tangle beneath her. Stiff and wiry, they tended to spring outward again, but by dint of great persistence, she forced some to remain as she desired. While engaged in this task, she turned sideways from time to time, slowly revolving on her nest and performing the same operation on all sides. The few tendrils beneath her hardly screened her abdomen when I looked up from below.

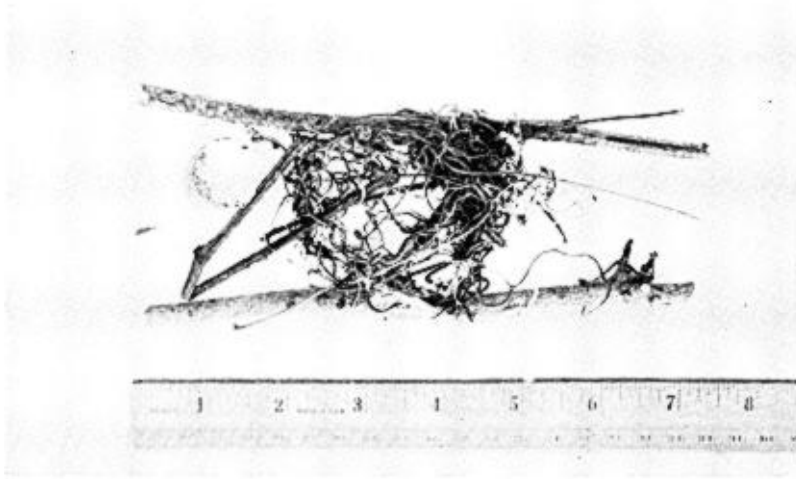


Fig. 2. Nest of Rufous Piha and shell of hatched egg collected in El General in 1950.

She worked in complete silence. At intervals I heard the sharp whistles of other pihas off in the forest, but none came in sight; even the fledgling did not reappear. At 8:00 the piha ended her 40-minute spell of shaping her nest and flew up into the treetops, and by 9:10 she had not returned. Never before had I seen a building bird devote so much time to arranging such sparse materials.

On the following morning, I watched from 5:40 until 9:05 a.m. The piha came to her nest only thrice, at intervals of about an hour, each time bringing a single tendril. She spent 2, 7, and then 3 minutes shaping her structure. All her movements were slow and deliberate, and she ignored me even when I stood almost beneath her. Once after leaving the nest she flew up into the trees and called *piha* loudly. As before, she was always alone. Although so little work had been done, the nest seemed to be about finished three days after the first piece was placed. During the additional week that elapsed before the egg was laid, I noticed scarcely any change in the structure, which was as slight as the nest already described.

Aside from the four piha nests found over a period of 17 years in a restricted area of forest on our farm in El General, I have seen only one other. This was discovered on April 21, 1967, in a fairly open part of the forest on a ridge near the Río Puerto Viejo in the Sarapiquí lowlands of northeastern Costa Rica. It was situated about 25 feet up in the open crown of a small tree, at the point where a nearly horizontal mossy branch, about 1½ inches thick, divided into two thinner, diverging branches. Resting upon the primary branch just inward from the fork was the tiny pad, hardly wider than the branch itself. As far as I could see from the ground, it was composed largely of tendrils and the rachises of compound leaves. This structure differed from the pihas' nests that I have seen on the opposite side of Costa Rica in being built upon a single fairly stout bough instead of on, or between, two or more much thinner twigs, but it was certainly no bulkier than the other nests. I should never have noticed it if I had not watched the parent catch a spider and carry it to the downy nestling that lay on the slight pad. After feeding, she settled down to brood, so concealing nest and nestling with her body that she

seemed merely to be sitting on the branch. She was plainly visible from a distance of 20 yards, for this nest was even less screened by foliage than the others that I have seen.

All five nests were on limbs of small trees, well out from the trunk, at heights ranging from 17 to about 35 feet. They were in the lower part of the forest, well protected from winds which sway the crowns of the dominant trees and would throw the eggs from such open receptacles. These nests were well above the reach of wholly terrestrial animals, and at the same time they seemed less likely to be visited by monkeys, toucans, and other arboreal nest robbers than if they had been situated on the boughs of large trees.

THE EGG

Evidently the Rufous Piha normally lays a single egg, for three nests in El General on the Pacific slope held no more, and the nest in the Caribbean lowlands had a single nestling. Beneath two of the nests I picked up shells from which the nestlings had just hatched. These shells were smoky gray, or grayish brown, heavily blotched and mottled all over with darker brown, which on the thick end nearly masked the ground color. They resembled eggs of the White-winged Becard but were much larger. Reconstructing one of the eggs by fitting the two parts of the shell together, I found that it measured about 31 by 22 mm.

In the valley of El General, the earliest recorded egg was laid about March 4, the latest on August 3 or 4.

INCUBATION

In the nest which I had watched being built, the egg was laid between 10:15 a.m. on August 3 and 1:45 p.m. the following day. On August 15, my son and I took turns watching the nest from dawn to dusk. All day the piha left her nest for only four intervals, from 5:44 to 6:17, 8:09 to 8:12, and 9:06 to 10:18 a.m., and from 12:26 to 1:20 p.m. The forenoon was sunny, but soon after the piha's return at 1:20 the sky clouded over and a hard rain began. By 4:00 p.m. the downpour had ceased, but the sky remained dark and the forest canopy continued to drip until nightfall. The piha sat steadily all afternoon, not even leaving her nest after the rain stopped. In this region where, in the wet season, hard, long-continued rain is typically confined to the afternoon, a number of incubating birds of other species that I have watched have done all their foraging in the forenoon and soon after midday, then sat steadily through the afternoon. This piha's sessions (until 1:20 p.m.) lasted 112, 54, and 128 minutes; her recesses, 33, 3, 72, and 54 minutes. She was on her egg for 77.5 per cent of the 12 hours from 5:44 a.m., when the forest had become light enough for foraging, until 5:44 p.m., when it was becoming dark. For a cotinga, she sat with high constancy.

Returning from an outing, the piha usually fluttered down from the higher trees to alight near her nest, where she paused to look carefully all around, turning her head slowly from side to side. Then she might advance to a point closer to the nest and continue her scrutiny, or she might go directly to it. She hopped gently onto the nest, alighting with her feet on either side of the egg. Spreading her abdominal feathers until her brood patch appeared in their midst, she settled on the egg. The fluffy feathers of her flanks stood up prominently above the edges of her wings, and other downy feathers overlapped the side of the nest, which was

almost hidden beneath her. She sat rather upright, often looking around from side to side. When alarmed or suspicious she stretched up her neck and held her upraised head nearly motionless, appearing strained and alert. Reassured, she contracted her neck to assume a more restful posture.

We never once saw this or another incubating piha adjust her egg with her bill, an omission which seems adaptive, when one reflects how easily the egg might be rolled off the nest. But at intervals the piha slid her abdomen over the nest from side to side, a movement of slight amplitude apparently made to adjust the egg beneath her, much as a broody hen does. During the clear morning the piha from time to time rotated on her nest, to face in another direction, but all through the wet afternoon she sat in the same position, her body upright.

Rarely while sitting the piha called loudly. After she had sat a long while her sideward movements became more frequent and she turned her head increasingly. Although sometimes she would become still again, often this restlessness presaged her departure. Then she would rise slightly, fold down the fluffy feathers that projected over the edges of her remiges, give her wings a few preliminary beats, and fly right up from her egg, much as a hummingbird leaves its nest. Usually she rose obliquely through the forest, rarely choosing a downward course. Alighting in the treetops, she might give a shrill whistle, sometimes followed by a trill, and perhaps be answered by another piha hidden amid the foliage overhead. While on or near the nest, all her movements were slow and careful, as indeed they needed to be to avoid knocking off her egg.

Learning the incubation period was a time-consuming endeavor. This piha, like others that I have watched incubate or brood a nestling, was quite fearless of me, looking down calmly while I moved around beneath her. Even tapping lightly on the slender trunk of the nest tree or gently shaking the foliage of a sapling that grew close by failed to make her budge. I feared that if I used more drastic means to drive her from the nest she might leave abruptly and throw out the egg, which I could see only when she was absent. When three weeks passed and the egg remained intact, I suspected that it was infertile and would not hatch, but I continued my daily visits.

When I arrived at 9:20 a.m. on August 29 I found the piha sitting restlessly, frequently rising up to look beneath her. Soon, when she rose up, I could see through my binoculars that her egg was hatching. At 9:30 she picked up the empty shell, the parts of which hung together, and dropped it from the nest while she continued to sit. Although most passerine birds carry empty shells to a distance if they do not eat them, this seems to be routine procedure with pihās.

The incubation period of this egg was between 24 days and 20 hours and 25 days and 23 hours. A 25-day incubation period is amazingly long for a bird the size of an American Robin. Even far larger ravens and crows have shorter periods. Of all the incubation periods of passerines that I have determined, this was the longest, although in certain small tropical American flycatchers with pensile nests the eggs take 22 or 23 days to hatch. As far as I can learn, the only passerine with an incubation period longer than that of the piha is the much larger Superb Lyrebird, whose eggs hatch in about six weeks. Probably the thin, open construction of the piha's nest, which affords slight insulation, is in part responsible for the long incubation period.

THE NESTLING

After dropping the empty shell from the nest at 9:30 a.m., the piha continued to sit, frequently rising up to look at the newly hatched nestling beneath her. Finally, at 10:40, the parent spread her wings and rose directly from the nest into the treetops. The nestling's light gray down was already dry and stood up prominently on its head and back. Its skin was pink. It tumbled around on the nest but avoided the edge. The female remained away for three-quarters of an hour, then she flew down from the treetops with some small object barely visible in the tip of her bill. Standing beside the nest, she gave the nestling its first meal, two hours after it hatched. Then she stepped onto the nest to brood.

A few days later, this nestling vanished. Fortunately, I had made extended observations on the care and development of the nestling at the first nest, where the egg hatched between nine o'clock on the morning of June 1, 1950, and the same hour on the following day. (In the ensuing account, this nestling's age is stated on the assumption that it hatched early on June 2.) During the young piha's 28 days in the nest, I devoted over 30 hours to watching it, without obtaining any evidence that a second parent assisted in its care. Yet I often heard another piha in the vicinity, and more rarely I saw another. Once, when two adults were in view, one chased the other, and they called sharply.

For a passerine of medium size, the nestling received an unusual amount of brooding. Until 11 days old, it was covered about as constantly as the eggs of many tropical birds are incubated, the female sometimes sitting uninterruptedly for well over two hours, once for 168 minutes (see table 3). Although when 17 days old it was fairly well feathered, two days later, during a morning which was at first lightly clouded and then sunny, the 19-day-old piha was brooded nearly half the time, including one session that lasted 70 minutes without interruption. When the nestling was 25 days old, and again on the following day, I found the parent covering it while rain fell in the late afternoon. She was also on the nest at daybreak on June 29, having evidently brooded the 27-day-old nestling through the night, but during the dark, misty forenoon which followed, she did not once cover it, although she rested beside the nest for considerable periods. Thus the young bird was brooded through its next-to-last night on the nest. For its final night in the nest, I lack observations. One morning, when a squirrel climbed over a neighboring trunk while the female brooded, she sat erect with her neck stretched far up, as already described. On leaving, she always flew up directly from the nest rather than from a point beside it.

Table 3
Brooding and Feeding of a Nestling Rufous Piha

Date in June, 1950	Age of nestling in days	Brooding in approximately six hours of the forenoon				Feeding	
		Shortest session in minutes	Longest session in minutes	Total time	Per cent of time	Times	Meals per hour
3	1	50	168	273	74.6	3 (4)*	0.5
7	5	1	157	232	63.6	6 (8)	1.0
13	11	26	61	232	64.4	8	1.3
21	19	5	70	168	46.7	10	1.7
29	27	0	0	0	0	11	1.8

* The figure in parentheses indicates the number of times the parent brought food when this was greater than the number of meals that the nestling accepted.

Feedings were infrequent, ranging from 3 times during the first six hours of daylight on the day after the nestling hatched to 11 times in the corresponding period of the twenty-seventh day after hatching. The rate of feeding was from 0.5 to 1.8 times per hour. Throughout the nestling period, I never saw more than one article of food brought at a time, but it was usually substantial. The insects intended for the day-old nestling were large and green, and after plucking them from the foliage the parent beat and rubbed them against her perch before taking them to the nest. The nestling received its third meal for the day at 8:32 a.m. Five minutes later, it was given another green insect; but when it was sluggish in swallowing this meal, the female removed it from the nestling's mouth and after a while ate it herself. Then she brooded for two hours and 48 minutes, and her chick received no more food that morning. Feeding rates are given in table 3.

When the nestling was five days old, its diet was varied with a large berry and a small scorpion. When 11 days old, the young piha was receiving, in addition to insects, large green fruits, probably from a tree of the laurel family, and spiders that were of impressive size. As the nestling grew older, fruits became increasingly prominent in its diet. On the last morning that I watched, the young piha, now 27 days old, received, in six hours, 5 fruits, 4 insects, and 2 unrecognized items. The nestling rarely seemed eager for nourishment, and even after it was feathered it did not greet its parent's arrival by promptly stretching up its gaping mouth, in the usual manner of passerine nestlings. On the contrary, it generally delayed a good fraction of a minute, and sometimes for several minutes, before opening its bill. On the day before it flew, the female perched beside the nest, holding a small unidentified object, for 49 minutes before it was taken by the young bird. In the absence of competing nest mates, a quick response to food appears to be of no great advantage. Probably young pihas are always solitary occupants of their slight nests, and this sluggish acceptance of food is innate.

The nestling's droppings were at first swallowed by its parent, and until the young bird was over three weeks old, I saw only this method of removing them. On the nestling's next-to-last day in the nest, however, I twice saw it void its excreta over the side, just after it was fed. On each occasion, the parent dived after the dropping, caught it in the air, and carried it away.

As already recorded, the newly hatched nestling was pink with sparse gray down on its head and back, and perhaps also on other parts of its body that I could not see from the ground. When it was only five days old, I saw it flap its stubby wings a few times. Its feathering was slow, and when 11 days old it was still largely naked. Six days later, it was fairly well feathered. When 19 days of age, it pushed its foreparts out in front of its brooding mother, then vigorously flapped its wings. Twice the active preening of the restless young bird seemed to cause the departure of the female. When a human or some other animal walked beneath the nest while the nestling was alone, it stretched up its neck and stood motionless in this posture, just as the parent did when alarmed. Once while it was standing so, the female alighted beside it with a big green fruit in her bill. Slowly the young bird sank down to the resting posture, then opened its mouth to receive the food.

On its next-to-last day in the nest, the young piha was restless, moving around, preening much, often flapping its wings, and from time to time walking out on a supporting twig for an inch or two beyond the nest, only to return promptly. When the parent called, the young bird replied with a similar trilled whistle that was

higher in pitch. It now stood rather than lay in the nest. The following day, I found it standing in this fashion at sunrise, and by noon it had flown, at the age of 28, or possibly 29, days. Its brown plumage resembled that of the adults, but it was much smaller than they.

At the nest in the Sarapiquí lowlands in 1967, the nestling, a few days old, was also brooded for long intervals and fed infrequently. After finding this nest by watching the parent take a spider to it at 9:10 a.m. on April 21, I continued observations until noon, and in this long period the nestling received only one more meal. On the following day it was fed only four times in the five hours from 6:00 to 11:00 a.m. The only item that I recognized was a cicada. The parent swallowed the nestling's droppings. While brooding, she sat with her body either parallel or transverse to the fairly stout supporting branch. Neither shouting nor clapping my hands while I stood directly below made her budge. No second piha was seen near this nest. Evidently the female always attends her egg and young alone.

The piha takes an astonishingly long while to rear her single nestling. Allowing 5 days for building, an interval of 6 days between the completion of the nest and laying, 25 days for incubation, and 28 days for the nestling period, 64 days elapse from the beginning of the nest to the departure of the fledgling. This is nearly twice as long as Gray's Thrush, a bird of about the same size, takes to raise a brood of two or three in a far more substantial nest, which is generally placed in a plantation or dooryard rather than in the forest. Yet despite its slow rate of reproduction, the piha, which seems to have increased over the years, is now the most abundant and conspicuous bird of its size, or larger, in the forest on our farm. Doubtless the virtual elimination, by trespassers, of toucans and other large birds that probably preyed on its nests, has contributed to the piha's increase.

No less surprising than the length of the piha's incubation and nestling periods is the fact that egg and nestling remain for so many weeks on the narrow platform where they seem to lie so precariously. They stay there thanks to the habitually careful movements of the parent bird and the quietness of the young piha, which need not compete with nestmates for food.

DISMANTLING THE NEST

As already recorded, on July 15, 1967, I watched a piha tear apart a nest, near which was a stubby-tailed fledgling that had evidently just left it. I saw the adult at the nest before I noticed the fledgling, and my first thought was that the piha was taking material from this nest to build another. Longer watching discredited this supposition, for the bird carried pieces beyond sight in opposite directions, dropped some directly from the nest, and took others to neighboring branches only to let them fall. Evidently it was demolishing this nest which the fledgling had quite recently left.

The successful nest in 1950 was still intact on the day following the young bird's departure, when I collected it. In 1965, both egg and nest vanished from one day to the next. At the nest on our farm in 1967, the nestling disappeared a few days after it hatched. The nest had been torn from the tree and its materials scattered over the ground below. When, after an interval of a week, I revisited the nest in the Sarapiquí lowlands, the nestling had vanished, although it was still too young to have flown, and very little of the nest remained. Predators do not, as a rule, tear apart the open nests that they pillage. Evidently pihas dismantle their

own nests when these have been left empty, whether by the departure of the fledgling or an act of predation. Although birds of many kinds pull apart their abandoned nests to procure material for new ones, few are known to demolish their nests without this motive. Blue Cotingas and Lovely Cotingas, however, scatter the materials of nests that have been visited by predators. Village Weaver-birds deliberately demolish their old nests so that they can build new ones in the same desirable sites (Crook, 1960). This can hardly be the reason why pihas do so, for with them there is no shortage of nest sites.

SUMMARY

The Rufous Piha lives high in the trees of the rain forest and is usually solitary. On the Pacific slope of southern Costa Rica, it occurs from sea level up to about 4000 feet.

It captures insects and spiders while hovering beside the foliage, without alighting, and it varies its diet with berries and other small fruits, including those of palms.

Its calls consist of clear, sharp whistles of from one to three notes and a variety of trilled whistles, which are often musical. These loud notes are uttered rather infrequently, rarely more than once per minute, and they are at times startlingly unexpected. They are often given in response to a sudden loud noise, such as a man's shout or sneeze, a dry stick snapping underfoot, or the whirring flight of a startled tinamou.

Pihas appear never to form pairs. In El General their breeding season extends at least from late February until September. The five known nests were situated on small branches or thinner twigs of slender trees in the undergrowth of the forest, at heights of 17 to 35 feet, where they were sheltered from the wind. An almost flat mat composed largely of coiled tendrils, the nest has been reduced to the absolute minimum compatible with its function of supporting egg and nestling. One nest was built in four or five days by a female unattended by a mate. She brought material at long intervals but spent much time shaping her slight structure.

Each of four nests contained a single egg or nestling. The protectively colored egg is smoky gray heavily mottled and blotched with deep brown, which on the thick end nearly masks the ground color.

While sitting on her nest the piha is almost wholly exposed and appears to be merely resting on a branch. She is amazingly indifferent to disturbance by man. One incubating female left her nest only four times, for a total of 162 minutes, between dawn and dusk, and she kept her egg covered for 77.5 per cent of the 12-hour day. To leave, she flew right up from her nest, like a hummingbird.

At one nest, the incubation period was 25 or 26 days. The female dropped the empty shell over the side of the nest instead of carrying it away.

Hatched with sparse gray down that fails to conceal its pink skin, the piha develops slowly. Still largely naked when 11 days old, one nestling was feathered when 17 days of age. When the feathered young piha was alarmed, it stretched up its head and stood motionless, just as the incubating or brooding parent did. It uttered a trilled whistle in response to a similar call by its parent. When, at the age of 28 or 29 days, it left the nest, it resembled the adults in plumage.

A single parent attended the nestling, which even when 11 days old was brooded 64 per cent of the time, and when 19 days old was brooded 47 per cent of the time. In the rain, and at night, it was brooded until it was at least 27 days old. Periods

of brooding were long, often exceeding an hour; and once, when the nestling was newly hatched, the parent brooded continuously for two hours and 48 minutes.

The nestling was nourished with insects, spiders, fruits, and an occasional small scorpion. A single article was brought on each parental visit. The rate of feeding varied from 0.5 meals per hour at one day of age to 1.8 meals per hour when the nestling was 27 days old. The lone nestling was surprisingly slow in taking its food, apparently because, in the absence of competing nest mates, a prompt response was of little advantage.

Droppings were at first swallowed by the parent. Later they were voided over the side of the nest, but if the parent was present, it caught them in the air and carried them away.

Pihas tear apart their empty nests, whether they are left vacant by the departure of the fledgling or pillaged by a predator.

TURQUOISE COTINGA

Cotinga ridgwayi

The Turquoise Cotinga is a rather stout bird, about seven inches in length, with a short bill and a fairly short tail. As in other species of this genus, the sexes differ greatly in coloration. The male's contour plumage, which is so glossy that it appears to be enamelled, is nearly everywhere an intensely bright blue, which changes from yellowish green to purple with shifts in the incidence of the light. A narrow black ring surrounds each dark brown eye. A shield of deep purple covers the lower part of the cheeks, the chin, and the throat. A large rounded patch of rich purple, separated from the purple throat by an isthmus of blue across the chest, adorns the center of the breast and abdomen. All but the outermost tail feathers are black with narrow blue margins. The lesser and middle wing-coverts are blue spotted with black, and the greater coverts and secondaries are black with blue edges. The female is grayish and buff, spotted and streaked almost everywhere. She bears no trace of the blue which imparts such unforgettable loveliness to the male, and only her size and form suggest her relationship to him. In both sexes, the bill and feet are blackish.

The Turquoise Cotinga has a restricted range on the Pacific side of Central America from Costa Rica south of the Gulf of Nicoya to western Panamá and from sea level up to about 6000 feet on the slopes of the continental divide. It is a wandering bird of the treetops which seems rarely to stay long in any locality. These cotingas venture forth from the forest into clearings with scattered trees, and they may even nest in such trees. Although often alone, they frequently associate in small flocks. The largest flock which I have seen contained at least four blue males and three grayish, spotted females, all of which rested in the tops of some low trees that were losing their leaves. They did not perch in a compact group but were scattered through neighboring treetops. After resting motionless for many minutes, they flew one by one into a different tree. Males appear to outnumber females, but this is possibly because they are more conspicuous. Sometimes two males rest together in the top of a tall tree, patches of more intense blue against the azure of the tropical sky.

The Turquoise Cotingas eat the fruits of *Psittacanthus*, a large, shrubby mistletoe, the long, tubular flowers of which form patches of vivid orange high in the trees. They also descend near the ground to feast on the small, blackish fruits of the pokeberry (*Phytolacca*), which flourishes rankly in newly burned clearings in the forest. They swallow small palm fruits, including those of the tall "palmito" (*Euterpe* sp.).

The only note which I have heard from this cotinga is a low, clear twitter or trill, which the males produce almost continuously while they fly. This pleasant flight note is also given by other species of *Cotinga*. Although its quality suggests that it is vocal, its constancy raises the suspicion that it may be produced by the air passing through the bird's feathers.

Late in the afternoon of May 13, 1962, I noticed a female Turquoise Cotinga resting at the very top of a tall *Inga* shade tree in a small coffee plantation near our house. She preened a little, and after a while she flew down amid the foliage. Here she settled on a slender horizontal branch, 40 or 50 feet up, where the leaves

formed a dense canopy above her but she was clearly visible from the ground. It was then about half-past five o'clock. The cotinga rested motionless in the same spot until, more than an hour later, she could no longer be distinguished in the gathering darkness. At the end of the night I found her in the same place. At 5:50 a.m., before sunrise, she suddenly flew away. Five evenings later, I again found this cotinga roosting, a few inches from the spot where she had slept on May 13, but after this I lost track of her. The site in which she roosted, the early hour at which she retired, and her solitariness, reminded me of a Masked Tityra that I once found roosting.

NESTING

The only nest of the Turquoise Cotinga that I have seen was placed in a muñeco (*Cordia*) tree whose tall, narrow crown of dark foliage rose above surrounding young trees and bushes. Although the nest tree grew in an area of light vegetation, it was near older and taller second-growth woods, which merged at no great distance into primary rain forest. The lowest limb of this muñeco tree left the trunk about 30 feet above the ground and extended almost horizontally above a path that was seldom used. About a yard out from the trunk, this limb divided into three fairly thick, nearly parallel branches, of which the middle one was slightly lower than the other two. The nest rested on this central branch, between the outer two which provided lateral support. It was a slight, shallow cup composed chiefly of coiled tendrils, mixed with which were some long, thin, wiry, gray strands, up to two feet in length, which were apparently the rhizomorphs of fungi. Much light passed through the thin walls of the structure.

I first saw the builder of this nest on the morning of March 2, 1948, when she perched in the top of a neighboring tree with a bit of material in her bill. She disappeared into the dense crown of the muñeco tree, but soon she emerged to fly away. I waited but did not see her return. I could find no trace of a nest until a few days later, when I noticed a few pieces of material in the trifurcation of the bough above the path.

In the following days, the little bunch of dry vegetation seemed not to grow; and although I looked eagerly for the cotinga, many days passed before I again saw her. At last, while walking down the pathway on the morning of March 24, I noticed the speckled bird on the nest above me. She moved all around, shaping the slight structure and paying no attention to the observer almost directly beneath her. When she had finished this work, she flew away, and I waited fruitlessly for her return. On the following morning, I watched for another hour without seeing her. On the afternoon of March 27, I set a 15-foot ladder against the trunk of the nest tree and looked into the nest with the aid of a mirror attached to a pole. The shallow bowl contained two eggs, which were buffy, speckled all over with brown which was heaviest on the thick end. The eggs almost filled the nest, which was so slight that I had supposed that it was still unfinished. In the evening of this day, the cotinga was incubating. She sat calmly while three horses, and later I, walked along the path below her. In the following days, I found her equally unperturbed by activity at the ground level.

From 5:30 a.m. to 1:30 p.m. on March 30, and from 1:00 to 6:00 p.m. on April 1, I watched this nest while seated in the pathway without concealment. The morning was clear; but in the afternoon the sky was blackly overcast, distant

thunder rolled, and for half an hour scattered drops fell, but not enough to soak the ground, which was dry and dusty after two almost rainless months. Compared with other members of this family which I have watched while they incubated, the Turquoise Cotinga sat most patiently. The four sessions which I timed lasted for 119, 36, 156, and 145+ minutes. The four recesses were likewise long, lasting 37, 44, 35, and 88 minutes. The five hours during which I watched in the afternoon were occupied by one long session, one long absence, and the early beginning of the nocturnal session. When I arrived at 1:00 p.m., the female was sitting, and she continued until 3:25. Then she flew away and did not return until 4:53. She then remained constantly on her eggs until I left at 6:00, when I judged that she had settled down for the night. She had incubated for 69.1 per cent of her period of diurnal activity.

The shallow nest contained so small a portion of the cotinga's body that while sitting she was above the nest rather than in it. To leave, she dropped straight down almost to the tops of the low bushes that surrounded the nest tree, then turned abruptly and flew away—a mode of departure widespread among birds whose nests are high in trees. Once when she returned she found a Squirrel Cuckoo in a lower tree near her nest. She drove this larger bird away, then proceeded, with several pauses to look around, to her eggs. Sometimes she preened while sitting. Coming and going, she was always perfectly silent save for the low whistling of her wings. I never heard a vocal sound from her. Even when she returned from an excursion one day and found me on the ladder holding the mirror above her nest, she uttered no cry of protest or alarm; but after looking on from a low perch, she flew off as though indifferent to what was happening there. She was always alone. I saw no male in the vicinity, either while she built or while she incubated.

On April 3 the cotinga was still incubating. By the following afternoon the nest site was bare, except for a few shreds of material in the crotch. The remainder of the nest was scattered over the ground below. Probably the cotinga herself tore apart her nest after a predator took her eggs. As told in the following chapter, other species of *Cotinga* have been seen to do this after losing their nestlings.

SUMMARY

The Turquoise Cotinga is confined to the Pacific side of southern Costa Rica and western Panamá, where it occurs from sea level up to 6000 feet. It is found singly or in small, loose flocks of up to half a dozen individuals. Males are seen more often than females. This cotinga rests in the tops of trees, but sometimes it descends low to eat the berries of the *Phytolacca* which springs up in recently burned clearings. It also devours the fruits of mistletoes and palms.

The only known note of this cotinga is a low, soft twitter or trill, which the males produce almost continuously while they fly.

The single nest for which there is information was situated 30 feet up in a tree standing above low second growth, not far from the forest. It was a slight, shallow cup composed largely of coiled tendrils, mixed with which were wiry fungal strands up to two feet in length. Building proceeded very slowly and took the greater part of a month.

At the end of March, this nest held two eggs, which were buffy, speckled all over with brown, but most heavily on the thick end.

In more than 12 hours of watching, the female took four sessions which ranged from 36 to 156 minutes and averaged 114 minutes. Her four recesses ranged from 35 to 88 minutes and averaged 51 minutes. She covered her eggs for 69 per cent of the day. She was not heard to utter a note.

No male was ever seen in the vicinity while the female built and incubated.

LOVELY COTINGA

Cotinga amabilis

The Lovely Cotinga closely resembles the Turquoise Cotinga, from which it differs chiefly in its slightly larger size and the longer tail-coverts of the male, which reach to the tip of the rectrices instead of leaving much of the tail exposed. As in the Turquoise Cotinga, the male Lovely Cotinga is clad above and below in glossy, intensely blue plumage. A patch of deep purple covers the lower part of the cheeks, the chin, and the throat. Separated from this by a sharply defined band of blue, a large shield of rich purple covers the breast and extends backward, gradually narrowing, along the middle of the abdomen. The wings and tail are largely black. The female, which lacks any trace of blue, has dark grayish brown upper parts, finely spotted with whitish on the crown and hindhead, and with coarser whitish spots on the back and shoulders. Her under plumage is dull white with crowded dark spots nearly everywhere, although on the chin and throat they are small and inconspicuous. Her eyes are dark, and her bill and feet are blackish.

The Lovely Cotinga is confined to the Caribbean rain forests from the Mexican state of Veracruz to eastern Costa Rica. It has a fairly wide vertical range, from sea level far up into the mountains. During the year that I spent at Vara Blanca, on the excessively rainy northern slope of Costa Rica's Cordillera Central, I saw this bird only from April to June, when a number of lowland species took advantage of the somewhat milder weather then prevailing to move up the slopes and nest. At about 5500 feet, I saw one male and one or two females. A tall, spreading tree of the laurel family, probably a species of *Nectandra*, stood in a narrow clearing in the epiphyte-laden forest and supported the long, swinging pouches of a colony of Chestnut-headed or Wagler Oropendolas. In June, this tree bore a profusion of small green fruits, which attracted birds of many kinds. The male Lovely Cotinga was to be found there almost daily for several weeks, and less often a female joined the feast. The male cotinga was especially fond of the fruits and ate quantities of them. Whenever he flew, even if only a few feet between neighboring branches, he made a sound intermediate between a rapid tinkle and a rattle. It was less sweetly melodious than the similar sound which the Turquoise Cotinga and some of the South American representatives of the genus make in flight. Its quality suggested, more than the softer notes of these other species, that it might be a mechanical rather than a vocal sound, perhaps produced by the attenuated outer primaries.

NESTING

At Vara Blanca, at the end of April of 1938, I saw a female cotinga fly northward with a fruit of the ira rosa (*Ocotea pentagona*, Lauraceae) in her bill. Soon afterward, I noticed a female, probably the same, flying southward with a lizard. Evidently she was feeding young, and the direction of her flight on these two occasions pointed to a certain yos (*Sapium*) tree as the probable site of her nest. This great, wide-spreading tree grew in the pasture not far from the forest's edge, in full view of the cottage I occupied. Scrutiny of the ample crown through binoculars from various angles failed to disclose a nest, although the topmost branches bore cushions of moss and clusters of epiphytes in which a nest might well

have been hidden. Sometimes I watched in the hope that the cotinga herself might reveal her nest's position. But I saw her only once more, and on that occasion she vanished into the abundant foliage. The drizzles and cloud-mist so prevalent at this season added to the difficulty of learning what occurred in the high treetops.

Late on the afternoon of May 10, as I descended the path which led from the cottage down the hillside, close by the great yos tree, I heard loud, full-voiced, seemingly agonized shrieks coming from the high treetop. Looking up, I saw a Blue-throated Toucanet standing on one of the upper boughs with its huge bill raised in a defensive attitude while the female cotinga darted back and forth above its head, uttering the painful screams which had directed my attention upward. Soon the toucanet flew down into the woods that filled the neighboring ravine, while the cotinga vanished into the cloud of verdure which covered the yos tree. But a little later I saw her go to the fork of a fairly thick, mossy branch at the very top of this tree, about a hundred feet above the ground. Here, standing on the cushion of moss which covered the crotch, she picked up a billful of fine twigs or some similar material and let them drop to the ground. She repeated this behavior, lingered for several seconds on the site of the nest, then turned and darted off through the foliage.

The cotinga's act of throwing down the twiglets revealed to me the position of her nest and showed of what it was made. Evidently it had been a slight structure, probably a shallow bowl; for if it had been bulky, I should have seen it from the ground. As I reconstructed the story from the fragments of action which I had witnessed, the toucanet had carried off or eaten the nestlings which I supposed, from having seen the cotinga carry food, must have been there. Then the distressed female had torn apart and thrown to the ground the empty and now useless nest. Some years earlier, Chapman (1929:128) had seen a Blue or Natterer's Cotinga pull apart her nest in similar circumstances. The reader may remember that at about the same time that the eggs vanished from my nest of the Turquoise Cotinga the materials of the nest were scattered, probably by the cotinga herself. Although such behavior is rare in birds, it has been witnessed also in the Sarus Crane, Ring Ousel, Scrub (Florida) Jay, and others (Armstrong, 1947:34).

Subsequent developments proved that my interpretation of the episode in the yos tree was only partly correct. On the second morning after I watched the altercation between the toucanet and the cotinga, I found the latter at the forest's edge near the yos tree. Resting on the broad, palmate leaf of a cecropia tree, she gave her plumage a thorough preening; and I was able to study her appearance more thoroughly than on previous occasions, when I had enjoyed only fleeting glimpses of her in the treetops. The arrangement of her feathers completed, she flew to the lowest branches on the uphill side of the yos. This descent by a bird who had hitherto stayed high up in the trees was so significant that it held my attention. Presently the cotinga dropped down to rest on one of the decaying, weed-covered logs which had been piled on the hillside to clear the pasture. After a moment she returned to the yos tree, while I went to search through the log pile and the surrounding herbage, for I was sure that a nestling was hiding there.

While I hunted, the cotinga flew excitedly back and forth among the lowest and nearest branches of the yos tree, constantly repeating a low, clear monosyllable, which sounded like *ic ic ic*. This note of protest, and the scream that I had earlier heard, are the only sounds, other than the trill made in flight, which I have ever

heard from an adult male or female blue cotinga of any species. It will be recalled that the female Turquoise Cotinga, whom I watched while she attended her eggs, was quite silent. It is perhaps significant that both of the female Lovely Cotinga's utterances were expressions of parental solicitude.

Once, while I searched, I heard a low, clear note emerge from the pile of logs, but possibly a frog had made it. I could find no young cotinga, so I withdrew to the edge of the pasture and watched. Soon the female flew down to the pile of logs, stood there for a minute or two while she looked around, then returned to the nearest branches of the yos tree. She repeated this descent to the logs eight or ten times, always going to the same part of the pile. Advancing now to the point indicated by the parent's actions, I found, resting among the herbage between the rotting logs, the nestling of whose presence I had been certain. Only strong parental devotion could have drawn to the ground a bird so strongly attached to the tree-tops as this cotinga.

Since the nestling could not yet fly, it must have fallen, or at best fluttered, to the ground when menaced by the toucanet two days earlier. It was completely clothed with feathers, but its remiges were still partly ensheathed and would not sustain it in the air. The young cotinga presented a remarkable and arresting appearance, unlike that of any other bird that I had ever seen. Its upper plumage was everywhere mottled with gray, buff, and blackish. Most of the feathers of its forehead, crown, back, rump, and wing-coverts, as likewise of the chin and throat, terminated in a short, dense tuft of white down, which reminded me of the pappus of a composite seed. These downy tufts were shorter and denser than the natal down of any other passerine nestling which I have examined closely; they somewhat resembled the interpterylar down of a nestling Yellow-bellied Elaenia, but these tufts of down are not the precursors of contour feathers (see Skutch, 1960a:303-304). The young cotinga's remiges were dull black; the primaries had buffy tips, and the secondaries were buff on the outer margins as well as the tips. The rectrices, which were just expanding, were, as far as they were visible, dull black with buffy tips. The ventral plumage was pale gray. The eyes were bluish; the strong, broad bill was black; and the feet were grayish flesh-color. Since the adult female's eyes were dark, the nestling's bluish eyes suggested that it was a young male.

While I examined the young cotinga, its mother darted several times above my head, voicing the same cries of distress that I had heard while the toucanet was by her nest. When she was not flying above me, she perched on the nearest bough of the yos tree and reiterated the clear *ic* already mentioned.

For three days, the young cotinga rested among the logs overgrown with vines and weeds, while its mother attended it. Almost every time that I approached, I found her watching from the yos tree, and she either repeated the short monosyllable or darted above me. Once, while I watched from a distance, I heard, as she flew down to her fledgling, a low, clear twitter such as I have generally heard from male but not from female blue cotingas. She was always alone. Almost a month passed before I saw my first male Lovely Cotinga in this locality. The more extended observations of Chapman (1929:122-132) on the Blue or Natterer's Cotinga, covering all stages of nesting, failed to reveal that a male took any interest in the nest.

On the second evening after I found the young cotinga, I went out in the dusk to bring it into the house, for the night promised to be wet, as were most nights at this season. At daybreak, I replaced it on the log whence I had taken it, so early

that its mother could not have missed it. During the day it vanished, and I did not again see either the parent or the young bird in the vicinity. I like to think that the dry night's lodging which I gave the fledgling favored the expansion of its plumage, so that on the following day it was able to fly into the trees where it would be safer.

SUMMARY

The Lovely Cotinga lives high in the trees of the rain forest on the Caribbean side from southern México to Costa Rica. It is found from sea level to an elevation of at least 5500 feet, where it nests. After the breeding season, it seems to withdraw to lower and warmer regions.

The Lovely Cotinga subsists largely on fruits plucked from the crowns of forest trees. One parent took a lizard to her nest.

In flight, males produce a sound intermediate between a rapid tinkle and a rattle. When a toucanet threatened her nest, a female cotinga screamed in distress, and later she repeated a clear monosyllable as I searched for her fallen nestling. Rarely she made the tinkling sound in flight.

In April and May, a female nested about 100 feet up in the top of a great tree standing in a clearing near the forest's edge. The nest was so inconspicuous that, although its presence was suspected, it was not found until the cotinga drew attention to it by threatening a nest-robbing Blue-throated Toucanet that stood beside it.

After the toucanet's visit, the cotinga scattered the twigs or other materials of which her nest was composed. Similar behavior has been observed in other species of *Cotinga* in corresponding circumstances.

A flightless nestling escaped the toucanet by falling or fluttering to the ground, where for several days it rested in a pile of rotting logs and was attended by its mother. No male was seen in the locality until almost a month after this occurred.

The contour feathers on the nestling's dorsal surface and throat were terminated by short, dense tufts of white down, quite different from the natal down of most passerine nestlings.

THREE-WATTLED BELLBIRD

Procnias tricarunculata

The Three-wattled Bellbird is a large, stout cotinga. The sexes differ greatly in appearance and size. The male is about 12 inches in length and is everywhere deep cinnamon-rufous, except for his pure white head, neck, and chest. From the base of his black bill hang three long, string-like, featherless, black wattles, one of which springs from his forehead, and one from each corner of his mouth. His eyes are brown and his feet are blackish. The female is about 10 inches in length and has dull olive-green upper plumage, of which the feathers have brighter, more yellowish margins. Her under parts are deep sulphur yellow striped with olive-green, except on the lower abdomen and under tail-coverts, which are immaculate. Her eyes are brown and her bill and feet blackish; she quite lacks the vermiform wattles of the male.

This northernmost of the bellbirds is confined to southern Central America, in Nicaragua, Costa Rica, and western Panamá. Because of its irregular vertical migrations, its altitudinal range is difficult to define. Although no information about its nesting is available, all the evidence points to the conclusion that it breeds in the highland forests from about 5000 feet upward, where the far-carrying calls of the males ring out frequently in the months from March to June, when most other birds are nesting. Although bellbirds have been found at lower altitudes, as between 2000 and 3000 feet above sea level in the valley of El General, in every month of the year, I have only rarely heard them in this region at the season when most birds are breeding. In this altitudinal zone, I have noticed bellbirds chiefly from January to March and from July until September, which suggests that they might be passing through on their upward migration early in the year and on their downward journey at the end of the nesting season. But if they are indeed travelling at these times, they often interrupt their journey for weeks together, for what seems to be the same individual may call from the same part of the forest almost daily for a month or more. The bellbirds' descent from the highland forests takes them to both coasts. The species was first described by J. and E. Verreaux from a specimen collected more than a century ago at Bocas del Toro on the Isla de Colón, at the western end of the Caribbean coast of Panamá. I have seen bellbirds on the Peninsula of Nicoya in December, and Mr. C. H. Lankester informed me that he found them on the Isla de Chira, in the Gulf of Nicoya.

The bellbirds' wanderings appear to be caused partly by changes in weather and partly by fluctuations in the abundance of the fruits on which they largely subsist. When I settled near Vara Blanca, at an altitude of 5500 feet on the stormy northern side of Costa Rica's Cordillera Central, in early July of 1937, bellbirds called frequently, although the prevailing wet weather prevented my glimpsing them in the high, mist-shrouded treetops. During long-continued rains in the middle of the month, these notes became less and less frequent, and soon I ceased to hear them. After the end of July, I had no indication of the bellbirds' presence in these rainy mountains until the second week of December, when I heard a call or two floating out of the mist. Toward the end of January of 1938, the bellbirds' notes became frequent at Vara Blanca; and then, in contrast to their behavior in the preceding year, they were still conspicuously present when I took my final departure on



Fig. 3. Three-wattled Bellbird, male (life-size).

August 11. I attribute this difference to the fact that in 1938 the months of July and early August were much less stormy than they had been in 1937. I have sometimes heard bellbirds, at points below 5000 feet where they are of sporadic occurrence, on wet and gloomy days when the higher mountains were doubtless enveloped in chill wind-blown clouds and rain. Yet, especially from July to March, they are often found at low altitudes in intervals of fine weather.

Of all the birds resident in Costa Rica throughout the year, the bellbird performs the greatest altitudinal migrations of which we have knowledge. A few birds, such as the Black-faced Solitaire, the Barred Parakeet, and, according to Carriker (1910: 326), the Spangled-cheeked Tanager, may descend in the nonbreeding season to points a thousand feet or so below the zone in which they nest. Others, like the Boat-billed and Gray-capped flycatchers, the Masked Tityra, and the Chestnut-headed Oropendola, may in February and March move a little higher up the moun-

tains to breed. Still others, such as the Scarlet-thighed Dacnis, may suddenly appear in great numbers in a district where they have not been seen for years, then completely vanish for another period of years. But the great majority of the Costa Rican birds that do not migrate to South America or temperate North America maintain very nearly the same vertical range at all seasons. One wonders why more of them do not, like the bellbird, escape the gloomy and chilling dampness that prevails on the heights for weeks together in the wetter part of the year, when an hour's downward flight would take them to warmth and sunshine.

At Vara Blanca, I sometimes saw a bellbird fly into a large *ira rosa* tree (*Ocotea pentagona*) that stood on the slope below my cottage. Here, in company with Quetzals, Blue-throated Toucanets, and other birds, he ate the hard, green-skinned fruits, each of which contained a thin layer of flesh surrounding the single big seed. He plucked these fruits while perching beside them instead of gathering them on the wing, in the manner of the Quetzal. Carriker (1910:326) stated that about the first of December the bellbirds begin to drift into the Caribbean lowlands, where they become very abundant in the upper part of the Humid Tropical Zone, between 600 and 1500 feet. Here they remain until late in February, feeding upon a small, nut-like fruit.

VOICE AND COURTSHIP

Although little is known of the habits of any of the bellbirds, their bizarre wattles, and even more their powerful voices, have won them wide renown, which extends beyond the narrow circle of readers who are familiar with the sparse and scattered references to them in the more technical ornithological writings. Some of the South American species deliver ringing metallic notes which are said to carry for a mile through the forest, and to hurt the human ear at close range. Not in his own right, but merely because of his relationship to the three more southern representatives of the genus *Procnias*, is the three-wattled species called a bellbird. His notes are wholly devoid of metallic timbre and at most might be imagined to emanate from a wooden clapper. He has a very limited vocabulary, consisting, as far as I could discover, of only two fundamentally different notes. The first, loud and strong but dull and throaty, is such as might be produced by striking once a wooden bell devoid of resonance; the second is much sharper and higher in pitch. These two notes are so dissimilar in character that, when I first heard them from a bird unseen in a mist-veiled treetop, I wrongly surmised that the deeper note was the call of the male and the sharper one the answer of the female.

The two notes together form a phrase which often sounded to me like *BUCK wheat*. The *BUCK* is not always delivered with full intensity, but often in a more or less subdued form (*buck*), as though the bird gave both hard and gentle strokes of his wooden clapper. A whole series of these notes is uttered while he keeps his extraordinarily large mouth wide open, revealing a cavernous black interior that attracts the attention of a watcher 50 yards away. Some of these series, delivered without closing the bill or even perceptibly moving the mandibles, might be expressed as: (1) *BUCK wheat*, (2) *BUCK wheat BUCK*, (3) *BUCK BUCK*, (4) *BUCK buck BUCK*, (5) *BUCK wheat BUCK wheat BUCK*, (6) *BUCK buck BUCK buck buck buck*—and so on to include almost every possible combination of these notes. The greatest number of notes that I heard a bellbird deliver without closing his mouth was seven, but in such a long series the *wheat*'s become in-



Fig. 4. Three-wattled Bellbird, female (reduced).

creasingly faint. Although the bellbird's calls do not sound remarkably voluminous when they come from a bird high overhead, they have tremendous carrying power and one may walk a long way without reaching the bellbird that he hears in the distance.

Toward the end of January, as has been said, the bellbirds' loud calls began to ring through the mountain forests with greater frequency, and in the following month I heard them often. By March, they were sounding their notes all day long and from every side. Late in this month, I found a male calling from the tops of tall scattered trees standing in the corner of a new clearing, with forest on two sides. How large and distinguished the bright brown and white bird appeared as he stood against the blue sky, on exposed dead branches a hundred feet above me! He did not remain on one special perch but divided his time between the tops of several trees, the most widely separated of which were about 50 yards apart. After calling a while on one, he would fly to another and continue to sound his dull wooden-bell-like call. Two weeks later, this bird remained more constantly on a single one of the lofty perches between which he formerly alternated. His favorite post was now the tip of an ascending dead branch at the very top of a tree no less than a hundred feet high. Here, day after day, I found him at all hours of the morning, broadcasting his peculiar calls afar over the mountainside. At intervals he flew into the neighboring forest, doubtless to seek food, but after a few minutes he returned to resume his calling.

As the bellbird calls with his huge black mouth gaping widely, he bends far forward, in what appears to be a strained posture. At the end of a series of notes, he often flies out horizontally for a foot or so, turns around sharply in the air, and regains his perch with his orientation reversed. At first, I thought that he left his perch because he had bent so far forward while calling that he lost his balance and found this the simplest method of recovering his equilibrium. Continued watching, however, convinced me that this short forward flight with rapid reversal in the air is in reality a simple display. On regaining his perch, the bellbird often spreads his brown tail and draws in his neck, a posture which he holds only for an instant. Sometimes, instead of turning in the air, he flies to another branch a few feet away, rests there for several seconds, then returns to his principal perch, where, as he alights, he fans out his tail and retracts his neck in the usual fashion.

From time to time, the bellbird shakes his head sharply, as though one of his long, loosely hanging wattles had fallen across an eye or otherwise molested him. I suspect that these dangling appendages are a great annoyance, a veritable infliction upon the bellbird, and I find it hard to imagine what compensating advantage they might have. To my eye, they add nothing to the beauty of a bird whose coloration is not only unusual but most elegant. Although this bellbird is sometimes depicted with his frontal wattle standing stiffly upright and the lateral ones projecting sideward, as far as I have seen, all three of them always hang limply.

In 1938, the adult male bellbirds continued into August to proclaim themselves at their usual stations through much of the day. As the season advanced, I became increasingly aware of bellbirds in greenish, streaked plumage, some of whom might have been females, although many were undoubtedly young males, for they had budding wattles. Moreover, these greenish birds often tried to call, opening their mouths widely like the adults and displaying the same sombre interior, but failing in a ludicrous fashion to emit the same powerful notes with voices still weak and

untrained. When these young birds alighted in the treetop of a displaying brown-and-white male, they were never chased nor threatened. One long-wattled adult perched very close to a green young bird and called; from the ground it looked as though he were showing the novice how to perform.

The young males evidently take more than a year, and possibly several years, to acquire the full adult regalia. At the end of April, I saw a bellbird whose head, neck, and chest were a very impure white. His lower breast was dull brown with lighter spots, and his upper plumage was brown of a shade much duller than that of mature males. His three wattles were less than half the full length. Yet he called much as the adults do. This young male had evidently been hatched no later than the preceding year. In early February I saw, in the forest on my farm in El General, a young male still in the greenish immature plumage, with lateral wattles that seemed about an inch long, while the frontal wattle did not fall below his bill and was hard to distinguish from my position on the ground. Yet he, too, called and displayed like the adults. Even bellbirds in full brown and white attire, with no trace of the juvenal green, exhibit wattles which differ markedly in length, suggesting that these appendages continue to grow after the adult plumage has been attained.

The habit of sending forth their far-carrying calls is so ingrained in the male bellbirds that they seem unable to refrain from them even in regions, and at seasons, when they almost certainly lack functional importance. Often a bellbird settles in the forest on my farm and calls for weeks together, especially in January and February, and again in July and August. In this present year of 1960, a bellbird was heard almost daily at the house from early July until the end of August. On a visit in mid-July to a farm in the highland forests on the northern side of Volcán Irazú, I failed to see or hear a single bellbird, although my host assured me that earlier in the season they had been present. Were it not for the bellbirds' persistent use of their stentorian voices, they would not often be noticed on their periodical visits to the Tropical Zone, for they seem to travel singly rather than in conspicuous flocks, and they remain high up in the treetops, where even birds so large and strikingly attired are hard to detect. The high mountains where the bellbirds breed are surrounded by foothills, valleys, and coastal plains which in aggregate cover a far greater area; so that even if every individual of the species simultaneously descended to these lower and warmer regions, each going its own way, they would be rather thinly scattered and likely to escape attention. Doubtless the females migrate altitudinally no less than the males, but because of their silence I have no record of their presence, in El General or elsewhere, below 3000 feet.

The bellbird's habit of calling day after day from the same station, and the constancy with which he sends forth his notes, put him in a class with male hummingbirds, manakins, and such flycatchers as the pipromorpha. I strongly suspect that, like these other birds, he does not pair and takes no part in the care of the nest. Indeed, I can hardly imagine this conspicuous bird feeding nestlings, which might mistake his long wattles for food and try to swallow them. Apparently, his only part in reproduction is to advertise his presence to the females whose developing eggs require fertilization, but I never had the good fortune to see an undoubted female visit a display station. I have succeeded in learning nothing at all of the nesting of the Three-wattled Bellbird, either from books, or by searching through the mountain forests, or by questioning the hardy mountaineers who are well

acquainted with the loud-voiced male "calandria," but who are probably unaware that the silent female wears a very different attire.

Three nests of the Black-winged or Bearded Bellbird in Trinidad were reported by Beebe (1954). They were flimsy, shallowly concave platforms of forked twigs, placed 15 to 20 feet up in cacao trees in plantations. One held a single egg. According to B. Snow (1961) the male of this species takes no interest in the nest.

SUMMARY

The Three-wattled Bellbird appears to breed only in the highlands, but it performs pronounced vertical migrations that take it to both coasts. It has been found in El General, well below its breeding range, in every month, but chiefly from January to March and from July to September. Its periodic disappearances from the wet highland forests where it nests fluctuate in date from year to year and seem to be influenced by weather and availability of food.

The bellbird feeds largely on fruits of forest trees, including those of the Lauraceae.

The bellbird's far-carrying call consists of various combinations of two basic notes, both quite lacking in metallic timbre. A series of two to seven notes is uttered with its cavernous mouth continuously gaping widely, revealing a black interior. These notes are poured forth from an exposed station at the very top of a tall tree, where the bird is to be found much of the time for months together. The bellbirds also call much while visiting the forests at lower altitudes.

At the conclusion of a call, the bellbird often gives a simple display, which consists of flying forward a short distance, turning sharply in the air, and regaining his perch, where he spreads his tail and draws in his neck, holding this posture momentarily.

Young males in greenish plumage with budding wattles attempt to call but do not succeed well until these appendages are somewhat longer. Adult males do not repulse these young birds from their display tree. Apparently, males take more than a year to acquire full adult plumage, and their wattles continue to lengthen even after this.

Nothing is known of the nest of this bellbird.

GENERAL SUMMARY OF INFORMATION ON THE COTINGIDAE

The approximately 90 species of cotingas, becards, bellbirds, umbrella-birds, and their allies form one of the most extraordinary avian families of the Americas, if not of the entire world. With the exception of one species endemic to the West Indian island of Jamaica, the family is confined to the American continent with its closely adjacent islands, and almost wholly to its tropical portions, although one species reaches as far north as the southern boundary of the United States. In size, this single family exhibits almost the entire range to be found in the whole order of Passeriformes, for some of its species are among the smallest of all birds, whereas others are as big as a crow; no other passerine family in this hemisphere exhibits such great variation in size, and in other orders perhaps only the woodpeckers and parrots show a corresponding diversity.

In coloration, this amazing group runs through the spectrum from almost uniform snowy white to unbroken black. Brilliant red, yellow, intense green, and bright cerulean blue with purple on the under parts, are among the colors worn by members of this family. But a large proportion of them are clad wholly in shades of brown or gray, and still others are conspicuously spotted or streaked. The peculiar forms of ornamentation displayed by cotingas include recurved, umbrella-like, erect crests; long, string-like, fleshy wattles; bizarre contractile appendages hanging from the foreneck, sometimes a foot in length, and either mostly naked or covered with overlapping feathers; areas of bare skin on the cheeks, or covering most of the head, or on the neck, and red, scarlet, or bright blue in color; loose, hair-like plumage billowing over most of the body; long, forked, swallow-like tails. Some species, including the Rose-throated Becard, have on the shoulders areas of concealed white which are revealed in moments of excitement. In the more brilliant and ornate cotingas, the sexes often differ greatly in appearance; but in many of the duller and less fantastic species, they are nearly or quite alike.

At the northern limit of its range, the Rose-throated Becard may perform short migrations (Bent, 1942:11). The Three-wattled Bellbird makes pronounced altitudinal migrations, breeding in the highlands but descending to the lowlands, especially in the wettest months. In general, however, the cotingas are not known to migrate.

Although in diversity of size, coloration, and ornamentation the Cotingidae far exceed all the related families, from the ecological standpoint they appear to be far more uniform than the Tyrannidae, Furnariidae, and Formicariidae, although possibly no more so than the Dendrocolaptidae and the Pipridae. As far as I know, the cotingas include no terrestrial forms, none that creeps over the trunks of trees, none that is wren-like or tit-like in habits—all of which are found in the Furnariidae. The cotingas known to me are all birds of the treetops, most of which inhabit heavy forest, although some are found in clearings with scattered trees, or in the lighter woods of somewhat arid regions. Some of the species which inhabit the lofty rain forest stay so consistently in the high upper regions inaccessible to man, that one may hear their cries day after day yet hardly ever glimpse the birds themselves. No other family of birds of the Western Hemisphere presents such great obstacles to study; in no other are nests more difficult to find, or so hard to reach if they have been located. Yet no family of birds, not even excluding the birds-of-paradise, so excites the wonder and curiosity of the naturalist, so challenges him to pry into the well-guarded secrets of their lives.

The food of the cotingas includes both fruits and insects in liberal quantities. Their method of picking fruits resembles that of the trogons and the manakins: they dart up to the cluster, grasp a berry in the bill, and pull it away without alighting. When hunting insects, they perch, peer around through the foliage of the treetops until they detect an insect at rest on a leaf, make a sudden dart to seize it without alighting, then return to a convenient perch, against which they may beat their prey before swallowing it. Some of the smaller and more agile members of the family may capture volitant insects in the manner of a flycatcher.

In voice, the cotingas present contrasts hardly less great than those in coloration and size. Their calls, often exceedingly difficult to trace to their source, are among the characteristic sounds of the tropical American forests. They range from the softest and most dulcet of liquid notes to some of the loudest, the harshest, and the most bizarre of all avian utterances. In the Costa Rican forests at lower altitudes, any sudden noise, such as a human sneeze, a shout, a gunshot, or the abrupt whirr of wings of a startled Great Tinamou, is likely to be answered by the loud, sharp whistle of the Rufous Piha, resting unseen in the treetops far above. Now and again through the day, especially in the early part of the year, the Bright-rumped Attila utters his clear, melodious, far-carrying *ooo weery weery weery weery weery woo*. The Masked Tityra voices most unbird-like, low, grunty notes. The Black-crowned Tityra makes dry nasal sounds and other sounds so faint that they remind one of the rustling of an insect's wings; all its notes are surprisingly weak for so stout a bird. At higher altitudes in the same country, the Three-wattled Bellbird fills all the forest with the loud peals of his wooden clapper, quite lacking in metallic timbre. The Snowy Bellbird of the Guiana forests utters a *kong kang* that sounds like striking an anvil with a hammer and a ringing, sonorous *kaaaaaaaaaaang*, said to be audible at a distance of three miles (Beebe, 1925b:159). The call of the Ornate Umbrella-bird is a deep, melodious *muuhh* like the lowing of cattle (Sick, 1954:238). The long, upward-sliding, liquid ripple of the Purple-throated Fruit-Crow calling in the distant treetops is one of the most beautiful sounds to be heard in the forest of Panamá. The notes of the White-winged Becard are among the softest and most soothing of avian utterances. At dawn, the male often sings for the better part of an hour, repeating interminably his sweet notes suggestive of unappeasable yearning.

In courtship and the relations between the sexes, this family also exhibits great diversity. In a number of genera, including *Tityra*, *Erator*, *Pipreola*, *Pachyramphus*, and *Platypsaris*, pairs are regularly formed and the male takes a share in attending the nestlings, sometimes even in building the nest. Others, including *Cotinga*, *Lipaugus*, *Procnias*, and *Carpodectes*, seem not to pair. At nests of the first two, males were not seen in attendance. Nests of the last two have apparently never been studied by ornithologists, but males are conspicuous in the nesting season, and their whole behavior indicates that they have no mates, but like male manakins and hummingbirds advertise their presence to all the females of their kind who are about to breed. The male Three-wattled Bellbird perches day after day in the same high treetop, sounds his loud wooden clapper with his great mouth gaping widely to reveal the black interior that contrasts so oddly with his white head and neck, gives his head little tosses to shake the three long wattles that dangle from the base of his bill, and flies out from his perch only to turn in mid-air and resume his former station. The male Yellow-billed Cotinga perches conspicuously in a dead

treetop rising above the roof of the forest or in an adjoining clearing; he may have several such trees between which he divides his time. Here he rests quietly, or sidles along a limb, or flies from one to another in a deep catenary loop. He needs no call; his snow-white form is conspicuous from afar against the blue sky; and any vocal utterance would be a superfluous expenditure of energy. When courting his mate, the male Purple-throated Fruit-Crow spreads his magenta gorget until it projects laterally like that of certain hummingbirds (Ellis, 1952:99). Snow (1961) has described the posturing and loud, synchronized calling by couples of Calfbirds perching side by side on special display branches which they have denuded of twigs and leaves, in the forests of Guiana. Nuptial feeding is not known to occur in the cotinga family.

The nests of the Cotingidae exhibit the same amazing variety as do most other features of this heterogeneous family. *Tityra* and *Eratyr* breed in old woodpecker holes or in natural cavities usually high in trees, carrying in many dead leaves, twigs, dry flower stalks, and the like to form a loose litter. Open nests are built by a number of genera, including *Lipaugus*, *Cotinga*, *Querula*, and *Cephalopterus*. Usually these nests are slight structures, shallow saucers or concave platforms, placed so high in trees that, although they are rarely seen, they are even more seldom reached by ornithologists for careful examination. The Rufous Piha's flat mat of tendrils is barely large enough to hold a single egg and nestling among slender leafy twigs. The nest of the Turquoise Cotinga, also composed largely of coiled tendrils, is somewhat more deeply cupped and placed on stouter branches. The nest of the Purple-throated Fruit-Crow is a shallow platform or saucer, composed of branches and vines, through which light passes; one was placed amid dense foliage "at the junction of steeply ascending branches about 75 feet from the ground" (Ellis, 1952:98). The big Ornate Umbrella-bird of the Amazonian forests builds a flat, open nest of sticks, including some that are two feet in length and half an inch in thickness, which form a structure so loose that the egg is visible through the bottom (Sick, 1954:240-242).

At the other extreme from nests which are as small and inconspicuous as is compatible with their function of holding eggs and nestlings are the great, roughly globular, closed nests built by *Platypsaris* and *Pachyramphus* of large quantities of the most diverse materials, including leaves, dry vines, lichens, moss, spiders' silk, sheep's wool, and whatever else is readily available to swell the structure's bulk. In *Platypsaris*, the pendulous nests are attached, usually high above the ground, to slender, drooping twigs, and the doorway at one side of the bottom is entered by flying almost straight upward; an unusually bulky nest of the Jamaican Becard found by Gosse (1847:192) measured about 2½ feet in height, more than 2 feet in width, and about 1 foot in thickness. In *Pachyramphus*, the nest is not pensive but is placed in a fork or some other position where it is supported from below; the doorway in the side faces out rather than down.

The nest is built by the female alone in the Blue Cotinga (Chapman, 1929:129), the Turquoise Cotinga, and doubtless also the Rufous Piha. In the White-winged Becard and Cinnamon Becard, the female does all the work of building but is attended by her mate. In the Masked Tityra and Black-crowned Tityra, the male follows the building female and often carries material back and forth, making a gesture of helping but rarely taking anything into the nest cavity. In the Rose-throated Becard, the male takes a substantial share in building; but as a nest

which I watched in the Guatemalan highlands neared completion, he placed all his contributions on the outside, leaving to the female the work of lining the great globular structure. In the Purple-throated Fruit-Crow, both sexes bring material, at times carrying a long piece of vine between them in a manner that is most unusual in birds; but the female appears to do all the construction and shaping of the nest (Ellis, 1952:99).

The eggs of the Cotingidae are even less known than the nests, because the latter, even when they are found, are so often inaccessible. In *Tityra*, *Cotinga*, *Lipaugus*, *Cephalopterus*, *Pachyramphus*, and *Platypharis*, the eggs are light gray, grayish brown, dark buff, or more rarely dull white or creamy white, mottled over most of the surface, but especially on the large end, with shades of brown or gray. The eggs of the Rieffer Fruiteater are cream with sparse red-brown spots chiefly above the equator (Miller, 1963:27). For the Masked Tityra, I have one record of two eggs. In a nest of the Black-crowned Tityra, three young were reared. A nest of the Turquoise Cotinga held two eggs, and one of the Blue Cotinga contained two young (Chapman, 1929:125). The White-winged Becard lays three or less often four eggs, and the Rose-throated Becard produces sets of four to six eggs. But a nest of the Ornate Umbrella-bird had only a single egg (Sick, 1954:242), and the same was true of three nests of the Rufous Piha.

Incubation is performed by the female alone in the Blue Cotinga, Turquoise Cotinga, Masked Tityra, Black-crowned Tityra, Rufous Piha, White-winged Becard, Cinnamon Becard, Rose-throated Becard, and apparently also in the Rieffer Fruiteater (Miller, 1963:27), the Purple-throated Fruit-Crow (Ellis, 1952:100) and the Ornate Umbrella-bird (Sick, 1954:241). The becards sit most impatiently in their huge nests, which must be close and stuffy inside; except at night, they rarely incubate continuously for as long as half an hour and they take relatively long recesses, so that they spend only about half of the daytime hours with their eggs. The larger tityras are more constant in incubation, sometimes sitting for an hour or more without interruption and, at three nests which I watched, covering the eggs about 65 per cent of the day. A Turquoise Cotinga attended her eggs still more assiduously, taking sessions which averaged nearly two hours and spending 69 per cent of the day in her slight, open nest. As they return to resume incubation, the becards often bring additional material to their bulky nests, or they may even use part of their recess to make several trips in succession bringing contributions to it. Tityras at times carry a few more pieces of dry leaves to add to the litter in the bottom of the cavity in which their eggs lie, and which serves to cover over and conceal them in the absence of the parent. The male of the Black-crowned Tityra and Cinnamon Becard sometimes guards the nest while the female goes off to forage.

The incubation period of the White-winged Becard is 18 or 19 days, that of the Masked Tityra about 21 days, and that of the Rufous Piha 25 or 26 days. These appear to be the only species in the family for which the length of this period is known.

The nestlings are, as far as known, hatched in a blind and helpless state. Those of the White-winged Becard bear no trace of down on their pink skin. A nestling Rufous Piha had sparse, light gray down. Nestling Blue Cotingas are covered with white down and have yellow-lined mouths (Chapman, 1929:125, 128). On a nestling Lovely Cotinga, which I did not see until it was well covered with plumage but still unable to fly, a considerable proportion of the feathers, especially on the upper

parts, bore at their ends dense tufts of short whitish down, in aspect very different from the down of most passerine nestlings, although somewhat resembling that of the Yellow-bellied Elaenia. If, as appears probable, these tufts of down had covered the skin of the nestling when newly hatched, it must have borne very little resemblance to the naked newly hatched White-winged Becard.

In both the Lovely Cotinga and the Blue Cotinga, the nestlings are attended by the female alone. A female of the latter species, as Chapman saw, brought berries in her throat and regurgitated them. A Rufous Piha also attended her nestling without a mate's help, bringing it insects, spiders, small scorpions, and fruits carried visibly in her bill, one at a time. In the genera *Tityra*, *Erator*, *Pachyramphus*, and *Platypsaris*, the nestlings are brooded by the female alone but they are fed by both parents, chiefly on insects that are carried in the bill. In this family, the meals of the nestlings tend to be widely spaced. As the single nestling of a Rufous Piha grew older, the female increased her rate of bringing food from 0.5 to 1.8 times per hour. After they no longer required brooding, nestling White-winged Becards were fed at the rate of 2.2 times per capita per hour. Nestling Black-crowned Tityras were fed slightly more frequently. A pair of Rose-throated Becards brought food to their nest at an average rate of 21 times per hour, and in one hour they brought 28 meals, which is the maximum that I have recorded for the family; but the size of their brood was not known.

I have never known a member of the cotinga family to give a distraction display. A female Lovely Cotinga darted above my head when I came near her nestling, which had fallen to the ground when its nest 100 feet above was visited by a Blue-throated Toucanet.

The nestling period of the White-winged Becard was 21 days at one nest, that of the Rufous Piha 28 or 29 days, and that of the Masked Tityra 28 to 30 days. These could be determined by inspection, but by watching the inaccessible nests of other species, I learned the approximate time that the nestlings were within: Cinnamon Becard, between 20 and 22 days; Rose-throated Becard, at least 18 days; and Black-crowned Tityra, at least 25 days.

In those species of which the sexes are strikingly different in coloration, the young of both sexes, in their juvenal plumage, resemble the adult female far more closely than the adult male. In the Rose-throated Becard, the male requires well over a year to attain fully adult plumage. When about a year old, he may breed in an attire only slightly different from that of the female. By means of the following annual molt, he takes on a plumage which, although essentially similar to that of the fully adult male, still reveals traces of immaturity (Dickey and van Rossem, 1938). For other species, there is a dearth of information as to how and when the adult plumage is acquired. I have never seen any member of the family nesting in an attire not fully adult.

FAMILY PIPRIDAE

BLUE-CROWNED MANAKIN

Pipra coronata

Manakins, at least those of the male sex, are rarely dull, either in attire or behavior. They are always springing surprises. Even when clad in formal black, they wear some bright dash of color: a scarlet or a blue cap, hidden gold in the wings, or lemon-colored pantaloons. The females are demurely clad in olives and greens but are not altogether devoid of the brisk mannerisms of the males.

One of the less ornate members of the family, the Blue-crowned Manakin is a stout, short-tailed bird about three and a half inches in length. The male, which is almost wholly deep, velvety black, with a large oval patch of bright cobalt or ultramarine covering his crown, is easily distinguished from other Central American manakins. The female, as with most manakins, differs greatly in plumage, being clad in a moderately bright shade of parrot-green. In both sexes, the eyes are brown, the bill is largely black, and the legs and toes are dark. Female manakins of different species and even genera are readily confused; but the female Blue-crowned Manakin can be distinguished from the females of the three or four other species with which she mingles in southern Central America by the brighter green of her upper plumage. She may also be separated from females of the Orange-collared and Golden-collared manakins by her blackish rather than pink or orange legs. The clear little trill which she utters with great frequency is also distinctive.

Blue-crowned Manakins range from southwestern Costa Rica to eastern Perú and western Brazil; the race which now occupies our attention, *Pipra coronata velutina*, is distinguished by the intense velvety black plumage of the male. It is found in the extreme northwestern corner of the range of the species, in southern Pacific Costa Rica and western Panamá. A lowland bird, it extends well up into the mountains, and near the southern border of Costa Rica I found individuals in female plumage not uncommon as high as 4000 feet, but adult males were rare.

The Blue-crowned Manakin is primarily an inhabitant of the lofty rain forest, where it lives in the dimly lighted underwood, among the shrubs and the lower boughs of the taller trees. Yet it occasionally enters and even nests in areas of second-growth woods at no great distance from the forest. One morning in December, while removing the runways of termites from the stone bases of my house, I noticed a small greenish bird resting quietly on a rafter beneath the eaves of the back porch, above the spot where I was at work. The bird looked so strange in this setting that I did not at first recognize it. Finally, I went for my binoculars and turned them on the diminutive bird for a critical scrutiny. It was a female, or possibly a young male, Blue-crowned Manakin. She was about 50 yards from the bushy edge of the forest, but the intervening distance was shaded by low trees. For over half an hour the manakin rested here, at first almost motionless in one spot, but toward the end of her visit she began to move around, hopping over some boards stored above the rafters. She was perfectly silent and from time to time she yawned. In a moment when my attention wavered, she darted away unseen.

Some years later, while I dwelt in a narrow clearing in lowland forest in a house set upon high pillars, I found a female Blue-crowned Manakin resting on a white

handkerchief that had been hung on a wire to dry, almost beneath the center of the house. A number of droppings beneath her revealed that she had already been in the same spot for some time. Ten days later, an adult male Yellow-thighed Manakin came to rest on a beam beneath the floor of the same house and stayed for ten minutes while we watched him. The two Blue-crowned Manakins came to the house in fair weather, but the Yellow-thighed Manakin rested on the beam late on a rainy afternoon. Manakins appear to seek sheltered places not only to keep dry but also to enjoy a spell of quiet repose. Perhaps in the forest large leaves give them similar protection.

FOOD

Small berries of various kinds enter largely into the diet of this and other species of manakins. The Blue-crowned Manakin also consumes many insects, most of which are plucked from the foliage or from slender twigs, at the end of a sudden swift outward or upward dart by the brisk little bird, but at times they are captured in the air. Blue-crowned Manakins often join a mixed flock of forest-dwelling birds, mostly larger than themselves, in foraging above and about swarming army ants. They perch in the bushes a few feet above the ants and make rapid darts to snatch up tiny fugitives that have taken wing or have vainly sought safety by crawling up the stems of saplings and over the foliage.

VOICE AND COURTSHIP

Notes.—The most common utterance of the Blue-crowned Manakin is a soft, clear trill. This is given frequently by the females no less than by the males and is the most musical sound that I have heard from any of the smaller manakins, although it is not as beautiful as the tripartite whistle of the Thrush-like Manakin. The male also delivers a loud, harsh note that sounds like *k'wek*. This call is most often heard from the males in their courtship assemblies, and we shall have more to say about it farther on. Males also utter a low *p'rrr* when their territory is invaded by a rival or by a man; but I have not heard this note from females, even when they are concerned for the safety of their nests or young.

The courtship assembly.—As in other members of their family, Blue-crowned Manakins do not form pairs, and the males take no interest in the nest and its contents. Several males gather in the same part of the undergrowth of the forest, forming a courtship assembly, where each is to be found daily through most of the year, and where by peculiar calls and movements they advertise their presence to the other sex. I have given attention to two of these assemblies. The first was in the forest on the ridge between the Buena Vista and Chirripó rivers in the basin of El General, at an altitude of about 3000 feet above sea level. I discovered this assembly in May of 1936, and from then until the following May I made numerous visits to it. From May until the end of August, I could count on finding the manakins present whenever I returned to this part of the forest. In October, the height of the rainy season, when scarcely any birds except hummingbirds nested, I failed to see them on my single visit during this month. But on December 25 the manakins were again performing in their old places, which they still occupied when I last visited them in May. During most of the time that I had this assembly under observation, it contained three males.

The second assembly to which I have devoted attention is on a forested ridge on our farm in El General, at an altitude of about 2500 feet above sea level. It has been present in this location for well over 11 years; although my written records of it cover only this interval, the earliest of them, dated April 20, 1954, mentions that the manakins had already been performing in this spot for several years. The courting males are spread out for a good distance along the ridge, and at one time I counted seven of them. Some of these males are stationed in dense undergrowth where they are difficult to observe, and I have given particular attention to the three at the southern end of the assembly, where the low vegetation beneath the tall trees is somewhat sparser and the birds are easier to watch. Two of these manakins have been present in the same stations for at least 11 years, or at least these stations have been occupied by a succession of individuals so similar in appearance and behavior that I failed to notice that one replaced another. They are to be found here, especially in the early morning, through most of the year, although females appear to nest only from February, or more often March, to June.

At his courtship station, the activities of the male Blue-crowned Manakin are not so narrowly focused at a central point as are those of the male Yellow-thighed Manakin, with his special display perch, or those of the male Orange-collared Manakin, with his bare "court" on the ground. The Blue-crowned Manakin's courtship activities are spread over a limited area of the forest undergrowth, the boundaries of which are so poorly defined that its size cannot be given with exactness. It is roughly 20 to 30 feet in diameter. Within this area are saplings or small trees with slender, horizontal limbs, on which the manakin spends much of his time resting and calling, at heights ranging from about 6 to 30 feet above the ground, but usually between 10 and 20 feet up. There are also numerous, slender, upright stems between which the manakin can fly rapidly back and forth near the ground; the low undergrowth which is essential for his courtship activities makes watching them difficult. Most important, but by no means easy to find, is the nuptial perch, a slender, more or less horizontal branch in the darkest part of the forest, about a foot above the ground. This nuptial perch may be part of a strongly inclined living stem; but more often it is a length of a slender fallen stick, one end of which rests on the ground while the other end is held up by low vegetation; or else it is one of the thinner branches of a large fallen bough. The three manakins which I watched most in the year 1959 all used fallen dead branches as their nuptial perches, although the year before one of them had chosen the thin stem of a living shrub.

In the assembly, each manakin spends most of his time about 75 to 100 feet from his nearest neighbors. Since the territory of each is poorly defined and they frequently visit each other, I do not know whether their territories are contiguous or separated by an unclaimed zone.

The male's activities.—Within his area, the manakin makes himself conspicuous by voice and movements. Since his voice is chiefly instrumental in drawing the bird-watcher's attention to him, we shall consider this first. He uses only two distinct vocal elements, the soft clear trill and the harsh *k'wek*; but by modifying the pitch and length of the trill and by combining these elements in different orders, he achieves a certain variety in spite of his very limited vocal endowment. Usually each *k'wek* is introduced by a trill, and very often this basic phrase, the trill followed by the harsh note, is given three times in succession, thus: trill *k'wek*, trill *k'wek*,

trill *k'wek*. Sometimes only a single trill *k'wek* is given, and at other times two or four of these phrases are delivered together. Likewise, two or three *k'wek*'s may follow a single trill; and occasionally the *k'wek* is sounded two, three, or four times without the introductory trill. The loud, unmelodious *k'wek* seems to play the chief role in guiding the females to the courtship assembly. Not only does it carry farther through the forest than the soft trill, but it is distinctive of the males, as the trill, which is frequently repeated by the females, is not. I have never heard the *k'wek* from a manakin who was undoubtedly a female (as, for example, one attending a nest) rather than a young male. These various calls are usually given by the male manakins as they perch on leafless portions of slender, horizontal branches, from 10 to 20 feet above the ground. The males frequently move from one such branch to another.

Often the manakin interrupts his calling to dart back and forth between perches a foot or two apart, perhaps on the same twig. Or he may fly back and forth between branches somewhat more widely separated, tracing a strongly curved course which first falls and then rises. As he flies back and forth he makes a low rustling sound with his wings. Rarely he executes a rapid "about-face" on his perch. He may flit both wings simultaneously, but in none of these exercises does he make the snapping noise that the Yellow-thighed Manakin frequently produces. I have never heard a Blue-crowned Manakin make loud explosive sounds, like the snapping of dry sticks or the detonation of small firecrackers, such as the Yellow-thighed Manakin and several species of *Manacus* commonly produce by beating their wings.

The foregoing performances are generally seen at the level where the Blue-crowned Manakin most frequently calls, above the watcher's head. From time to time he descends to fly back and forth among the lowest shrubs, within three or four feet of the ground. Darting swiftly from stem to stem, he traces an erratic course through the crowded vegetation. The successive flights in this zigzag journey vary as much in length as in direction; sometimes he goes only a foot between turning points and sometimes he covers several yards. He crosses and recrosses the same small area, which may be 10 or 12 yards in diameter. I once watched a manakin make about 50 of these low flights with hardly a pause. Then, after a rest, he flew back and forth through the same patch of low vegetation about 46 times.

This wild darting to and fro usually leads the manakin to his nuptial perch, but he may approach it by a much shorter series of low flights. The flight which finally takes him to this perch is of a special character: starting from another low perch, often on an upright stem four or five feet from the nuptial perch, he first drops slightly downward, then inclines his course upward, tracing a sigmoid curve and dropping down to the nuptial perch from a few inches above it. The moment he touches his perch, he depresses the forepart of his body, bends down his head, and emits a little, harsh, grating sound while rapidly beating his wings. Or, when the display is less intense, the grating noise is made without the wing beats. This grating or growling note is rarely heard except from manakins on their nuptial perches. They do not deliver it every time they alight there, but only when they approach it by means of swift dartings back and forth in its vicinity, culminating in the special flourish of the sigmoid flight.

At the height of the breeding season in April and May, each manakin visits his nuptial perch in this fashion repeatedly in the first hour in the morning. Later in the day, one may watch for a long time without discovering these sticks, which have

nothing to distinguish them from the fallen branches and leaning stems amid the ground vegetation. Some manakins use two nuptial perches alternately, but each seems to have a preferred perch on which he beats his wings as he emits his grating note. He often does so even late in the year, when the nesting season is months away.

A female visits the nuptial perch.—Despite many hours of watching, I only once had the good fortune to witness the behavior of a Blue-crowned Manakin when a female came to his nuptial perch. At 9:07 a.m. on April 11, 1958, I sat on my folding stool in the undergrowth to watch manakin 3 of the assembly on the ridge near our house. At rather long intervals he trilled, but he seldom voiced the sharp *k'wek*. He often flew rapidly back and forth, both in the crowns of the lowest trees, 10 to 20 feet up, and among the saplings near the ground. At about 9:35, a green female arrived and I glimpsed her flitting back and forth among the lowest shrubs, while the male darted about more obviously, much as he did when alone. Although intervening vegetation prevented my following all the movements of these two manakins, there seemed to be no formal dance in which the flights of the male and female were coordinated.

Finally, the female went to the nuptial perch and rested there about a foot above the ground. At once the male flew up and alighted on her back, fluttering his wings and uttering the usual grating note. Their union lasted only a moment, then the male flew off. The female also moved away, but after a few seconds she returned to the same perch, without inciting the male to a second attempt at coition. She must have been familiar with the male's special perch from earlier visits. While she was in sight, I saw him do nothing to direct her attention to it; she went to it before he did. During these activities, the other males stayed at a distance. The behavior of the male when the female alighted on his nuptial perch, his flying approach, fluttering wings after he alighted, and harsh grating notes, were very much the same as on his more frequent visits to this perch when no female was in view.

Relations between males.—The Blue-crowned Manakin's relations with his neighbors in the courtship assembly are on the whole friendly, but they are less intimate than in the case of the Yellow-thighed and Orange-collared manakins. When a male visits another's area, one often hears a *p'rrr*, a slightly harsh utterance that seems to be a modification of the soft trill. I do not know whether this note of irritation is uttered by the resident bird alone or by both him and the visitor. On April 1, 1959, the territory of manakin 3 was frequently invaded by another adult male, and this gave rise to spirited pursuits, in which one bird flew a few yards behind his fleeing rival, in a circuitous course which wove among the low trees and shrubs of the underwood and sometimes rose to the lower branches of the tall trees. One of these chases lasted for several minutes but most were shorter. I never saw the rivals touch each other. I could not tell whether the holder of the territory or the invader was the pursuer. On later visits, I found the area of manakin 3 still occupied, apparently by the individual which had long been there.

On other occasions, the visit of one adult male to another's area leads not to a pursuit but to a kind of irregular and brief dance. The two descend into the undergrowth and fly back and forth within a yard of the ground, their paths crossing. Often three individuals fly back and forth together in this fashion. Once I found four males together in the undergrowth, but one flew away as soon as I came in view and three continued their erratic flights. I have not seen two or three males

fly back and forth together for as long a time as a single male often does in the breeding season. Sometimes, when two or three manakins are flying about in the undergrowth, one or even two of them alight momentarily on the nuptial perch of the resident bird. Although these visits appear to be friendly, one sometimes hears the *p'rrr* which reveals annoyance or anger. The social flights of males are rare in April and May when breeding is at its height, but I have often seen these flights later in the year, especially from August to December, when the females have no need of the males, although the latter still pass much time at their courtship stations.

Persistence of the assembly.—Blue-crowned Manakins may be found at their assemblies at all times of day and in all months, but they are most active in the early morning and in March, April, and May, when chiefly the females lay their eggs. In June and July, there is a slump in their activity, perhaps associated with the molt.

When I last visited the courtship assembly on the ridge between the Buena Vista and Chirripó rivers on May 7, 1937, I found that several trees had been felled in that part of the forest, including a small one right in the midst of the assembly ground. At the edge of the area, two men were at work with axes, hewing a beam from a fallen trunk. Yet one of the manakins was even then calling in almost the same spot where I had found him a year earlier, only about 30 feet from the woodchoppers, with all the noise of their axes. His trills sounded very small and weak amid the thuds. The other manakin that was nearest the axemen also performed in his customary position. Thus these birds exhibit great attachment to their chosen stations. After a while, the men went off to lunch, and then the manakins trilled and called *k'wek* more constantly and with less distracting noise.

Behavior of an immature male.—As in other manakins, young male Blue-crowned Manakins begin their special courtship activities before they acquire the adult plumage and take up stations in the assemblies. On October 17, 1956, I found a Blue-crowned Manakin trilling and calling *k'wek k'wek*. In the dim light of a cloudy afternoon, I could detect no blue feathers on his crown and no black ones on his greenish body; and he was not near a courtship assembly. Since the numerous females that I have watched at their nests never called *k'wek*, I doubt that this green bird was a female. I have not found young males, nor those in transitional plumage, occupying stations in an assembly.

Comparison with other manakins.—The Blue-crowned Manakin is morphologically one of the less highly evolved members of its remarkable family and even of its genus. The male is, for a manakin, very plainly attired. He lacks a crest, elongated tail feathers, bright-colored thighs, and other adornments that some of his relatives display. He likewise lacks the capacity to produce loud snapping sounds by means of highly modified wing feathers. Correspondingly, his courtship is of a relatively primitive type, standing midway between that of *Schiffornis* and the highly developed performances of *Manacus*, *Chiroxiphia*, and his congener *Pipra mentalis*. He does not, like the Yellow-thighed and the Orange-collared manakins, center his displays at a single focal point but he spreads them over a comparatively wide area. In the Yellow-thighed Manakin, the display perch is also the nuptial perch; and the same may be said of the Orange-collared Manakin and related species, if we concede that the upright stems between which they jump above the bare court are the equivalent of display perches. The Blue-crowned Manakin's nuptial perch is an

inconspicuous twig near the ground, where he spends little time and does not call and display. His antics are simpler and less varied than those of the Yellow-thighed Manakin, and his vocabulary is more limited.

Although the Blue-crowned Manakin's courtship is far less brilliant than that of the Yellow-thighed and Orange-collared manakins, it combines in an interesting manner features from which the more spectacular performances of these two species and some of their relatives might with time evolve. By a gradual reduction of the area over which he flies back and forth through the lowest shrubbery of the forest, he might at last confine his flights between a few upright stems only a few feet apart, and then, with his activity narrowly centered, he might clear the leaves from the ground between these stems and make a bare court like that of *Manacus*. His flights between neighboring branches higher above the ground and his rare about-faces are suggestive of features which have achieved greater elaboration in the Yellow-thighed Manakin; and his wing flapping while he remains stationary might be the first step in the evolution of the structures that produce snapping sounds.

THE NEST

In the valley of El General, the Blue-crowned Manakins sometimes build their nests in February, but few are completed and contain eggs before March. The nests are nearly always situated in the undergrowth of primary forest, but sometimes they are in tall second-growth woods that adjoin the forest, and rarely I have found them in light woods that were separated from the forest by open fields or low thickets. Twenty-two nests ranged in height from 17 inches to 7 feet above the ground, but only three were below 2 feet and only three were above 5 feet in height. Rarely a nest is within hearing of a male at his courtship station.

The nests are nearly always built in a fork of a slender horizontal branch of a sapling or shrub, but one was between two parallel petioles of a small, spiny palm. Each shallow, hammock-like structure is suspended between the slender arms of the fork, to which its rim is attached. It is constructed principally of fine, light-colored fibers, and the bottom is more or less covered with dry, papery pieces of leaf and sometimes also with a varying amount of green moss. For this outer covering, whitish dead pinnae of fern fronds are often used, but sometimes there are fragments of the leaves of dicotyledonous plants. These pieces of leaf may be an inch or two in breadth and 3 or 4 inches in length and drape below the shallow structure. Mixed with the dead foliage are sometimes strips of fibrous inner bark, which in one nest hung 14 inches below the bottom. Cobweb is used to bind the materials together and attach the nest to its supports. The nest measures $2\frac{1}{8}$ to $2\frac{1}{2}$ inches in overall diameter by $1\frac{1}{8}$ to 2 inches in height, not including the pieces that dangle below it. The interior is from $1\frac{3}{4}$ to 2 inches in diameter and $\frac{5}{8}$ to 1 inch deep.

Although I have rarely watched Blue-crowned Manakins construct their nests, I have no reason to suppose that males ever take an interest in the work; I have never even seen a male near a nest that contained eggs or young. The nest of the Blue-crowned Manakin resembles that of the Yellow-thighed Manakin in its general form and its covering of dead leaves on the bottom; but I have never found any moss in the outer layer of the Yellow-thighed Manakins' nests, which are consistently placed higher than those of the Blue-crowned Manakin. The nests of the Orange-collared Manakin occupy about the same vertical range as do those of the Blue-crowned Manakin, but they rarely have dead leaves attached to them, so that

they resemble the fibrous inner part of the Blue-crowned Manakin's nest without the covering of leaves and moss. Moreover, Orange-collared Manakins' nests are usually situated in light second-growth woods and even in shady pastures and plantations; they are seldom far within the forest.

THE EGGS

Of 22 nests found in El General, 17 contained two eggs or nestlings. The other five held a single egg or nestling, but probably an egg or nestling had been lost from each of these. An interval of two days may separate the laying of the first and second eggs. The egg, or at least the one that completes the set, is deposited in the middle of the day, as in other manakins. At nest 16, the second egg was laid between 10:00 a.m. and 3:50 p.m.; at nest 21, it was laid between 9:00 a.m. and 12:30 p.m.; and at nest 22, it was deposited between 11:00 a.m. and 12:52 p.m. The eggs are dull white or pale gray, heavily mottled with light or medium brown, sometimes with rufous-brown, with the marks as a rule most concentrated in a band around the thickest part of the egg. The measurements of 23 eggs average 19.4 by 14.4 mm. Those showing the four extremes measured 21.0 by 15.1 and 18.3 by 12.7 mm.

We sometimes wonder what a female does with her eggs when she has lost the nest in which she was about to lay them. On April 10, 1962, I watched a Blue-crowned Manakin finishing a nest two feet up in a small coffee bush. Four days later, this nest had disappeared. At about 11:20 a.m. on April 16, while I sat nearby watching the nest of another bird, the female manakin came and flitted around the site of her vanished structure, uttering little trills. At least twice she tried to sit between the twigs to which her nest had been attached. At 11:30 I searched for an egg beneath this spot but found none. Returning at 12:40 p.m., I found an egg lying unbroken on the dead leaves beneath the nest site, with fire ants crawling over it. Two days later, I watched for this manakin to lay her second egg, but I failed to see her at the nest site in the middle of the day, and I could not find another egg beneath it.

In 22 nests in the valley of El General, 2400 to 2800 feet above sea level, eggs were laid as follows: February, 1; March, 4; April, 6; May, 9; and June, 2.

INCUBATION

Incubation is performed by the female only. From 5:45 a.m. to 2:26 p.m. on June 3, 1949, I watched a nest containing two eggs, which had already been incubated an unknown number of days. The female took three sessions, lasting 117, 74, and 171 minutes and averaging 120.7 minutes. Her four recesses lasted 34, 14, 22, and 32 minutes and averaged 25.5 minutes. After she ended her night session at 6:18 a.m., this manakin covered her eggs for 82.5 per cent of the eight hours that I watched her. Excluded from the record is a session which was interrupted after she had been sitting only six minutes, when a band of White-faced Monkeys passed above the nest. At that time she left the nest for 18 minutes. Although she left her eggs when the monkeys passed by, she stuck to her post while a family of Fiery-billed Araçaris fed in a neighboring tree. She sat quite motionless, without the constant movement of her head in which she indulged when no danger was evident. Yet both Fiery-billed Araçaris and White-faced Monkeys eat birds' eggs.

At intervals, the manakin backed onto the nest's rim and lowered her head to turn her eggs with her bill, and once she rose up to preen the feathers of her breast

and abdomen. She also moved backward on the nest to void her droppings over the edge, after she had been sitting a long while; but there was no accumulation of waste matter beneath the nest, probably because the hard rains of this season washed it away. Once she flew straight from her eggs to pluck something, evidently a small insect, from a neighboring leaf; then she flew off into the forest for an outing. Returning from this recess, she found a mixed flock of small birds passing by, and she perched at a distance from her nest, trilling over and over, until they drifted farther away. At the end of my vigil, she remained on her eggs watching me take down my blind, ten feet from her.

Ten years later, on May 27, 1959, I watched, from 5:45 a.m. to 3:24 p.m., a nest in which the second egg had been laid 11 days earlier. The early morning was wet, and the manakin did not end her night session until 6:58 a.m., more than an hour after daybreak. Thereafter she took four sessions lasting 78, 44, 96, and 197 minutes and averaging 103.8 minutes. During her long session of 3 hours and 17 minutes, rain fell for an hour; but she remained on her nest for about an hour after the rain had stopped and gleams of sunshine penetrated the clouds. Her five recesses lasted 15, 21, 20, 19, and 16 minutes and averaged 18.2 minutes. She covered her eggs for 85 per cent of the eight and a half hours after her first departure of the day. She always sat in silence, although I heard trills while she foraged in the distance. Like the other manakin, she sometimes dropped her excreta over her nest's rim.

As in manakins of other species, the Blue-crowned Manakin sits steadfastly, sometimes watching a man approach to within reach of her before she forsakes her slight, low nest. But none has ever permitted me to touch or handle her on the nest, as I have done with a Yellow-thighed Manakin. After she quits her eggs, the Blue-crowned Manakin often drops downward and flies away close to the ground, sometimes almost skimming it as she glides away with slow, fluttering wing beats. When I visited the nest of one female manakin, she would linger on her eggs until I almost touched her, then drop down to a low branch where she spread and fluttered her wings, trying to draw my attention away from her nest.

At one nest, the period of incubation was approximately 19 days. At a later nest, the second egg was laid between 11:00 a.m. and 12:52 p.m. on May 16 and it hatched between 5:15 p.m. on June 2 and 7:15 a.m. on June 3. The incubation period in this instance was more than 17 days and 4 hours and less than 17 days and 20 hours.

THE NESTLINGS

The newly hatched manakin bears scant gray down, insufficient to cover its skin, which at first may be light or dark flesh-color, but which rapidly acquires a more dusky hue. Its eyes are tightly closed, and the interior of its mouth is yellow. The nestling develops rapidly. When it is two days old its eyelids begin to separate, and after two more days the eyes are almost fully open. When the nestling is a week old its feathers begin to unsheathe, and at the age of nine days it is fairly well feathered. At times the nestlings are infested with *tórsalos*, dipterous larvae which form relatively huge swellings beneath the skin.

From 5:55 to 9:55 a.m. on June 5, 1959, I watched a nest containing two young, two and three days of age, respectively. In the first four hours of the morning the female brooded them five times, for periods ranging from 14 to 50 minutes and totalling 138 minutes. Her five absences varied from 12 to 24 minutes in length

and totalled 85 minutes. On each return to the nest she fed her nestlings, five times in all. Their food consisted of insects and much fruit, including mashed berries and red pulp. Most of the food was carried in her throat, with a few additional pieces held in her mouth. She cleaned the nest by swallowing the nestlings' droppings.

On April 13, 1947, when the two nestlings in nest 6 were a week old and becoming feathered, I watched them from a blind set amid low second-growth trees, while migrating Swainson Thrushes and Baltimore Orioles sang all around me. From 6:20 to 10:20 a.m., the female manakin brought food 5 times in the first hour, 5 times in the second, 7 times in the third, and 2 times in the fourth hour, making a total of 19 meals in four hours. She gave her nestlings liberal quantities of both berries and insects, which she carried largely in her throat, with at times the last article, a berry or a winged insect, held conspicuously in her bill. On some visits to the nest, she brought only whole, small, blackish berries, of which seven was the greatest number that I counted in a single load. A few red berries of greater size were at times included in the same throat-full with the black ones. On other visits, the food seemed to consist wholly of insects, which were as a rule smaller than the berries and more difficult to count. Once she brought a fairly big winged insect and once a small moth. Again, she came with a mixed cargo of both berries and insects, of which the latter were generally deepest in her throat and the last to be produced. Alighting on the twig beside the nest, she would place the article held in her bill into the first yellow mouth to be raised gaping in front of her. Then she would rapidly bring up other pieces of food one by one and divide them between the two nestlings. Rarely, she came to the nest with only a single insect. After delivering the food, she sometimes delayed beside the nest, and if she espied an insect crawling over the neighboring vegetation, she would dart out or even vertically upward to catch it, then return and pass this additional morsel to a nestling.

The parent brooded her nestlings only three times in the four hours, for 1, 11, and 8 minutes; this last session ended at 8:04 a.m. But after delivering food, she would sometimes rest quietly on the twig beside the nest without brooding; once she rested so for 23 minutes. She removed the nestlings' droppings, either swallowing them or carrying them off in her bill. Older nestlings sometimes drop their excreta over the edge of their nest, just as the female does while incubating.

Female Blue-crowned Manakins are as a rule very solicitous when their nestlings appear to be in danger. Sometimes they move excitedly around the human visitor, alighting only a few yards away or hovering on rapidly beating wings, facing the intruder, and often repeating their clear trill. One female with nestlings would hover about me, uttering this trill, until I looked at her. Then she would drop to a low perch, spread her wings widely, and beat them slowly as though in distress, sometimes seeming almost to fall from her perch and thereby increasing her imitation of a disabled bird. When I followed, she fluttered ahead to another low twig and repeated the act; she did this again and again, until she had led me a good distance from the nest, when she "recovered" and vanished into the vegetation. Sometimes she almost skimmed over the ground as she retreated, but she never alighted on it. I have witnessed such displays at several nests, both when I disturbed the female while she brooded and after she had ceased to cover her feathered nestlings. Sometimes, when surprised on the nest, the female would fly out of sight in the undergrowth, then promptly return to a low perch in view of me and display with spread

and fluttering wings. However, other females whose nests I repeatedly visited never displayed to me.

One afternoon, as I walked along a path through a coffee plantation, I heard a manakin's trills issuing from a neighboring grove, where I had found a nest earlier. They were repeated so often that I suspected she was in trouble and went to visit her. I found that her flightless nestling had tumbled from its shallow cradle and I replaced it. Female Blue-crowned Manakins use their soft trill very freely, often repeating it interminably as a human passes through the woods where they seem to have neither eggs nor young.

Nest 6 began to break away from the supporting crotch when the nestlings were 12 days old and well feathered. For a day or two the young manakins perched on the highest part of the rim of their strongly sagging nest. Then, after a torrential afternoon rain, I revisited the nest in the evening and found that it had become completely detached from one of the supporting arms and hung below the other. One of the nestlings had vanished at the age of about 13 days; the other rested on the twig where the nest was still attached. It was wet and bedraggled and continuously repeated a low *peep*. The next morning it was resting two inches from the nest, and by the middle of the afternoon it was out of sight, having left at the age of 14 or 15 days. Another nestling, reared alone, departed spontaneously when 15 or 16 days old. From another nest the two nestlings departed, apparently spontaneously, at 13 and 14 days of age. The nestling period seems to vary from 13 to 15 or 16 days.

One morning in April, in the fringe of low trees, vines, and bushes on the bank of a stream beside a pasture, a female Blue-crowned Manakin alighted on a low branch in front of me with a fairly big, lacy-winged insect in her bill. Swallowing the insect, she spread both wings widely and beat them slowly up and down, at the same time appearing to maintain a precarious hold on her perch. She repeated this demonstration several times on neighboring twigs. While I searched for a nest or a fledgling, the manakin came repeatedly to rest on perches close in front of me, and again and again fluttered her extended wings as though trying vainly to fly. Twice she dropped from her perch and skimmed low, in slow, fluttering flight, over the neighboring open pasture. For a while, it appeared that she would alight and struggle over the grass in a conventional "broken-wing" display; but each time she rose again into the shrubbery without having touched the ground. At last I found her fledgling, a wee, tailless bird with tufts of gray natal down still adhering to its head. It flew into the trees leaning over the water and its mother followed. I discovered no nest and could not learn whether the young manakin had been reared in the fringe of vegetation along the stream or in the woodland across the narrow, shady pasture. I have rarely seen an arboreal bird make so great a display to draw attention from a young bird already able to fly.

When they leave the nest, the young manakins are grayish olive-green above and grayish buff on the under parts. They are not nearly as bright in plumage as the adult female. The few males that I have noticed in transitional plumage were seen in April and May. On April 30, 1949, I found a male whose crown was blue and whose black body was slightly flecked with olive. On May 12, 1957, I met a male somewhat less advanced: a few olive feathers interrupted the blue of his crown, and there were conspicuous patches of greenish olive on his black body, especially on the back and the throat. His remiges were mostly black, although a

few olive ones remained, but his tail was wholly olive, like that of the females. Although it is possible that these males in transitional plumage had hatched earlier in the year in which I saw them, it is probable that they were about a year old. All of the males that I have seen holding stations in the courtship assemblies were in full breeding plumage.

SUMMARY

The Blue-crowned Manakin inhabits the lower strata of the rain forest, whence it ventures into neighboring areas of second-growth woods, in which it occasionally nests. On the Pacific side of southern Costa Rica, it occurs from sea level up to about 4000 feet. It sometimes rests for considerable periods beneath houses near the forest.

The Blue-crowned Manakin eats many berries and it likewise devours numerous insects, which are plucked from foliage or the air by means of a swift dart. It often joins the mixed flocks of small birds that follow army ants, capturing the small fugitives that try to escape by flying or climbing up on the vegetation.

Both sexes frequently utter a soft, clear trill. A loud, harsh *k'wek* and a low *p'rrr* seem to be given only by the male. The last is a note of irritation.

A number of males gather in the undergrowth of the forest to form courtship assemblies, in which they are to be found through most of the year. In these assemblies, each male occupies a poorly defined area about 20 or 30 feet in diameter, and neighboring males are 75 or more feet apart. Essential features of the male's territory are: (1) young trees with slender, leafless, horizontal branches, (2) fairly dense undergrowth, and (3) the nuptial perch, which is a thin, more or less horizontal branch, often a fallen dead stick held up by standing vegetation, about one foot above the ground.

Much of the time, the male at his courtship station rests on a slender, horizontal branch from 6 to 30 feet above the ground, but usually between 10 and 20 feet, and delivers calls which consist of various combinations of the soft trill and the harsh *k'wek*, which last is the distinctive note of the assembly. From time to time, he flits back and forth between neighboring perches or makes looping flights between those a little farther apart. He may flap his wings while perching, but, unlike some other kinds of manakins, he never makes loud snapping sounds. At intervals, he descends to the undergrowth and flies back and forth a few or many times, tracing an irregular zigzag course and keeping within three or four feet of the ground. Finally, with a flourish, he alights on his nuptial perch, where with depressed head and beating wings he emits a harsh, grating note. When a female goes to the nuptial perch, he alights on her back in just the same manner.

At times, especially after the end of the nesting season, males visit each other and two or three of them fly back and forth together in the undergrowth, crossing and recrossing each other. In the breeding season, one male's intrusion on another's area is more likely to lead to a pursuit.

The courtship behavior of the Blue-crowned Manakin is of a relatively primitive type, but it exhibits features which might evolve into the elaborate procedures of *Pipra mentalis* and *Manacus*.

In El General, these manakins breed chiefly from March to June. All nesting activities are carried on by the female, with no male in attendance. The nest is attached by its rim to the arms of a slender fork, at heights ranging from 17 inches

to 7 feet, but usually between 2 and 5 feet. It is a slight, open cup, composed of fine, light-colored fibers. To the bottom of the nest are attached pieces of papery dead leaves, which sometimes hang far below it, and often also tufts of green moss.

Apparently never more than two eggs are laid. An interval of two days may separate the laying of the first and second eggs. The second egg is laid in the middle of the day, probably usually around noon. The eggs are dull white or pale gray, heavily mottled with shades of brown, especially in a band around the thickest part.

The female is steadfast in her incubation of the eggs, taking sessions which are rarely less than an hour in length and she sometimes continues for more than three hours. Her recesses last from about a quarter to half an hour. One female covered her eggs for 82.5 per cent of 8 hours and another for 85 per cent of 8½ hours.

At one nest the incubation period was about 17½ days, and at another nest it was approximately 19 days.

The nestlings are hatched with sparse gray down and closed eyes. The interior of their mouths is yellow. The female nourishes them with berries and insects which she carries chiefly in her throat, with an additional article often held visibly in her bill. Up to seven berries may be crammed into the parent's throat, and on reaching the nest she regurgitates them and divides them among the nestlings. Two nestlings, one week old, were fed at the rate of 2.4 times per capita per hour. The female may swallow the nestlings' droppings or carry them away in her bill; but older nestlings sometimes evacuate over the nest's rim, as the female occasionally does while she incubates.

While incubating or brooding, female Blue-crowned Manakins permit a human to approach very close but they have not permitted themselves to be touched. On leaving the nest, the female may fly close above the ground with slow, fluttering wing beats. When she finds a man by her nestlings, she may hover in front of him, or cling to a low perch slowly beating widely spread wings in an effort to lure him away, repeating this act on a slightly more distant perch as he advances toward her. Females have not been seen to give a conventional distraction display on the ground.

The nestling period is 13 to 15 or 16 days. Fledglings are much duller than adult females. Young males were found in transitional plumage in April and May, when they were probably about a year old.

YELLOW-THIGHED MANAKIN¹

Pipra mentalis

The Yellow-thighed Manakin inhabits the rain forests of the Caribbean side of Middle America from southern México to Darién, and on the Pacific side of the continent it occurs from southern Costa Rica to northwestern Ecuador. On the Pacific slope of Costa Rica, it extends from sea level up to 3500 feet and breeds at least as high as 2500 feet. Despite his diminutive size of less than four inches and his generally black plumage, the male attracts attention, even in the dimly lighted forest, by his flaming red head, bright yellow eyes, yellowish bill, and lemon-colored thighs, by his sharp whistles, loud snapping sounds, and brisk movements. The female, clad in dull olive-green, is likely to be overlooked. Her eyes are usually brown, rarely yellow as in the male.

FOOD

This manakin subsists chiefly on small berries and insects, which it plucks or catches at the end of a rapid dart, without alighting. Sometimes, with manakins of other species, it joins the motley throng of small birds which follow the army ants and seizes the smaller of the fugitives, often capturing on the wing those which try to escape by flying. Once a female caught a little lizard, which soon slipped from her small bill, scurried beneath the fallen leaves, and was lost.

VOICE AND COURTSHIP

The conspicuousness to eye and ear of the male Yellow-thighed Manakin is significant in relation to his manner of courtship. This manakin does not form pairs and the male takes no interest in the nest and young. Throughout a long breeding season, his chief business in life is to advertise himself to the females and to be ready to fertilize their developing eggs. To this end, he selects at the outset of the breeding season a definite display perch, which is typically a straight, slender, more or less horizontal branch, which for a length of several feet is free of foliage and of lateral branchlets, and is unobstructed by the surrounding vegetation. Rarely a thin vine stretching across a fairly clear space between the trees is chosen as the display perch. Here the manakin is to be found through a large part of every day over a period of several months.

On Barro Colorado Island in the Canal Zone, the display perches of nine manakins ranged from about 20 to 45 feet above the ground and were favorably situated for observation. In El General, however, the perches are consistently higher than this, usually above 50 feet; so that, despite the abundance of the manakins and the frequency of their calls, I have not in many years found a group of displaying males which could be satisfactorily watched. This difference in the height of the display perches in the two localities may be correlated with the fact that in the forests of El General an abundant congeneric species, the Blue-crowned Manakin, displays and nests in the understory, and several other kinds of manakins are also present in the lower half of the forest. On Barro Colorado, however, the Yellow-thighed Manakin is the only representative of its genus, and the only manakin that I saw there except the Golden-collared, whose habits are very different.

¹ This life history is a résumé of Skutch (1949), with the addition of a few later observations.

The display perches of the courting male Yellow-thighed Manakins are not scattered at random through the forest but gathered into groups or courtship assemblies. On Barro Colorado in 1935 I studied two of these assemblies. The first contained five adult males: one who was the most active in courtship and spent most of his time alone, two who usually rested close together about 20 feet to the south of this solitary central manakin, and two who perched close together about 40 feet to the north of him. The second courtship assembly contained four adult males whose stations were from 75 to 125 feet apart.

On their display perches the manakins make themselves conspicuous by a variety of vocal and mechanical sounds and by curious antics. Among the vocal notes are: (1) an exceedingly short, high, *psit*; (2) the same note delivered very rapidly but more softly about five times—*psit psit psit psit psit*; (3) the same note given two or three times and followed by a buzzing sound; (4) *psit psit psit p'tsweweee*—*psip*, with the whistled *p'tsweweee* long drawn out, high-pitched, and thin, the final *psip* sharp and emphatic; (5) a high, shrill, rather harsh *tseeee* or *eeee*, voiced as the manakin returns to his display perch after a short, circling flight, or as he alights on the back of a female after a similar flight. If one member of an assembly utters this shrill call while his neighbors are resting quietly, it stirs them to renewed vocal and bodily activity. Perhaps the note most characteristic of the manakin is the long-drawn *p'tsweweee*. This note is uttered at intervals by the males as they sit quietly on their display perches during the hours of the day when they are least active, and it reveals their presence to the wanderer in the forest.

The male manakins also produce various whirring and rustling noises, either in flight or by beating their wings while they perch. In addition, there are louder, sharper notes which seem to be made by striking together the thick shafts of the enlarged, curved, stiffened secondaries. As he flies rapidly back and forth between his display perch and another limb a few feet away, the manakin customarily delivers, each time he takes off, a single loud, sharp *snap*, that resembles the sound made by suddenly breaking a dry stick. While perching, he often fans his wings so rapidly that they are scarcely visible, to the accompaniment of a snapping *whirr*. At other times, he raises his wings high to beat out a series of resounding *snap*'s in somewhat slower tempo; and it is then easier to see that the wing movements are closely associated with the sharp, crackling sounds. Both the staccato *snap* and the rolling *snap* closely resemble noises made by species of *Manacus* but are not so loud. As the Yellow-thighed Manakin approaches his display perch in the short, circling flight already mentioned, he makes a surprisingly loud noise such as can be imitated by holding a piece of stout cloth between both hands and suddenly jerking it taut.

The male manakin's flaming head is at all times so eye-taking that it is difficult to imagine anything that he might do to make it more conspicuous. His display movements are accordingly directed largely to showing off his pale yellow thighs, which in his resting posture are largely concealed. In the "about-face," the manakin stands on his display perch with his legs stretched up so that the thighs are exposed. His body is horizontal or even tilted forward. In this posture, he swings back and forth through an arc of about 180 degrees as rapidly as he can, keeping one foot on his perch as a pivot and moving the other from side to side of his stationary foot so swiftly that it is difficult to follow its movements. Each time he turns

around, the manakin gives his wings a resonant flap. When excited by the presence of a female, the male may execute 40 about-faces without a pause.

In the "backward-slide," the manakin stretches up his legs to reveal his yellow thighs, as in the "about-face." At times his legs are so elongated that his aspect becomes almost spidery. His body is inclined forward until at times his head almost touches the perch; his tail is elevated. By means of short and very rapid mincing steps he seems to slide or glide backward along the perch. The foliage at the end of the branch is set into rapid vibration by his innumerable short steps. After covering a few inches, he may turn and slide backward in the reverse direction. Often he whirrs his wings or shakes his tail rapidly from side to side as he glides tail-foremost along the branch.

A very different display consists in darting back and forth between the display perch and another branch a few feet away, to the accompaniment of staccato *snap's*, as already described. In the "circling flight" the manakin flies out several yards, veers around, and returns to his display perch. As he nears the bough, the smoothness of his flight is momentarily broken while he makes the arresting noise that has been compared to jerking a piece of cloth between one's hands. As he regains his perch, he voices the loud, shrill *tseeee* or *eeee*.

The arrival of an olive-green female stimulates all the males in the assembly to perform their various antics and make their sounds at a quickened rate; their activity becomes so complex and rapid that it is difficult to follow. This is especially true of the favored male on whose display perch the visitor finally alights. When one male, after running through a series of other stunts, advanced backward along the perch toward the female with his head lowered and tail elevated, she slid toward him in somewhat similar fashion, with rapidly beating wings. Whereupon he leapt into the air, circled around, approached the perch with a loud flourish of wings, and alighted directly on her back. On another occasion, the female slid away from rather than toward the male who glided tail-foremost toward her; nevertheless, he circled around in the air, returned with the usual sonorous flourish of his wings, and with a shrill, harsh *eeee* alighted on her to consummate his strenuous courtship display. It is noteworthy that at the assembly of the five males, the solitary male who stayed most constantly on his perch and displayed most vigorously twice won a female while I watched, whereas his rivals were never so favored.

While the chosen male displayed to his visitor, his competitors were never seen to interfere; but each performed vigorously on his own display perch, as though trying to draw her from him. The choice of a nuptial partner rests wholly with the female, and the unchosen males do not attempt to win her by forceful intrusions.

In the long intervals when no female visits the courtship assembly, two males often rest close together on some bough between their respective display perches. Some, while in the assembly, spend most of their time in close association with another and are rarely to be found alone on their display perches; others seldom visit a neighbor. At times with a long, harsh whistle one manakin invites another to meet him at a point between their respective perches. Apparently the males have particular perches for visiting together as well as special perches to which they entice the females. The visiting manakins usually rest about six or eight inches apart on a slender, horizontal branch, where they go through many of their courtship antics in a mild, subdued manner. The act most frequently performed on these occasions is the "backward-slide," but it is not executed in the whole-hearted manner of actual

courtship. The attentions which the manakins pay to their companions are reciprocal but not simultaneous; one rests passively while the other slides toward him, then after an interval their roles are reversed. One male did not appear to be dominant over his companion, as in species of *Manacus*.

In March, when the season of courtship was at its height, the male manakins arrived at their display perches early, while the light was still dim beneath the forest canopy. At first they called and performed with great energy, just as other birds sing most heartily at dawn; but their activity soon waned, and through most of the day they were rather quiet unless a female arrived to arouse them. Those males who habitually rested in pairs would absent themselves for long periods; but the lone performer remained more constantly on his perch, where much of the time he sat quietly, head drawn in and feathers puffed out, doing nothing save look around with bright yellow eyes and utter an occasional lazy whistle. His foraging excursions were brief, for much of his food consisted of insects which he snatched from the surrounding foliage by means of a quick dart. On their display perches, manakins are almost fearless of humans, who may move noisily beneath them without interfering with their normal routine. They merely peer down inquisitively and perhaps voice a sharp whistle.

On Barro Colorado Island, Yellow-thighed Manakins display on their chosen perches from December until at least the end of May, and probably later. In El General, 2500 feet above sea level, the manakins' whistles and snaps are often heard from mid-December to the end of August, although the birds themselves are hard to see. On Barro Colorado in November, young males in olive-green plumage, but flecked with red on head and hindneck, were practicing in a subdued manner the courtship antics of the adults on typical display perches.

I have repeatedly seen Yellow-thighed Manakins in olive-green plumage, with no trace of red or black, display rather vigorously at a distance from an assembly. These birds may have been females but more probably were males younger than those just mentioned. But on two occasions I watched spirited displays given by females whose sex I could not doubt, because they attended a nest or a fledgling. One of these females had yellow rather than brown eyes and was more than ordinarily attentive to her nest. When pushed from her eggs, she performed the "about-face," at the same time showing off her thighs, which were more yellow than is usual in her sex. As she flitted from perch to perch, she sometimes audibly snapped her wings. Another female, attending a fledgling, "about-faced" and snapped her wings, once giving a rolling *snap*. She also darted rapidly back and forth between branches a few feet apart, in the manner of a displaying male; and she uttered a loud, shrill, long-drawn *eeee* that resembled the note given by the male as he mounts a female. It is evident that the courtship displays of the male are latent in the female and may find expression, at least in a subdued form, at times of emotional stress, as when nest or offspring appears to be in peril. Apparently this is particularly true of the older females.

NESTING

In El General, some females begin to build their nests in late February. On Barro Colorado building evidently starts at about the same time, as I found a full set of eggs on March 10.

The nest is situated in the primary forest, or rarely in adjoining high second-



Fig. 5. Female Yellow-thighed Manakin on nest. Unlike most adult females, this bird had yellow eyes. Barro Colorado Island, Canal Zone, March 23, 1935.

growth woods, where it is suspended between the slender arms of a horizontal forked branch of a shrub, a sapling, or a small tree. Just as the Yellow-thighed Manakins choose higher display perches in El General than on Barro Colorado, so they place their nests higher in El General. Six nests on Barro Colorado ranged from 5 to 10 feet above the ground, with an average of 7.8 feet. Five nests in El General were situated from 10 to about 30 feet up, with an average of 18.6 feet. My failure to find, in many seasons in El General, as many nests as I discovered in one season on Barro Colorado reflects the greater difficulty of encountering these slight structures when they are well above one's head, rather than their relative abundance in the two localities. The female builds at a leisurely pace, and at three nests in El General I counted eight visits with material in half an hour when she was working most actively. Usually her visits were more widely spaced.

The completed nest is a slight, frail, shallow structure, attached by its rim to two thin, diverging, horizontal twigs, between which it hangs. It is composed chiefly of fine vegetable fibers, usually brown in color, sometimes lighter. Rarely, the short, fine, curled secondary rachises of acacia-like twice-compound leaves are mixed with the fibrous materials; and slender, black fungal filaments, the so-called "vegetable horsehair," may be coiled into the bottom as lining. Attached to the outer or lower surface are a variable number of small dead leaves or fragments thereof. Sometimes bits of the pinnae of ferns are fastened here along with the leaves of dicotyledonous plants. Some nests have a complete covering of these dead leaves, others are so sparsely covered that the eggs are visible through the meshes of the bottom. The nest is bound to the supporting arms by cobweb as well as by

passing the constituent fibers over them. A typical nest measured $1\frac{3}{4}$ inches in internal diameter by $\frac{5}{8}$ inch in depth. The depth of the bowl is about equal to the transverse diameter of the eggs that it holds. The incubating female, who sits above rather than in it, would be conspicuous if she were not so small and dull in color.

A nest found under construction on February 24, 1949, was still without eggs on March 6, but three days later there were two eggs in it. A nest that was less than half finished on March 17, 1943, received its first egg about March 26 and the second egg on the following day. Another nest, which on April 14, 1954, seemed to have been just begun, appeared to be finished on April 16; by April 21 it held two eggs. Thus the interval between the start of building and laying seems to shorten as the season advances. In ten instances, the full set consisted of two eggs. At one nest, an interval of at least three days separated the laying of the first and second egg, but I suspect that this is an abnormally long interval. The eggs are dark grayish buff, heavily mottled with brown, especially in a wreath around the thicker end. The measurements of eight eggs average 21.5 by 15.4 mm. Those showing the four extremes measured 22.2 by 15.9 and 21.0 by 14.3 mm.

My earliest dates for eggs are March 9 in El General and March 10 on Barro Colorado. On this island I found six nests with eggs: three in March, two in April, and one in May. For the same locality, Eisenmann (1952:38) records two additional nests, both of which held eggs in early July. In the valley of El General, about 2500 feet above sea level, I found two nests with eggs in March, one in April, and one in June.

The female incubates with great steadfastness and constancy. At a nest which I watched for 12 hours, she took 7 sessions ranging from 29 to 108 minutes and averaging 65.1 minutes and 7 recesses that varied from 6 to 21 minutes and averaged 14 minutes. Accordingly, she incubated with a constancy of 82.3 per cent. A second female, which I watched from daybreak until past noon, began her day by leaving the nest at 6:26 a.m. and was absent until 6:52. She then sat until 8:30, returned at 9:04, and remained continuously until 12:38 p.m., when she left for another outing. The entire morning was taken up by two long sessions of 98 and 214 minutes and two recesses of 26 and 34 minutes. She covered her eggs for 83.9 per cent of the observation period.

On returning to her nest, this manakin flew directly onto her eggs, without first alighting on the rim, much in the manner of a hummingbird. From time to time she regurgitated a small seed, held it in her bill for a few seconds, then dropped it to the ground. Occasionally she preened while she warmed her eggs. Like the first female, she incubated in perfect silence. The nest of the first female was the only one that I have found within sight and hearing of a male's display perch; but he rarely came near the nest and showed no interest in it. The female seemed to ignore him.

Depending on their dull plumage and immobility to escape detection, most of the Yellow-thighed Manakins whose nests I have studied permitted me to come very near while they incubated but flew away before I could touch them. Far bolder than all the others was one female with yellow eyes, pale yellowish thighs, and unusually dark dorsal plumage, tending toward the black of the male. Even before her eggs hatched, she stuck to her ten-foot-high nest while I placed a ladder and climbed up to her. She permitted me to smooth the silky feathers of her back and even to touch her head. Since she would not allow me to see what her nest



Fig. 6. Nest and eggs of Yellow-thighed Manakin. Barro Colorado Island, Canal Zone, March 30, 1935.

contained, I tried to push two fingers beneath her to feel. It was not the weight of her tiny body that made her so difficult to raise; she was clinging to the nest with her feet. The first time that I touched her bill she attempted to bite, but afterward she made no hostile move.

Photographing this manakin was a unique experience, for she remained on her nest while I set up the camera, focussed, took time exposures, and changed films. She even permitted me to push her around into the pose that I preferred! This remarkable female not only had yellow eyes like the males but she performed some of their courtship antics, as already described. On the evening of the day when her eggs hatched, she alighted on the rim of her nest just as I approached with a ladder for my daily examination, which I usually made by inserting a finger beneath her. Standing above the nest, she "froze" and remained perfectly immobile while I climbed the ladder to look in. The legs of a small spider projected from her bill.

Newly hatched Yellow-thighed Manakins have pink skin with sparse gray down, tightly closed eyes, and yellowish bills. They develop slowly. When they are five days old their bills begin to darken, their eyes begin to open, and pinfeathers push out from their skin. At eight days they are still nearly naked, but their feathers are beginning to escape from the ends of the sheaths.

I watched a nest with two nestlings eight and nine days old, respectively. The female, who had brooded through the night, flew from the nest at 6:27 a.m., but she gave the young no breakfast until 7:33. By 10:27 she had brought food to the nest only five times. As she approached to feed, nothing was visible in her bill, although at times it was slightly open. Standing beside the nest, she regurgitated

a number of objects from her throat, sometimes as many as ten, and divided them between the nestlings. Small purple berries seemed to enter largely into the young birds' diet. When the nestlings were satiated and sank back into the nest before she had exhausted the contents of her throat, she coaxed with low twitters until they rose up to take more. Once she brooded for 52 minutes, and often she remained standing near the nest either before or after delivering a meal, as though guarding its occupants. Once she lingered so for a quarter of an hour before she gave them what she had brought.

The parent did not remove the droppings of these older nestlings, who voided over the edge of their nest. Their excreta contained many small seeds.

One parent, after remaining on her nest until I almost touched her, fluttered downward to a perch only a few inches above the ground, where she spread and beat her wings somewhat in the manner of the Blue-crowned Manakin. But as injury simulation this display was not convincing, and other parent Yellow-thighed Manakins have tried even less to lure me away.

I know the outcome of eight nests that were found before the eggs hatched. Eggs disappeared from four nests and unfledged nestlings from four others. None was successful, and I was unable to learn the incubation and nestling periods.

The young of both sexes resemble the females in their olive-green plumage. In November, young males in olive-green attire, but flecked with red on head and hindneck, were not uncommon on Barro Colorado Island. At the end of March, I found in El General an olive-green bird with yellow eyes and a single red spot on the back of its neck, evidently a young male just beginning to acquire the adult colors. From the date, it is likely that he had been hatched in the preceding year, if not earlier. In another part of El General, I saw in mid-April a male farther advanced in the transitional plumage, his head largely red and his body dusky.

ORANGE-COLLARED MANAKIN

Manacus aurantiacus

The Orange-collared or Salvin Manakin is a short, stocky bird about four inches in length. The top of the male's head, to the level of the eyes and the base of the bill, is black. A broad collar encircling the neck, and including all the head below the eyes, the upper back, and the chest, is intense yellow or orange, changing in shade with the angle of vision. A narrow black band across the back separates the orange collar from the olive-green of the lower back, which becomes more yellowish on the rump and upper tail-coverts. The ventral plumage posterior to the orange collar is yellow, tinged with olive on the sides and flanks. The tail is greenish olive, becoming blackish at the tip. The wings are largely black or dusky, with the lesser coverts yellowish orange. The short bill is black; the eyes are deep brown; the legs and toes are bright flesh-color or orange. The female is golden olive-green on the upper parts, becoming more yellowish on the rump and upper tail-coverts. Her under plumage is lighter and more yellow, with a band of darker yellowish olive-green across the chest. Her bill, eyes, and feet are colored much as in the male; and the bright pinkish legs serve to distinguish her readily from the rather similarly attired females of the Yellow-thighed Manakin, Blue-crowned Manakin, and White-ruffed Manakin, which occupy the same region, but whose legs are dark.

The Orange-collared Manakin has a restricted range on the Pacific side of Costa Rica, south of the Gulf of Nicoya, and in adjacent parts of the Republic of Panamá, but it is obviously closely related to the Golden-collared or Gould Manakin of central and eastern Panamá and Colombia. In Costa Rica Orange-collared Manakins are resident from the lowlands up to about 3500 feet above sea level. They inhabit the rain forests, neighboring second-growth woods and taller thickets, shady pastures, plantations, and even dooryards with abundant shrubbery. The females are found in the more open situations far more often than the males. The former nest in a variety of situations within and beyond the forest. Near Buenos Aires de Osa, I found these manakins not uncommon in dry thickets remote from taller woods.

In their social habits, manakins resemble hummingbirds. Although a number of them gather to form a courtship assembly, or may congregate at a favorable source of food, they are not truly gregarious; and they move from place to place as individuals rather than in flocks. Their flight is swift and direct, and their short, rapidly beating wings produce a whirring sound, particularly noticeable in the males.

FOOD

The diet of the Orange-collared Manakin is varied and includes both fruits and insects in liberal quantities. These manakins are fond of berries of numerous kinds, especially those of the shrubby or arborescent members of the melastome family so abundant in the lowland rain forests. They sometimes venture from the woodland shade into adjacent clearings which have been burnt a year or two earlier and now support many rank bushes of pokeberry (*Phytolacca rivinoides*), whose juicy, deep purple berries they pluck from the long racemes. They eat the seeds of the tree, *Alchornea latifolia*. These seeds are enclosed in a thin, bright red aril, which is unpleasant to the human taste but doubtless agreeable and nourishing to the

birds, for these arillate seeds are eagerly sought by many species. I have often seen Orange-collared Manakins, along with larger birds of various kinds, gathered above swarming army ants, where they were capturing some of the small insects stirred up from the ground litter by the ants. The manakins snatch both berries and insects in much the same manner, darting up to the cluster of berries or to the leaf over which an insect crawls, seizing the food in the bill, and carrying it off without alighting.

COURTSHIP

Like other members of the genus *Manacus*, the brilliant male Orange-collared Manakins, who take no interest in the nests, perform elaborately during a long breeding season at "courts" which they establish in the crowded vegetation. Each court is an area of ground a foot or two in diameter which the bird itself clears of fallen leaves and litter and keeps clean as long as it is in daily use. Where one court is found, diligent search through the surrounding undergrowth will usually reveal several more; for a number of male manakins congregate to form a courtship assembly or lek, and apparently they never pass the breeding season far from others of their own kind and sex.

The courtship assembly.—When I first came to El General 32 years ago, I found the courtship assemblies chiefly a short distance within the forest's edge, beside the new clearings which the settlers had made to plant their maize, beans, and pasture grass. The courts were also found on the back of a sharp wooded ridge. In both of these situations, the light near ground level was often somewhat stronger than in the midst of heavy forest, and in consequence there was a denser growth of slender saplings and shrubs, especially those of the melastome family, which furnished the thin upright stems that are indispensable for the courtship "dance." As, with the passage of the years, the once-magnificent forests of El General have receded before the axe and fire, I have noticed an increasing tendency of the manakins to make their courts in secondary vegetation. Even in the primary forest, the courts are usually well screened by the surrounding bushes, and beyond the forest they are sometimes situated amid such dense and tangled growth that they are difficult to find and most unsatisfactory for watching the performances which take place at them. It was not easy for me to find a courtship assembly that invited close study.

In February of 1959 we cut down for purposes of planting maize a tract of woods which had grown undisturbed since the original forest had been felled and burned early in 1941, just before I bought the farm where I now reside. After the removal of a single crop of maize, this area had been permitted to rest and recuperate for nearly 18 years. I had long known that some manakins' courts were located here, but the density of the swiftly springing vegetation made this part of the farm difficult of access. The preparation of the cornfield in 1959 not only provided an easier approach but evidently caused the relocation of some of the courts. I now found them concentrated on a wooded knoll, which had been left untouched while the more fertile lower ground was cleared for sowing. This round knoll had a flat top and steeply sloping sides, and it was about half encircled by the new cornfield; the remainder of its perimeter adjoined low thickets which had overgrown the cornfields of recent years. The taller of the slender trees on this little elevation were 60 or 70 feet in height, while beneath them there was a fairly dense, but in spots

rather open, undergrowth of shrubs, tangled vines, and clumps of low, spiny palms. In addition to the numerous courts on this knoll, I found two on the opposite side of the cornfield, in a strip of rather similar secondary woods that adjoined primary forest. Before the clearing was made, the secondary woods where all these courts were situated had been continuous across the intervening depression. I made periodic observations on these courts from April, 1959, to the end of June, 1960.

On May 29, 1959, when I believed that I had located all the courts on the knoll, I surveyed their positions with a prismatic compass and tape, as accurately as the rather dense vegetation would permit, and afterward I plotted the courts on a map. There were then ten courts situated within an area that measured approximately 235 feet from north to south by 160 feet from east to west. One of these courts was 102 feet northeast of its nearest neighbor and another was 101 feet southeast of its nearest neighbor. If these two outlying courts are omitted, there were eight courts in a rectangular area of 185 by 70 feet, or 12,950 square feet—somewhat less than a third of an acre.

By the following February, when the number of occupied courts on the knoll had again reached its maximum, I found 14. The most distant of the outlying courts of the preceding year, on the northeastern side of the knoll, had been abandoned; but the occupied area had been extended slightly to the southeast by the creation of three new courts. These 14 courts were scattered over an area of about half an acre, which in woodland with a rather dense undergrowth seems much greater than an equal expanse of open ground.

In 1959, the closest occupied courts on the knoll were 31 feet apart. Five courts were from 30 to 40 feet from their nearest neighbors, whereas the outlying courts were 101 and 102 feet from their closest neighbors. In 1960, two occupied courts were only eight feet apart. Such close spacing is exceptional and apparently is not always tolerated. On January 13, 1960, I found a new court (no. 15) about eight feet from well-established court 3, but two weeks later court 15 had been abandoned. When, in January of 1960, a new court (no. 16) appeared nine feet from a court (no. 14) that had been made late in the preceding year, the latter was abandoned. Usually, when courts were somewhat close together, the intervening undergrowth was dense. It was exceptional to find two courts which could be watched simultaneously from a single observation point without clearing away so much vegetation that the surroundings would have been greatly altered. Of all the courts, the two in the woods across the cornfield from the knoll were most satisfactory for simultaneous study. They were 16 feet apart, with little undergrowth between them.

The separation of the courts of the Orange-collared Manakin shows about the same range as that of the courts of the closely related Golden-collared Manakin, which Chapman (1935:483-484) found from 12 to 200 feet apart, with the majority between 30 and 40 feet from their closest neighbors. But these courts were in smaller assemblies than those on the knoll; from four or five to seven and possibly more were associated together (*op. cit.* 490). If my memory is accurate, the assemblies of the Golden-collared Manakin which I visited with Dr. Chapman on Barro Colorado Island in 1935 were in forest with less undergrowth than is found in the areas where the Orange-collared Manakin carries on its courtship, so that it was easier to watch several birds at once; and the Golden-collared Manakins were less shy of their human observers.

In striking contrast to these manakins of southern Central America, the Black-

and-White Manakins of northern South America crowd their courts together. On the island of Trinidad, Snow (1956) found them very closely grouped, from three to six feet apart. In an area of approximately 60 by 30 feet he counted 70 courts; and some of the estimated 100 males that he found at this assembly were displaying without courts. On the same island, Darnton (1958:52) found the courts of this manakin equally crowded, "some almost touching, others at intervals of a yard or so."

The courts.—The courts, or areas from which the attendant manakin removes all the litter that he can pick up and carry away in his bill, vary considerably in size. The largest of these bare patches of ground that I measured were 27 by 26 inches, 26 by 26 inches, and 27 by 18 inches; the smallest were 12 by 12 inches, 11 by 11 inches, and 12 by 10 inches. In shape they ranged from roughly circular to strongly elliptical. Most of the courts had two slender, erect stems of saplings or shrubs, no thicker than one's fingers, growing at their edges; but sometimes they had only one such stem; and one court had four. An exceptional court had two stems standing only seven inches apart in its center, rather than at its edges. In addition to these stems in or at the margin of the denuded area, there were usually several stems standing a short distance away from the court area. These might be used for the courtship dance. Indeed, where only a single stem grows at the edge of the court, these slightly more distant stems must be employed, for the manakin requires several of them as the stage for his performance.

Old, well-established courts are clear of all removable forest debris, as though they had been swept repeatedly with a stiff broom. Only exposed rootlets remain, defying the manakin's efforts to tear them away with his small bill. One morning I saw a manakin go again and again to a particular spot on his court, where he plucked at something on the bare ground, after which he wiped his bill repeatedly against a branch. Newer courts are often carpeted with a layer of matted, well-decayed leaves and other litter, which the bird can only gradually carry away as, in drying, it peels from the underlying soil. If one wishes to convince himself that these areas of the woodland floor are actually cleared by the manakins, he has only to drop a few leaves or flowers in the area and then watch from a distance. Often he will see a brilliant little bird approach and carry them off, one by one, in his bill. When objects of different colors, as green leaves, brown leaves, and red flowers, are placed simultaneously on the court, the caretaker removes them regardless of color, although red objects are likely to remain longer than green leaves. Once, when I laid in the center of a court a segment of yellow banana peel, longer and perhaps heavier than the manakin, the bird alighted on the ground beside it, seized it, and flew up just high enough to flip it beyond the edge of the bare area.

The manakin often carries a leaf from his court at the end of a round of jumping across it. This suggests that the bird does not first clear a court and then perform above it, but that the bare area on the ground gradually develops as the bird performs repeatedly between suitably situated upright stems. Rarely, a manakin plucks a green leaf from a plant growing close beside his court, but I have noticed no extensive defoliation of the surrounding vegetation.

Period of occupancy of the courts.—As long as courtship displays are performed at a court, it is kept clean. When the manakin relaxes his attention, leaves soon sift down on it, revealing that the season of daily displays is drawing to a close. The easiest way to learn whether a court is still frequently used is to lay a few leaves on it and return after a half-hour or so to see whether they remain. To be

convincing, this test should be made early in the morning; later in the day, the owner's attendance is less constant.

In earlier years, I learned that in El General the Orange-collared Manakins clean their courts and begin to perform above them before the end of January, the first of the two or three months of scant or no rainfall. Thus the courtship assemblies are well established long before the females begin to build their nests in March of an average year. If the dry season is severe and late February and early March are very dry and hot, activity at these courts may languish, although the courts themselves are still kept clean, to be used more freely after the first showers have cooled and refreshed the air and many females have begun to build their nests. After July, when few females are still nesting, the manakins allow leaves to litter their courts; although, as we shall see, courtship activity does not wholly cease with the termination of the breeding season. A courtship assembly may occupy the same area year after year.

In 1959, I began to make more systematic observations on the occupancy of courts in the knoll assembly and in the woods on the opposite side of the cornfield. Of the 12 courts which were active in April and May, only nine were still clean in mid-June. By the end of this month, five were clean and seven were neglected. By July 10, only two courts looked well swept. By the beginning of September, a single court was free of litter. This court, no. 3 on the knoll, was large (24 by 20 inches), and even when I first found it the earth had been denuded of all vegetable mold. Although in late November it showed signs of neglect, by early December it was clean again; it received almost continuous care from the breeding season of 1959 to that of 1960. Court 11, which measured 12 by 10 inches, was neglected from late June to early September. On five visits from September 18 to October 30, I found it clean. In November and early December it was again neglected, but from mid-December to the following June I always found it well kept. After a period of neglect, court 10 was found clean on two visits in October.

A new court, 14, was first noticed on October 5, at a point where I probably would not have overlooked it had it been present much before this. From then until the middle of the following January, I found it clean on most, but not all, visits, and sometimes I found manakins performing above it. Apart from these few courts which were made, or more or less continuously maintained, during the long nonbreeding season, and whose significance will be discussed later, there was no increase in the number of recognizable courts on the knoll until December. On December 2 there were only two more or less clean courts, 3 and 14, as already told. On December 7 I found three courts, while from the 17th to the 30th I had four under observation. On January 13, 1960, I found six clean courts. On January 27 I noticed 11. On February 6 there were 14 courts, the maximum number of well-established courts that I found on the knoll at one time. A few bare spots that I took to be courts were soon abandoned, for unknown reasons.

On the knoll, three courts (3, 10, and 11) were in use in both 1959 and 1960; and one of these, as already mentioned, was almost continuously attended through the intervening nonbreeding season. On the opposite hillside, one of the two courts was also attended in both years, while the other court of 1960 was close beside the site of that of 1959. In three instances on the knoll, there was in 1960 a court within a few feet of the obliterated court of the preceding year. Probably when the

same court persists through successive years, or a new one appears very close to an earlier site, the same individual is in attendance.

In 1960, when there were frequent showers in the "dry season" and birds of various kinds, including the Orange-collared Manakin, began to breed exceptionally early, the males deserted their courts earlier than in 1959, when the dry season was severe and the rains began late. By June 1 of 1960, the number of well-attended courts on the knoll had dropped from 14 to 11. By June 26 all the courts were littered with fallen leaves. It will be recalled that at the end of June of the preceding year nearly half of the courts were still clean.

Sounds made by the males.—The displaying male Orange-collared Manakin performs such varied antics, to the accompaniment of such diverse sounds, that an account of his performance might bewilder the reader who had not been prepared by a description of the setting and an analysis of the manakin's movements, vocalizations, and mechanical noises. From a study of the courts, we shall proceed to consider the sounds that one hears at them.

With the outstanding exception of the mellifluous Thrush-like Manakin, I am familiar with no member of the family that might be considered a songster. The notes of the Orange-collared Manakin are few and unmelodious. At the courtship assembly, a loud, clear *cheeu* is often heard, especially at the end of a snapping roll, soon to be described. When annoyed or disturbed, the manakin may call *chee-yú*, with the emphasis on the second syllable. At times the note of annoyance is a thin, tense *chee*. The usually silent female voices a somewhat weaker *cheeu* when perturbed, especially at her nest. All these notes, with subtle variations difficult to recognize and describe, appear to be modifications of a single basic utterance.

To compensate for his lack of vocal expression, the male manakin produces a considerable variety of sounds that are evidently mechanical and are made by the wings, although some writers have questioned whether this is indeed their origin. His ordinary flight is accompanied by a fairly loud rustling or whirring sound. But at times he makes a fuller, deeper *whirr*, which he is likely to do as he approaches his court, or takes short flights in its vicinity, or leaves it after displaying. On flights of several yards or more, this deep *whirr* is made intermittently, with an undulatory effect. The bird's trajectory is at this time somewhat or even strongly undulatory, instead of being straight as is usual in manakins. This seems to be the sound which Chapman (1935:492) called the "reedy *whirr*"; his suggestion that it is produced by the bird's incised outer primaries is probably correct.

A loud *grrrt* seems to be a variant or intensification of the reedy *whirr*. It is most frequently heard when the manakin, after alighting on his bare court in the midst of a round of jumping above it, rises sharply upward to resume his sideward jumps. The *grrrt* may also be made while the manakin perches beside his court during a pause in his jumping. Aside from marking a definite spot for the courtship display, the provision of a firm base for the sonorous ascent appears to be the bare court's only function. All the rest of the manakin's antics are performed above rather than on it. The Black-and-White Manakin also rises from his court making a growling *grrrt*, which evidently closely resembles that of the Orange-collared Manakin (Darnton, 1958).

Next to be noticed is the sound which Chapman called the "rolling snap." This is a very rapid series of sharp, crackling notes, which the manakin most often makes while perching near his court. Lifting his wings well above his back, he beats them

so rapidly that they become blurred, at the same time producing the loud, sharp notes, which may be imitated by holding a thin, flexible strip of wood against the teeth of a rapidly revolving cogwheel. Usually the rolling snap is followed by a loud *cheeu*. This sequence of sounds may stimulate neighboring males to repeat it, and often it preludes a bout of jumping over the court.

Finally, there is the staccato *snap*, a single sharp note, which has often been compared to the sound of a dry twig which is suddenly broken or to the detonation of a small firecracker. This explosive note is produced by the manakin as he jumps over his court from an upright stem on one side to a stem on the opposite side. The amazingly loud noise carries a long distance and is often heard issuing from dense vegetation where the manakins perform unseen. More than any other sound made by the bird, it serves to advertise the presence of the courtship assembly. A subdued version of the *snap*, which may be given by a perching male, was called a *snip* by Chapman.

Because young males resemble females in their greenish plumage, it is difficult to be sure which sounds are restricted to the males. "Green" birds (as I shall henceforth refer to all individuals whose sex is not definitely known) often snap loudly as they jump back and forth, perhaps above courts not their own. These are probably young males. Birds attending nests may with confidence be designated as females, for I have never seen a male in adult plumage, nor two manakins in green plumage, take an interest in a nest or in the young. From the undoubted females who attend the nests, I have never heard any varieties of the *snap*. But breeding females sometimes make a faint *whirr* while they fly.

As to the mode of production of all these sounds which are not, like the *cheeu*, obviously vocal, there is room for differences of opinion. Having often watched an Orange-collared Manakin make the rolling *snap*, I can hardly doubt that it is produced by the beating of the wings which always accompanies it. The Yellow-thighed Manakin makes a similar sound. It seems impossible, without high-speed photography, to follow the movements of the wings at the instant when the manakin makes the staccato *snap* while shooting rapidly across his court; but it is most improbable that this noise is produced by one organ and the rolling *snap* by another. Hence, I attribute all the *whirr*'s and *snap*'s which have just been described to the highly modified wing feathers of the male manakin. Chapman (1935:481) wrote of the wings of the Golden-collared Manakin: "The shafts of the male's secondaries are not only laterally curved and stouter than those of the female, and their vanes, particularly the outer one, broader, but the vanes themselves are much heavier and the wing, in consequence, stiffer. It is also flatter and less arched than in the female." Other male manakins, notably *Machaeropterus deliciosus*, have still more strikingly modified secondaries. Although one may doubt that feathers can produce so strong a note, it is even harder to believe that the manakin's small bill can be snapped shut so explosively. Moreover, the *snap* differs greatly in quality from any undoubtedly vocal note that I have ever heard from any animal of whatever kind. Apparently, sufficient muscular force to produce the staccato *snap* can be generated only on a rapid jump, such as that across the court. Although the subdued *snip* is sometimes made while the manakin perches, the full *snap* is not.

Courtship movements.—The loud calls and *snap*'s issuing from a number of male manakins gathered in a small area should suffice to guide the female to them from afar, as they guide the birdwatcher. Only the youngest females, seeking a male

to fertilize their first eggs, appear to require such advertisement; since assemblies are in the same place year after year, older females must remember their location. After reaching the area where the males are congregated, the female manakin, like the human observer, should have no difficulty in picking out the vividly colored, mobile forms, even in the dimly lighted undergrowth where visibility is restricted by interfering vegetation. The special movements which we are now about to describe appear to serve chiefly to establish a rapport with the female after her arrival, rather than to guide her to the male. But they are often performed in her absence.

The principal activity of a male at his court is jumping from vertical stem to vertical stem, across or occasionally around the bare area, about a foot above the ground. He describes an arching course from stem to stem, and in the midst of each rapid dart he emits an explosive *snap*. Sometimes, when the display is less intense, he jumps without a *snap*. If, as usually happens, his course is back and forth rather than around the court, he regularly alights on the upright stem facing inward, in the direction of his next leap. This skillful maneuver of reversing his direction as he alights speeds up the series of jumps. Suddenly the manakin interrupts his horizontal jumping to descend to his bare court, whence, after a pause which may last two or three seconds, he shoots upward to a height of a foot or less, to the accompaniment of the harsh *grrrt* already mentioned. This ascent often carries him to an upright stem, from which the horizontal jumps are immediately resumed.

Since the manakin often uses stems standing somewhat beyond the edge of his court as bases for his jumps, these leaps may exceed the diameter of the bare area. The number of jumps in a single display is variable and difficult to determine. Pauses of all lengths, while the manakin clings to the upright stem to which the last jump has taken him, may interrupt the continuous leaping; so that one must rather arbitrarily decide how long a pause is permissible within a series of jumps, and how long it must be to constitute an intermission between two performances. Once I watched a practically continuous series of 14 jumps, including a descent to the court with subsequent sonorous ascent, by a manakin performing without a partner, although a green bird resting nearby probably spurred him to greater effort. Usually the series is somewhat shorter than this; sometimes it is reduced to two jumps with one descent to the ground. I have not recorded more than one descent in the midst of a series of jumps of whatever length.

At the end of a performance, the manakin sometimes alights on his court and carries away a fallen leaf. One male concluded a dance by plucking a living leaf from a low plant beside his court and carrying it off. Sometimes at the end of his performance he tugged at a larger leaf which he failed to detach. Such defoliation of the surrounding vegetation may increase the visibility of the court, but the Orange-collared Manakin seems not to carry out this procedure to a significant extent. The Blue-backed Manakin, which does not clear an area of ground, plucks away the green foliage surrounding the display perch in a low bush, apparently removing much of it. The significance of this defoliation may be that it allows more light to fall upon the male's splendid plumage, or that it makes approaching enemies more visible to the displaying birds (Gilliard, 1959b:7-8).

The "beard."—A minor element in the display of the male Orange-collared Manakin is the forward projection of the feathers of the chin and throat to form

a sort of orange "beard." When the displaying male pauses between jumps across his court long enough to be clearly seen, it may be noticed that his neck is stretched forward and his chin feathers are turned in the same direction, their tips reaching to, or slightly beyond, the end of his short bill. Sometimes he perches with his head inclined upward and his beard extended; more rarely he depresses his neck and holds his head horizontally with protruding beard. To judge by the sketches and descriptions of various authors, the white beard of the Black-and-White Manakin is more prominent and extends farther beyond the bill than the orange beard of our species. Likewise the White-collared Manakin has a prominent beard. Long ago I saw this manakin in the Caribbean lowlands of Honduras, shaking his head from side-to-side with his white beard projecting beyond the end of his bill. From Chapman's (1935:480) description, it appears that the Golden-collared Manakin's yellow beard is more conspicuous but less colorful than the beard of the Orange-collared Manakin.

Diurnal periodicity.—The male manakins begin to snap and jump at their courts at sunrise or a little earlier. The period of greatest activity lasts for the next hour or more; but between seven and eight o'clock their zeal falls off sharply and their absences from the court and its vicinity grow longer. After 8:00 a.m. so little occurs at the courts that one grows tired of sitting in a blind waiting for something to happen. Yet throughout the morning, and even in the afternoon, bursts of loud snapping issue from the assembly ground from time to time. I have often heard this snapping while passing by or attending my vegetable garden in the vicinity.

Even in the early morning, the manakins do not, of course, jump and snap continuously. Such vigorous display would soon exhaust them if they did not rest frequently. Much of the time they perch on a horizontal branch or vine, from 1 to 3 yards above the ground and perhaps an equal distance to the side of their court, waiting for a female to arrive. The perching manakin sometimes puffs out his body plumage so strongly that his wings are concealed in a ball of feathers. From time to time he gives a rolling *snap* followed by *cheeu*, or else he calls without first snapping. Sometimes two males rest close together, in a manner soon to be described.

The courtship "dance".—The approach of a green bird stimulates the waiting males to renewed activity. The passage of such a visitor through a large assembly is greeted by salvos of loud snapping. The males do not pursue the visitor, but each goes to his own court and tries to attract its attention. Unfortunately, I am obliged to use the neuter pronoun, because nearly always I was uncertain of the green manakin's sex. Once, when coition followed a dance, it seemed evident that a female was present; and once an indistinct collar revealed that the visiting manakin was a young male, just beginning to acquire adult plumage. On no other occasion was I quite certain of the green bird's sex, and I am not sure that the owner of the court could always tell it.

All my observations of the courtship dance were made from a blind, set about eight feet or more from the court. It is more necessary to conceal oneself to study courtship behavior than it is to watch the females at their nests. This was unexpected, because on Barro Colorado Island I had found female Golden-collared Manakins more shy than are female Orange-collared Manakins in El General. Chapman (1935:484) made his classic study of the courtship of the former species without concealment "beyond the cover afforded by the vegetation." I have watched

nests of the Orange-collared Manakin while sitting unconcealed, but I have had no satisfactory view of the courtship dance except from a blind.

Watching from concealment, I have frequently seen a green manakin fly up to a court where a male was trying to win its attention. The ensuing activity was so rapid that it was difficult to discern all the details that I wished to notice. The brilliant male and his plainly clad companion shot back and forth above the court, between the upright stems on opposite sides, to the accompaniment of loud, staccato *snab*'s that seemed to be made by the resident male alone. Once each partner made about nine jumps; but usually the dance was briefer than this, sometimes consisting of only two or three jumps. The two participants, going in opposite directions, commonly passed each other above the court; but sometimes I received the impression that the green bird followed the brilliant one, who left his perch just in time to avoid the other. This may have been a subjective effect, due to selective attention to one aspect of this very rapid action; but other observations, soon to be mentioned, make me believe that it was not wholly an illusion.

The dance ends suddenly, and often the adult male goes off a short distance, leaving the green bird clinging to an upright stem beside his court. A good example of such behavior is provided by an entry in my journal under date of May 1, 1959. In quoting it, I have changed "female," which appears in the original, to "green bird," as I was not certain of the visitor's sex:

"This morning, from 6:10 to 8:00, I watched manakin 3 of the knoll assembly. During the first 25 minutes he danced alone a few times, once making 11 jumps with one descent to the ground. At 6:35 a green bird arrived and both jumped over the court a number of times. Then the male flew off to a perch several yards away, where he rested with his head inclined strongly upward while the green bird remained clinging to a stem at the court's side. Soon he returned and they jumped over the court, crossing each other, a few times more. Again he withdrew, this time to an upright stem a short distance away. After a brief interval, the green bird, who had been left alone at the court, flew to this stem; and as 'she' approached, the male flew back to the court for another bout of jumping with 'her.' Finally he flew away leaving 'her' at the court, and presently 'she' vanished. Again I received the impression that during the dance the green bird pursued the male, and he left the stems to which he clung in order to avoid 'her.' But the performance is so rapid that it is difficult to follow the movements of the two birds simultaneously and to interpret what occurs."

Sometimes the visitor goes to the perch close to the court where the male rests between rounds of jumping over it. At 6:45 a.m. on June 13, when courtship activity was waning, male 3 was resting above his court when a green bird suddenly flew up and alighted beside him. He abruptly flew out of sight. Soon he returned and jumped back and forth between saplings beside rather than above his court, but meanwhile the green bird had gone away. Forty minutes later, male 3 danced briefly with a green bird, while a second green manakin rested close by. Shortly afterward, a green manakin alighted on the favorite perch of male 3, but he paid little attention to the intruder. Even at the end of April, when courtship intensity was at its height, I have seen an active male promptly fly away when a green bird alighted on one of the vertical stems beside his court.

Probably some of these green visitors are young males rather than females. Although the human observer cannot distinguish them, the manakin may be able to do so. This may account for his refusal to dance, as in the incident just mentioned. In other cases, he may somehow learn the visitor's sex while jumping over the court with it; the sound of its wings, for example, might reveal this to him; and when he

discovers that he is dancing with another individual of his own sex, he breaks off the performance. On April 26, and again two days later, I watched a green bird with an indistinct collar, which seemed to reveal the beginning of the molt into adult plumage, dance successively at both of the two isolated courts across the cornfield from the knoll. I detected no orange in this bird's collar, but its appearance suggested that it might have been formed by a number of brighter feathers still ensheathed. If young males were frequent visitors to the courts, one would expect to see more of them in transitional plumage. Yet with the exception of the individual just mentioned, I have neither record nor recollection of seeing Orange-collared Manakins in such plumage. Nothing appears to be known about the age and season when the full breeding attire is acquired in this species.

At the courts just referred to, which could be watched simultaneously from a blind set on a slight elevation above them, I sometimes saw a visitor go to one court, jump a few times with the owner, then proceed at once to the other court and dance with its owner. Usually the visitor went first to the court at my right (R), then to that at my left (L), which was larger, and whose owner was clearly dominant over his neighbor. Once for a few moments two green birds jumped simultaneously with the manakin on my left.

At court L, at 6:47 a.m. on April 28, 1959, I watched the only dance in which the green participant revealed itself clearly to be a female. After jumping across the court a few times with the resident male, she clung to the slanting base of a sapling that stood just within the edge of the bare area. The male mounted her and remained for a moment; then they resumed the dance. After a few more jumps, the male flew off, leaving her clinging to the same stem, as though she desired him to mount her again. Soon he returned and they jumped a little more, after which the female flew away.

In June, when the breeding season was drawing to an end, I watched male 3 jump back and forth over his court. Then, clinging to an upright stem beside it, he slid downward with vibrating wings for about an inch. Soon he repeated this performance, this time sliding downward several inches. This seems to correspond to the behavior of the male Blue-crowned Manakin when he alights on his nuptial perch in the absence of a female (p. 101). He acts as though a female were present.

The manakins' assembly, in which the female makes an uncoerced choice among the males who vie for her attention, offers excellent conditions for the operation of sexual selection as conceived by Darwin. Unfortunately, the males that I watched were, to my eye, all so much alike in plumage that I could discover no basis for preference. But they differed considerably in the constancy of their attendance at their courts and in the length of their performances. It was probably no accident that, in the one instance when I witnessed the consummation of the dance, the female had chosen, of the two males I had in view, the more persistent and vigorous performer. It appears that, at present, sexual selection in this species operates chiefly to promote persistent and vigorous courtship activities rather than to intensify the colors of the males.

Relations between mature males.—In the first half of the year, when courts are well established and courtship behavior is at its height, I have never seen two adult males dance together at a court. However, later in the year, when most courts are abandoned, they may dance together above one of the few existing courts or else-

where. As we have learned, a male rarely tolerates another court as close as 8 feet to his own; and usually, if the courts are less than 50 feet apart, the intervening vegetation is dense. But these males, who are simultaneously cooperators and competitors in their life's mission of attracting the females and fertilizing their eggs, by no means ignore their closest neighbors, or treat them with hostility. On the contrary, while waiting for a female to arrive, they frequently visit each other and rest close together, much as occurs in the Golden-collared Manakin (Chapman, 1935:495-496) and the Yellow-thighed Manakin.

The two manakins who rest close together do not behave as equals, but one seems ascendant over the other. At the two isolated courts, manakin L often visited R; and at the knoll assembly, manakin 3 visited both of his nearest neighbors, 4 and 12. Manakin L had a larger court than R, and his performances at it were longer and more frequent. Likewise, the court of manakin 3 was larger than those of manakins 4 and 12. The visits always took place on a perch much closer to the smaller of the two courts belonging to the manakins who came together. The twig where R and L often rested was only about a yard to the side of R's court and four feet above it. In other ways, too, the owner of the larger court showed that he had the stronger personality. Sometimes the two manakins rested for several minutes, a foot or so apart, with feathers all puffed out, making them appear quite roly-poly. If the dominant bird sidled closer to his companion, the latter slid away. Sometimes the submissive manakin turned his head from side to side, twitched his folded wings, and made his whole body quiver, continuing this for about a minute. His dominant companion might at the same time begin a similar twitching, but his movements were less pronounced and were stopped sooner.

Manakin L sometimes flew over the court of his submissive neighbor R. Once when this occurred they flew about in what seemed an angry mood, after which one chased the other out of sight. Even while R was absent, as he often was, L might rest much nearer R's court than to his own. But the approach of a green manakin would always send him straight back to his own area. While a male danced over his court with a green partner, I never saw another adult male interfere.

One morning, while I watched courts R and L, I heard annoyed calls of *chee-yú* coming from the neighboring undergrowth. Here I spied three adult males, two of whom appeared to be R and L, while the third must have come from a considerable distance. There was much flitting through the bushes and vigorous twitching of head, wings, and body, as the submissive bird does while his dominant neighbor rests close by him. I believe that all three of the manakins participated in this action. I inferred that both of the birds whose courts were before me resented the intrusion of the stranger.

In an area far from an assembly but in which I frequently found nests, I once watched two green birds who were evidently females twitch their bodies while they rested close together. I have never seen manakins of either sex engage in a fight.

Courtship activities of adult males after the breeding season.—As already related, court 3 of the knoll assembly was kept more or less clean throughout the long interval between the breeding season of 1959 and that of 1960. Court 11 was, after a period of abandonment, attended in September and October, but it was neglected again in November and early December. A new court, first noticed in October, was maintained until the middle of the following January. Although these courts were attended through part or all of the nonbreeding season, they did not receive such

constant care as courts receive while courtship is at its height from January to June. Leaves which I laid on them might remain for several days. On the other hand, they were sometimes promptly removed, even while I stood watching, in September and October.

In the second half of the year, when scarcely any courts were maintained, I sometimes heard a good deal of snapping and calling on my early morning visits to the knoll, although on other days I heard little from the manakins and saw less of them. Sometimes loud noises would draw my attention to a group of three or possibly four males jumping back and forth together, calling and snapping in the dense undergrowth, at a place where there was no court and had been none in the preceding breeding season. Intervening vegetation always prevented a satisfactory view of these proceedings, and before I could come close enough to see well the manakins would disperse. No green birds were evident when these bachelors' dances took place. Once I watched two adult males flitting back and forth above and close by court 3, one of the three courts which were recognizable at that period. Then one of these males jumped across the court and snapped a few times.

In October of 1959 there appeared to be a minor renaissance of courtship activity. When I discovered court 14 on October 5, two adult males spent much time flitting around it, and sometimes they leapt and snapped. Later in the month, I again found two adult males at this court, flying back and forth between the saplings beside and near it, but not with the sustained vigor of a dance. They called often, probably in protest to my presence, but snapped scarcely any. These two males seemed to be good friends, and I did not notice that one was dominant over the other. At times one or two additional adult males were near this court, making four in all. Apparently the few courts which were clean at this season attracted a number of birds.

The Satin Bower-bird, whose elaborate bower corresponds to the simpler court of the manakin, also engages in sporadic courtship activity in the nonbreeding season. "From time to time a male will revisit his territory to rebuild the bower and indulge in snatches of out-of-season bower display with freshly plucked flowers; or perhaps even to paint a little. . . . After brief display, the male will desert his territory and return to the flock as suddenly as he left it" (Marshall, 1954:30). The male Three-wattled Bellbird, on his periodic visits to lower altitudes, may sound his wooden notes day after day in the same part of the forest, although there is no reason to suppose that breeding occurs at this season and altitude.

Arboreal display.—Even at the height of the manakins' breeding season, I have sometimes seen very abnormal display. On April 25, 1955, I found an active, noisy company of Orange-collared Manakins in an area of second-growth woods adjoining primary forest. The party included a number of green birds and at least one male in full breeding plumage. There was much snapping of wings and uttering of the sharp *cheeu* note. The manakins kept well above the ground; and I saw the adult male perform his courtship dance in the second-growth trees, no less than 20 feet up. He jumped between ascending branches in the treetop, snapping as he darted back and forth with rapid reversals of direction, much as though he were performing above a court. The party moved gradually toward the primary forest, at the edge of which the male again displayed with snapping, no less than 60 feet up in a tall tree. This was odd behavior for a bird of the undergrowth. On April 27, 1949, Darwin Norby (MS) watched three adult males jumping and snapping in the crowns of small trees, about 25 feet above the ground, not far from the place where I later saw similar

behavior. Chapman (1935:504) noticed arboreal snapping and whirring by the Golden-collared Manakin in the breeding season, but the calls were "half-hearted." In the Satin Bower-bird, too, arboreal displays are sometimes witnessed, in the feeding flock (Marshall, 1954:30-31).

Courtship behavior of young males.—As we have already learned, a male in greenish plumage sometimes dances with an adult at his court at the height of the breeding season. Perhaps such behavior is frequent, but the difficulty of distinguishing the majority of the young males from the females makes it impossible to learn how often it occurs. On the other hand, green birds that are evidently males sometimes perform with each other, and at times they dance alone.

On April 23, 1957, I found an adult male dancing above a bare area that seemed to be a court, beneath a tall second-growth thicket. Setting up my blind, I watched at this point for two hours on the following morning, without seeing an adult male. Toward the end of my vigil, a green manakin jumped a little in front of me. Ten minutes later, three green birds arrived and simultaneously shot back and forth over the bare area, keeping out of each other's way, alighting on upright stems around the edges of the court and sometimes descending to it, to rise at once and go to one of the stems. They made loud *snap*'s and uttered sharp *cheeu*'s. In the distance, I caught glimpses of similar performances, and the performers were mostly in green attire. No courtship assembly was established in this area; possibly the bare spots which resembled courts had been made by the scratching of the domestic chickens that foraged here. While Norby watched the three adult males dancing in the treetops, four green birds performed near them in the undergrowth, jumping back and forth between saplings and snapping but displaying little coordination in their movements.

On October 14, 1944, I watched a solitary green manakin jumping beneath tall second-growth woods. In a spot where the young trees stood close together and the deeply shaded ground was almost bare of herbage, he darted rapidly from stem to stem, making a loud *snap* with each leap. He repeated this performance again and again while I watched. There was no bare court at this point, either then, or in the preceding years, or in those which followed. Although this green manakin bore no trace of the adult colors, the bird was evidently a young male, practicing the nuptial display before he had acquired the nuptial dress.

On the knoll, in the second half of the year, I sometimes found two green manakins jumping and snapping together over one of the few recognizable courts. Once two green birds jumped over a court in company with an adult male. These out-of-season performances are most exasperating to the observer, who hears them in the distance and laboriously makes his way through obstructing vegetation toward them, only to have them cease when he comes within view.

Here, again, we notice parallel behavior in the manakin and the Satin Bower-bird. Males of the latter do not acquire full breeding plumage until they are from four to seven years of age, although they reach full breeding condition before acquiring a single spot of the darker adult color. The green young males make primitive display platforms which are frequented by a number of green birds of both sexes and occasionally by a blue adult male (Marshall, 1954:36-37).

Relations with birds of other species.—When an Orange-billed Sparrow hopped over court 3 and delayed there, pecking a little at the ground, manakin 3 jumped over the intruder's head a few times but made no attempt to drive him away.

Similarly, a Streaked-chested Antpitta which stood on court L and uttered a series of full, melodious whistles was not molested by the manakin. I have on several occasions watched a female or immature male Blue-crowned Manakin approach courts whose owners were present, without exciting them to the activity that a green bird of their own kind would have stirred up. Manakin 3 even ignored a Blue-crowned Manakin in female plumage who rested on his favorite perch beside his court. Clearly, these males could distinguish the bright green, dark-legged Blue-crowned Manakins from the slightly larger, duller green, orange-legged females of their own kind. I never received the impression that the intruding Blue-crowned Manakins were attracted by the males so different from those of their own species. Apparently they were merely foraging through the area of the assembly.

Chapman (1935:520), experimenting with stuffed birds, concluded that the male Golden-collared Manakin failed to distinguish the female Yellow-thighed Manakin from the female of his own kind. Females of these two species resemble each other more closely than do females of the Orange-collared and Blue-crowned manakins. In addition the latter species often repeats a soft trill quite unlike any note that I have heard from any other manakin. In the forests of El General, where four kinds of small manakins occur and three kinds are common, I have never found evidence of hybridization.

A morning at the courts.—I shall end this account of the Orange-collared Manakins' courtship by giving an excerpt from my journal, which brings together in their living context and true temporal sequence many of the activities which, for clearness, it was necessary to treat separately in the foregoing discussion. These observations were made at the two isolated courts, R and L, which could be watched simultaneously.

April 28, 1959, 5:57 a.m. I arrive, without hearing manakins as I approach.

- 6:05. L and R arrive at about the same time with rolling *snap* and *cheeu*. Then more *cheeu*'s. They jump back and forth over their courts without snapping.
- 6:10. A young male with the suggestion of a collar dances a little with R and then with L.
- 6:13. R makes seven jumps over court and one from the ground.
L makes four jumps and one from the ground.
- 6:14. R makes four jumps and one from the ground.
L makes two jumps and one from the ground.
- 6:15. L dances with green bird briefly.
- 6:20. Both males go off.
- 6:22. L returns.
- 6:30. L jumps over court nine times and rises once from ground, ending his display by pulling a small green leaf from a low plant beside his court and carrying it off a few feet before dropping it. (He sometimes ends a dance by pulling at a large green leaf beside the court but fails to detach it.)
- 6:40. R jumps over court three times then carries a dead leaf from it.
- 6:42. L jumps over court 12 times. R dances at same time.
- 6:47. A female visits L. [Here follows the account, already given on page 128, of a dance that led to coition.]
- 6:55. R dances several times.
- 6:58. L engages in a subdued dance, keeping within a few inches of the ground and sometimes alighting on it, giving low *snip*'s instead of loud *snap*'s. He terminates the dance by carrying a leaf from his court. Then he goes to perch close to R, by R's court. They rest with feathers puffed out, making them look very round.
- 7:12. They fly away.
- 7:15. R returns.
- 7:30. I place on each court two small green leaves, two red bracts of *Cephaelis*, and a segment of yellow banana peel, much longer than the manakins.

- 7:43. A green bird flits silently through the neighboring undergrowth; but the males seem not to notice her, although at least one of them is nearby.
- 7:55. A male returns to near the courts but seems not to notice what I placed on them.
- 8:00. Neither court has been visited for at least half an hour, during which I heard occasional calls and rolling *snap's* from the neighboring undergrowth.
- 8:05. At last L returns and sees objects on his court. He clings to the leaning base of the sapling and pecks or pulls gingerly at the peel, uttering a low *chee* and *cheeu* (much like the call already noted, but in a higher, thinner voice, as though irritated). He tries to lift the peel and fly off with it rather than to drag it away, and at last he succeeds in carrying it just outside the court, although its weight perhaps exceeds his own. Then he alights on the court beside a green leaf, seizes it, and flies off with it. He removes the second leaf in the same way. Then he rests a few yards from the court, leaving the two dull red bracts on it.
- 8:15. R now alights beside the peel on his court, seizes it, and flies up just high enough to flip it over the edge of the court. He utters *chee* and *cheeu* like L. He neglects the leaves and bracts in the middle of his court.
- 8:20. L flies back and forth over court with the red bracts, without snapping, then goes off without removing them. A Streaked-chested Antpitta walks(?) on to court L, where it stands on its long, slender legs, facing me, rhythmically puffing out and contracting the streaked feathers of its breast. Then it half opens and shuts its wings several times. It utters a rapid series of soft, clear notes, melodious and plaintive, diminishing in volume.
- 8:30. A manakin has continued to rest between the courts, doing nothing. Now he leaves. I go. The morning has been cloudy.

NEST BUILDING

From this point onward in our account, interest centers in the greenish females, who alone build the nest, incubate the eggs, and rear the young. I have never known a male manakin to participate, even briefly, in nesting activities, and I have found no mention of such participation in published reports. Just as male hummingbirds, which like manakins form courtship assemblies and in general remain aloof from the nest, attend the nest in a few species which appear to be exceptional, so it would not be surprising to find male manakins of some kinds helping to rear the nestlings. But this is far more likely to occur in those less specialized species of which the sexes differ little than in strongly dimorphic species like those of *Manacus*, *Pipra*, and *Chiroxiphia*.

Rarely, in years when occasional showers keep the vegetation in El General fresh through February, an Orange-collared Manakin may begin her nest toward the end of this month. In 1958 I found one nest, and in 1960 two nests, that were built toward the end of February. One of these nests was newly begun when discovered on February 28; and another had evidently been completed by this date, for the first egg was laid in it about March 1, 1960. But building does not become widespread before mid-March, and the nesting season does not reach its height until the following month.

The nests are placed in a variety of situations, ranging from the heavy primary forest to the taller second-growth thickets, shady pastures, coffee plantations, and even dooryards with abundant trees and shrubbery. Sometimes they are built above a narrow, shady watercourse or even a wide, noisily rushing mountain torrent. But they seem never to be situated in the low, densely entangled thickets that have grown for only two or three years on resting land. The manakins prefer second growth that has reached a height of 25 feet or more, with a closed canopy and rather sparse lower vegetation, through which a man can walk without much difficulty. About half the nests that I discovered before 1948 were in the primary

forest, often near its edge. Since then, the majority have been beyond the forest. Just as, with increasing deforestation, the males are locating their courtship assemblies in secondary woods; so the females show an increasing tendency to nest in areas where man has profoundly altered the character of the vegetation. But they often choose situations far too open for the courtship assemblies.

Often the female builds far from the courting males, and I have found nests up to 1000 feet from the forest and about a quarter of a mile from the nearest known assembly. Rarely a nest is close to, or even in the midst of, an assembly. In April of 1959, I found a nest with two eggs in the large knoll assembly, 40 feet from one court and 60 feet from another. On the following day, I watched another female begin her nest in a small sapling only 12 feet from one active court of this assembly and 28 feet from another court. This nest advanced with unusual slowness, and I never found an egg in it. About the beginning of March of the following year, a new nest was begun in the same small sapling, but the nearest court was now somewhat farther away. This nest was also built with extreme slowness, and I found no egg in it until March 24. Apparently only one was laid. Neither of these nests in the knoll assembly produced a fledgling, although the female who built 40 feet from the nearest court hatched nestlings which vanished after a week or so. In view of the very small proportion of all manakins' nests which are successful, I have no reason to attribute the failure of these two nests to interference by the surrounding males. The passage of these nesting females through the assembly often started an outburst of calling and snapping; but, as we have seen, the males try to attract, but do not pursue, the females. On Barro Colorado Island, I found a female Golden-collared Manakin building 40 feet from an occupied court. The nest was completed, but apparently the female failed to lay in it.

The Orange-collared Manakin's slight, shallow nest is suspended between the thin arms of a small branch that forks in the horizontal plane. More rarely it is attached to two diverging branchlets of a sapling, in which case it will be close to the upright main stem. In the forest and thickets, a shrub or sapling of the abundant melastome family often furnishes the nest site. In plantations, a coffee bush is not infrequently used. However a densely leafy orange or mandarin tree is more attractive to the manakins, who often choose one of these citrus trees that happens to be growing in a coffee plantation in preference to the scores of coffee bushes that surround it. In our dooryard, the adjoining shady pastures, and a neighboring small coffee grove, I have found no less than 14 nests in orange and mandarin trees. A nest beside a woodland path was in the middle of a broad, lacy frond of a young tree fern, between the rachis and a primary pinna, and the large leaf of a melastome formed a roof about it. This exceptional and most attractively situated nest was unfortunately knocked down by a falling stem before the eggs hatched.

The nests are usually situated lower than a man's head. Of the 80 nests whose height I have recorded, 66 were between 2 and 6 feet above the ground. Only two of these nests were below 2 feet: one at 19 inches and one at 20 inches. Of the remaining nests, ten were between 6 and 8 feet up. One was about 12 feet above the rushing water of a mountain torrent. The highest was 18 feet up in a tall bush standing in second-growth woods. In this instance, however, the shrub grew close to the foot of a cliff about 12 feet high. Apparently the building manakin had approached her nest from the higher ground at the top of the cliff.

Once, while sitting in my blind in the knoll assembly, I had the good fortune to witness the very first steps in building a nest. Early in the morning, I happened to notice a female snuggling in the top of a low sapling, as though building or investigating a nest site. When I examined this sapling half an hour later, there was still no trace of a nest; but after another hour I found a single strand of cobweb stretched between the bases of two diverging horizontal branchlets, with just enough space for a nest between this filament and the upright main stem. The ends of the filament were wrapped around the branchlets.

At this point, I turned my attention from the male whose court was in front of me to the building female to my right. From 8:35 to 9:35 a.m., she visited the nest site six times; from 9:35 to 10:05, four times. On some visits, she came with fibers or rootlets; on others, I noticed nothing in her bill, but probably she brought more cobweb. She often sat in the fork and made shaping movements with her body. When I left at 10:05, the strand of cobweb joining the twigs had broken. A little cobweb and a few rootlets were attached to the supporting branches, but some of the manakin's contributions had fallen. This building female was not molested by the surrounding males. One male, whose court was only 12 feet from the nest site, sometimes advanced toward her and called *cheeu* as she approached, but he did not come near her nor evince any interest in the nest itself. After this good beginning, this nest, as already told, progressed so slowly that two weeks passed before it was half finished.

Norby (MS) watched a building female gather caterpillar silk from a leaf in a thicket. Since she found no twig where she could rest while detaching the silk, she hovered momentarily on wing while she pulled a little from the leaf. Then she returned to a perch with her acquisition, and after resting briefly she made another attack on the silk. Sometimes, with closed wings, she hung from it by her bill. After four or five such visits, she had enough of the material to satisfy her and took it to the nest site, where she carefully wrapped it around a branchlet.

After plastering a certain amount of cobweb or insect's silk over the supporting arms, the manakin stretches vegetable fibers from one to the other, thereby forming a loose platform or hammock in the crotch. Working other fibers into this weft and often wrapping them around the supporting twigs and pulling their ends up through the bottom of the nest, she strengthens her fabric until she has a substantial concave receptacle, which she then lines with finer materials. Manakins seem rarely to work fast, and five or six visits in an hour is the maximum activity that I have recorded. Usually visits are so widely spaced that it is difficult for the watcher to maintain interest in the proceedings.

The time required for building a nest is variable and difficult to determine with exactness. One morning Norby found a few shreds of dry grass hanging from a crotch in a thicket. By 8:40 a.m. the next day this crotch held a well-formed cup, which had been made in an interval of 24 hours or a little more. At 2:45 p.m. on the same day, an egg was present in this hastily built nest. Usually, however, construction takes considerably longer, probably three or four days. From five to nine days often elapse from the beginning of building to the laying of the first egg.

The completed nest is a shallow cup or hammock attached by its rim to two horizontal twigs, between which it is suspended. Usually light but rarely dark in color, it is constructed of fine materials, including strips of inner bark, black or brown fungal filaments or rhizomorphs, fine fibrous rootlets, and frequently liberal



Fig. 7. Nest and eggs of Orange-collared Manakin, a typical nest of *Manacus*. Barro Colorado Island, Canal Zone, May, 1935.

quantities of shredded bast fibers, especially in the lining. Some nests consist almost wholly of fine, light-colored fibers, others of the thread-like divisions of richly branched inflorescences of grasses. Cobweb liberally applied reinforces the attachment of the nest to the arms of the fork and is sometimes spread over the outer surface. Often the fabric is so thin and open that the eggs may be seen through the bottom; but some nests are of thicker, more solid construction. As a rule, they are neatly finished, with little or no material hanging loosely beneath them, although exceptionally a few strands dangle conspicuously. They almost never have a number of dead leaves or pieces of moss attached to the lower side, as in nests of manakins of the genus *Pipra*. In a single nest of the Orange-collared Manakin a few dead leaves, up to 6 inches in length, dangled beneath the structure, making it bear, at the first glimpse, considerable resemblance to a nest of the Blue-crowned Manakin. Possibly the leaves had not been placed there by the builder. A typical nest measured 3 inches in diameter by 2 inches high. The concavity was $2\frac{1}{4}$ inches in diameter by $1\frac{1}{2}$ inches deep; but some nests are scarcely an inch in depth.

The cryptically colored female Orange-collared Manakin makes the smallest nest that will safely hold her two diminutive eggs. Sometimes one of them rolls out of the shallow receptacle, especially if the sitting bird is alarmed and leaves suddenly.

THE EGGS

Rarely, as in 1958 and 1960, I have found eggs in the first few days of March. However, few sets are laid before the middle of the month, and the peak of laying is not reached until April and May. Although on one occasion less than a day elapsed between the completion of a nest and the deposition of the first egg, often this interval is from four to eight days, and once it was about 14 days.

Both the first and second eggs of a set are usually laid in the middle of the day or in the early afternoon rather than in the early morning, as is true of many passerine birds. I have a record of one first egg that was laid before 11:45 a.m. One was laid between 12:15 and 1:30 p.m., one between 12:10 and 2:25 p.m., and another between 11:00 a.m. and 5:00 p.m. This last-mentioned egg was probably laid at about 2:00 p.m., when I found the manakin sitting far forward in the nest with her foreparts held high, in a posture that contrasted strongly with the horizontal position of an incubating manakin.

The second and last egg of a set seems invariably to be laid two days after the first, so that one knows when to watch for its appearance and can accumulate more records of the hour of laying. Fourteen of these second eggs were laid after 11:00 a.m.; eight of these appeared between 11:00 a.m. and 1:20 p.m., two were laid between 11:00 a.m. and 12:15 p.m., and one additional egg was laid between 10:00 a.m. and 12:00 noon. On the other hand, seven eggs are known to have been deposited after midday. The latest definite records are of an egg laid between 1:15 and 2:25 p.m. and another laid between 1:35 and 3:35 p.m.

I have records of 69 nests with two eggs or nestlings. Four nests contained a single egg; but considering how easily eggs are knocked from the shallow receptacle and other causes of loss, it is not improbable that another had been laid in these nests. The eggs are pale gray or pale blue-gray, heavily mottled with shades of brown. On some eggs the dark marks are rather uniformly distributed over the whole surface; on others, they are concentrated in a wreath around the large end or around the middle, leaving the two poles only lightly pigmented. Eggs of the same set may vary considerably in this respect. The brown blotches on the sides are usually elongated in the direction of the long axis of the egg. The measurements of 55 eggs average 20.5 by 14.9 millimeters. Those showing the four extremes measured 23.0 by 15.9, 19.4 by 14.7, and 21.4 by 14.3 mm.

In 80 nests in the valley of El General, 2000 to 3300 feet above sea level, eggs were laid as follows: March, 13; April, 25; May, 29; June, 10; July, 1; August, 1; September, 1. In view of the fact that the courts of the males are generally neglected after June, the records of eggs in the following months demand consideration; we wish to know whether these eggs were fertile. A set laid on July 6 and 8 yielded two nestlings. The August record is based on a nest with two unfeathered nestlings shown to me on August 29; but I do not know whether the set which I found, already completed, on September 10 hatched. We have already learned that an exceptional court may be kept more or less clean throughout the year.

INCUBATION

In the two days which separate the laying of the first egg and the second, the female is sometimes found covering the former, but more often the nest is unattended in this interval. At nest 68 I saw the manakin sitting on her single egg



Fig. 8. Nest of Orange-collared Manakin in orange tree in dooryard. El General, Costa Rica, May, 1965.

in the late afternoon of May 4, the day on which it was laid; but she was absent after nightfall. On May 5 she was absent at each of my five visits between 7:00 a.m. and 1:25 p.m. Ten minutes after the last of these visits, I found her covering the single egg in the rain which then began, and she was present also in the late afternoon. On the morning of May 6, she was sitting four of the five times that I visited her, and later in the same day she laid her second egg. The difference in the time of hatching of the two eggs likewise reveals that the first egg receives some, but far from continuous, incubation before the set is complete. The first egg often hatches some hours before the second, and once it hatched at least 19 hours before the second; but I have not known the first egg to hatch two days before the last, as should happen if incubation in this interval were fairly constant.

Plainly clad in olive-green, the female Orange-collared Manakin is far from conspicuous as she sits motionless amid the green foliage on a nest so shallow that it leaves most of her body exposed. Like other manakins, she permits an extremely close approach by man. With rare exceptions, the more timid of them have remained at their post on the eggs until I came within a yard or two. The braver females have continued steadfast while I stood looking at them with my face a foot or less from theirs. Sometimes I have been almost able to touch them, but none has permitted this familiarity before the eggs hatched, for they do not sit quite so firmly as some female Yellow-thighed Manakins. Sometimes, while walking through the forest, I have stirred up a female Orange-collared Manakin who has clung to her nest until I brushed past it, her sudden departure revealing its position to me. The manakin who built her nest 12 feet above the middle of a broad stream evidently felt exceedingly secure as she sat over the rushing water. I could not make her flee by shaking the long supporting bough, nor by standing in the river below and waving my hat at her.

At a forest nest which I often visited, I almost always found the female manakin covering her two eggs. Her nest was at the level of my eyes, and she would permit me to bring them within a foot or less of her own brown eyes before she jumped off and flew down among the bushes, where she vanished without vocal protest. One morning she allowed me to advance my face a few inches closer to her than ever before, and her departure revealed a single newly hatched nestling, not yet dry. When I returned early that same afternoon, the manakin was sitting, but now she flew from the nest while I was still a good way off. As I came closer, I saw that only the thin outermost layer of the structure remained. The greater part of its material lay on the ground; nestling and unhatched egg had vanished. The female had been brooding emptiness in the shadow of a nest! A pair of Fiery-billed Araçaris with two fledglings in the treetops above noisily protested my intrusion and made me suspect that they were the despoilers of the nest.

At a nest situated eight feet up in an orange tree in front of my house, I studied the rhythm of incubation from 5:35 a.m. to 12:05 p.m. on May 28, 1946, and from 12:47 to 5:30 p.m. on May 30, a nearly rainless afternoon such as is rare at this season. The female manakin began her day while the light was still so dim that I could not with certainty follow her movements; at 4:16 p.m. she settled on the nest, apparently for the night, since she had not budged when I went away in the rain at 5:30. The 14 completed sessions that I timed ranged from 10 to 64 minutes in length and averaged 33.9 minutes. An equal number of recesses varied from 3 to 17 minutes and averaged 7.1 minutes. During 9.5 hours the manakin spent 82.6 per cent of the time on her eggs. Her longest diurnal session was taken in the last hour of the forenoon; her next longest, from 3:04 to 4:04 p.m.

On leaving the nest, she usually flew into the crown of the orange tree, thence across the open pasture to the edge of the woods, 50 feet away. More rarely she flew directly from the nest to the woodland, without first vanishing into the foliage of the orange tree. At the edge of the woods was a bush of the melastome family laden with small black berries, which provided food for the manakin and many birds of other kinds. On returning from her usually brief absence, she invariably went first to the top of her orange tree, entered among its dense foliage, then dropped down to her nest, approaching it from the inner rather than the outer side and making her movements difficult to follow. She did not attack small birds of other species that came near her nest, and she was perfectly silent while I watched her. At times she stood for many minutes on the nest's rim, billing something in the bottom; but just what she tried to accomplish I could not learn.

Twelve years later, I watched a manakin incubate in a different orange tree in the same pasture. This nest was only 30 inches above the ground; and to study it at close quarters, I set a blind four feet away. To conceal myself was perhaps an unnecessary precaution, for the manakin sat steadfastly on her eggs while I set the cloth tent near her. On April 8, 1958, six days after this manakin laid her second egg, I watched her from 12:15 until 6:00 p.m., when the light was failing. On the following day, I resumed my vigil in the dim light at 5:25 a.m. and continued until 12:15 p.m. While I watched this nest the weather was fair, although the sky clouded over in the late afternoon. In the course of 12.5 hours, this manakin took eight sessions on the eggs, ranging from 17 to 258 minutes and averaging 71.4 minutes. Her nine recesses varied from three to 25 minutes and averaged 12.2 minutes. Computing by these averages, she spent 85.4 per cent of the day on her

eggs. Computing on the basis of the total time elapsed between 5:30 a.m. and 6:00 p.m., which may be taken as the manakin's period of daytime activity, her constancy in incubation was 83.6 per cent.

Like the former female, this manakin began her first outing of the day very early, while the light was still dim. Her sessions lengthened greatly as the day grew older. One long spell of sitting, lasting 4 hours and 18 minutes or 258 minutes, occupied most of the afternoon. Her two absences in the afternoon lasted only 15 and 20 minutes, and her longest recess of 25 minutes came in the middle of the forenoon.

To leave her nest, this manakin jumped up to its rim and promptly took off from there, sometimes flying directly out into the pasture but at other times passing through the foliage of the orange tree. On returning, she always made her approach inconspicuous by passing through the foliage of the tree, as did the first female. Except for the occasional whirring of her wings as she took flight, I heard not a sound from her all day. She often changed her orientation in the nest, facing now in one direction and now in another, and from time to time she rose up to turn her eggs with her bill or merely to look down at them. In the course of the morning she turned her eggs at least 16 times, but in the afternoon she did so only five times.

Darwin and Barbara Norby kindly gave me records of incubation at two nests, made while they studied with me in 1949. The two manakins that they watched, each on the twelfth day after the laying of the second egg, sat much less constantly than those that I studied. In 8 hours and 19 minutes, the first of these manakins took 22 sessions ranging from 3 to 41 minutes and averaging 15.2 minutes, while her 22 recesses varied from 2 to 16 minutes and averaged 7.5 minutes. She spent 66.8 per cent of the observation period on the nest. In 8 hours and 43 minutes, the second manakin watched by the Norbys took 20 sessions ranging from 6 to 28 minutes and averaging 15.7 minutes, with 21 recesses that varied from 3 to 32 minutes and averaged 10 minutes. She covered her eggs for only 61.0 per cent of the first nine hours of the day. However, this record is based only on sessions that were watched until the bird left the nest. The last of these completed sessions ended at 2:33 p.m., to be followed by a recess of five minutes. Soon after her return from this excursion, rain began to fall and continued until it drove the observer, Mrs. Norby, to shelter at 4:20 p.m. The manakin, which had already been sitting for 102 minutes, remained on her eggs in the downpour. The hard afternoon rains, so frequent in the months when the manakins nest, cause the incubating females to do most of their foraging in the forenoon; but, as is shown by the record that I made on clear days in early April when rains are much lighter, this schedule is maintained even in dry weather.

At night, the manakin sleeps on her eggs with her feathers so widely spread that they form a mound covering the nest from rim to rim and rising well above it. Her head is turned back and buried in this downy mass, and her only distinguishable feature is her short, narrow tail, sticking out from one side of the mound. Her contour feathers are not, however, so loosely spread as those of antbirds sleeping in the nest, which appear to be detached from the bird and dropped in a fluffy pile.

At nest 29, the second egg was laid between 12:10 and 1:30 p.m. on April 13; it hatched between noon and 5:15 p.m. on May 2, giving an incubation period of between 18 days and 22.5 hours and 19 days and 5 hours. At nest 30, the second egg was laid between 10:00 a.m. and 12:00 noon on May 19; it hatched between

5:40 p.m. on June 6 and 6:40 a.m. on June 7, after an incubation period of between 18 days and 6 hours and 18 days and 21 hours. At nest 46, the second egg was laid between 11:00 a.m. and 1:00 p.m. on May 8; it hatched between 5:45 p.m. on May 27 and 5:45 a.m. on May 28, giving an incubation period of between 19 days and 5 hours and 19 days and 19 hours. At nest 65, the second egg was laid between 9:00 a.m. and 4:00 p.m. on April 2; it hatched about 4:00 p.m. on April 20, after an incubation period of between 18 days and 18 days 7 hours. These and four other less precise determinations show that the incubation period varies from a little over 18 days to nearly 20 days, with an average of about 19 days. At one nest of the Golden-collared Manakin, Josselyn Van Tyne found the incubation period to be 19 days (*in* Chapman, 1935:506).

THE NESTLINGS

The newly hatched manakin has pink skin, shaded by sparse gray down, and tightly closed eyes. The interior of its mouth is yellow. During the first few days after the nestlings hatch, the female clings to the nest even more closely than while she incubated. One female with four-day-old nestlings allowed me to touch her tail lightly while she brooded, but this is unusual; as a rule, the parent bird darts off while the approaching hand is still a few inches distant from her. Another female with young nestlings remained steadfast on her nest, which was only 25 inches above the ground, until I almost touched her; then she dropped to the floor of the forest and fluttered over it for several yards, until she was nearly screened from my view by the undergrowth. This was the nearest approach to injury simulation that I have seen in the Orange-collared Manakin; but the bird disappeared too quickly to give the impression of being disabled or to tempt one to follow with the prospect of overtaking her. The manakin with the relatively high nest in the orange tree continued to cover her naked nestlings, or stood on the rim of the nest above them, until I shook the surrounding foliage. Then she would either dart into the center of the tree and thence drop downward, or else she would descend more directly, until almost in contact with the pasture grass below, over which she would skim for possibly 20 feet. She also left too rapidly to suggest that she was disabled. Other parents of nestlings have acted similarly. However, one female whose eggs were hatching jumped from her nest and clung to neighboring upright stems, a few inches above the ground, where she quivered her spread wings somewhat in the manner of the Blue-crowned Manakin in similar circumstances.

On June 12, 1946, when the two nestlings in the orange tree were two days old, I devoted five hours of the morning to watching their nest. The female alone attended them; no male manakin was ever seen in the neighborhood of the orange tree. In the five hours, the female brought food 11 or 12 times, or at the rate of about 2.4 times per hour. On returning to the nest from the nearby woodland, she would fly first into the crown of the orange tree, as she had done when she was incubating, then suddenly drop down from the abundant dark foliage to the rim of the tiny nest. This indirect approach made it difficult to see what she brought; for the moment that she alighted beside the nestlings, she bent down and began to feed them. As far as I saw, she brought all the nestlings' food inside her mouth or throat and held nothing visibly in her bill. Most conspicuous among the articles that she gave the nestlings were small, shiny, black berries, apparently of a shrub of the melastome family that fruited abundantly at this season. These berries were

brought on almost every visit to the nest and fed to the nestlings whole or slightly crushed. Apparently the tiny nestlings often experienced difficulty in swallowing them, for the female would pick them from the nest again and again. There were also small insects of various sorts, and one inch-long, naked, brown caterpillar which was offered to the nestlings many times over. After each presentation of the caterpillar to the nestlings, the parent would draw it almost wholly back into her mouth, then extrude and offer it once more. At last it vanished—swallowed, I believe, by one of the nestlings. After delivering food, the parent ate the nestlings' droppings.

In the five hours, the manakin brooded 11 times, for periods ranging from 3 to 16 minutes and averaging 10.5 minutes. The intervals between brooding ranged from 6 to 48 minutes, but during the longest period when the female was not brooding she was standing beside the nest. Her next longest period off the nest was 19 minutes, of which she spent four minutes standing on the rim of the nest. While resting beside the nest, she would busily pluck or push something in its bottom. First she worked from one side, then from the opposite side. Now she was occupied with the inside of the nest, now she turned outward and leaned over to pluck at the exterior with her bill. Probably she was ridding the nest of ants. I saw her take some minute creature in her bill, and after her departure I discovered a small ant on the supporting twig.

When the nestlings are about nine days old, their pinfeathers, which have grown long, begin to unsheathe, and two or three days later the young birds appear well feathered. When the two young manakins in the orange tree were 13 days of age, I again watched them for most of the morning. They received their first meal at 5:42 a.m., and in the next five hours they were fed a total of 17 times. Sometimes they were given food at the rate of 2 to 4 times in one hour. The average rate for the entire period was 3.4 feedings per hour for the two young birds.

Arriving from the neighboring woodland, the parent would, as formerly, fly into the top of the young orange tree, well above the nest. Her throat was swollen with food. Sometimes her bill was tightly closed, but at other times she held it partly open, apparently because the fullness of her throat made closure impossible. Once she held an insect in her bill, but as a rule no food was visible in it. She would remain perched in the treetop, motionless, for from 2 to 8 minutes, then drop down to the nest and promptly begin to feed its occupants. She regurgitated the articles of food from her throat one or two at a time and placed them in the upturned open mouths of her nestlings, alternately. The little, sweetish, black berries of a shrubby species of *Miconia* still formed the great bulk of the nestlings' meals. These were delivered whole, or rarely slightly mashed, on every one of her visits to the nest. Sometimes a few small insects were brought along with the berries. The rapidity of the parent's movements made it difficult to learn the number of separate articles brought on a single visit to the nest; but often there seemed to be seven or eight, and once I counted nine.

After delivering the food, the parent would on rare occasions fly promptly away, but nearly always she lingered beside the nest for from 2 to 7 minutes. In all, she remained standing on the rim 15 times, totalling 57 minutes, or on the average about four minutes each time. Sometimes while standing there she would pluck at the nest, apparently removing small insects, but more often she stood inactive and almost motionless, as though guarding her nestlings. Since they were feathered, she no

longer brooded them on fair days. On leaving, she usually flew back into the center of the orange tree, thereby making her departure as inconspicuous as her indirect approach. More rarely she flew directly out across the pasture to the neighboring woodland, where a fruiting *Miconia* bush supplied an abundance of easily gathered food.

After receiving a meal, the young manakins often evacuated by pushing their hindquarters over the edge of the nest and allowing their droppings to fall directly to the ground. Although the female was often standing at the nest when this occurred, she never made a move to take the waste matter, as passerine birds of most kinds would have done. There was a conspicuous deposit of blackish excrement on the grass beneath the nest. The manakin resembles some of the hummingbirds in removing droppings from the nest when the nestlings are small and in later permitting the young to dispose of them over the nest's edge.

From time to time, the thirteen-day-old manakins preened, or stood up in the nest to flap their wings, although the remiges were still largely ensheathed and exposed little surface.

Before these nestlings were feathered, their nest began to break away from one of the arms of the fork that supported it, and I sewed it up with thread for greater safety. The female brooded the nestlings by night until they were at least 14 days old and well feathered. Sometimes, as the day waned, I watched her standing beside the nest in statuesque immobility, continuing so for a quarter of an hour or more, until I stole away in the dusk. Returning after nightfall with a light, I would find her brooding. Late in the afternoon of June 25, when these nestlings were 15 days old, I found both perching on the twig that supported their nest. One nestling was several inches away from the nest. Forty minutes later, one was resting in the orange tree about two yards from the nest; the other had gone farther and could not be found. The former returned to pass the night roosting on the supporting twig close by the nest, and it remained there until the middle of the following morning, when it, too, vanished. This is probably the usual method of quitting the shallow nest, for I have found several other fledglings perching close by their nest shortly before they vanished.

Of the many nests of the Orange-collared Manakin that I had found over a decade, this nest in the orange tree was the first observable nest, of those discovered before the eggs hatched, that escaped predators until the young were fledged. The following year, a manakin, doubtless the same individual, returned to build in the same tree, a foot or two from the earlier site. In 1946, she laid her first egg on May 20; in 1947, on May 17; and in both years she reared two young at least to the age of flight.

In subsequent years, I have followed other nests to a successful conclusion. In all, I have learned the period in the nest of 13 young manakins. Three left two nests at the age of 13 days; four left three nests at 14 days; five left three nests at 15 days; and one departed at the age of 17 or 18 days. The development of this last nestling was obviously retarded. It was hardly feathered before its thirteenth day, and I found its mother brooding it in the rain when it was 15 days old. Two days later, in the afternoon, I found the seventeen-day-old manakin perching a few inches from its nest. On my approach, it fluttered to the ground and tried to hop away; it could fly no better than other nestlings when only 13 days old. Next day it had vanished.

Fledglings are clad in olive-green plumage so plain and unrevealing that one would hardly recognize them as manakins but for their brighter legs, which range from yellowish to orange-pink in color. One young manakin, with tufts of gray natal down still sticking to its crown and hindneck, had probably lost its mother. On a drizzly afternoon, it repeated with scarcely a pause a full, plaintive *peer*, unlike any note of the adults. At intervals it flew straight and swiftly to another perch and continued its calls, but no adult responded to them. Somewhat older juveniles repeat a thin, whistled *psee*.

THE SECOND BROOD

In 1960, when breeding began unusually early after a showery February, I found on March 4 a nest from which two nestlings departed on April 5. The eggs from which they hatched had probably been laid about March 1 and 3. On May 18, this nest again contained two eggs, which vanished a week later. This nest is my only evidence that the Orange-collared Manakin may attempt to rear a second brood. In view of the very high percentage of nests which are destroyed, most late sets of eggs are probably replacements rather than second broods.

NESTING SUCCESS

The Orange-collared Manakin is a satisfactory bird to study for reproductive success. The height and structure of the nests make them easy to examine without disturbing them, and perhaps making them easier for predators to find. Table 4, column A, summarizes the results of 54 nests of known outcome. Of these nests, 11, or 20.3 per cent, escaped destruction until the young were ready to leave, hence they have been counted as successful. Of the 105 eggs in these 54 nests, 17, or 16.2 per cent, yielded fledglings. All of these nests were found before the eggs hatched, but some were not seen until after the eggs were laid. Since predation begins as soon as eggs are laid, a nest found after some days of incubation has already survived part of the hazard to which it is exposed; and a sample containing such nests is a partly selected sample. Accordingly, I have made a separate computation for the 23 nests of known outcome that were found before the set was complete (column B). These nests are included among the 54 that appear in column A. In the larger sample, I am in some cases uncertain whether the nest was despoiled before or after the eggs hatched; but more frequent visits were made to the nests for which I had recorded the dates of laying, and I know that only 17 of the 46 eggs in these 23 nests yielded

Table 4
Nesting Success of Orange-collared Manakins

	A	B
	Nests found before eggs hatched	Nests found before comple- tion of set
Total number of nests	54	23
Nests which yielded a fledgling	11	3
Per cent of successful nests	20.3	13.0
Total number of eggs	105	46
Number of eggs which hatched		17
Per cent of eggs which hatched		36.9
Eggs which produced a fledgling	17	6
Per cent of successful eggs	16.2	13.0

nestlings, of which six survived until they were old enough to leave. (Two of these young would probably have perished if I had not tied up their nest, which was breaking away from its support.) This smaller group affords a more exact measure of nesting success. As is to be expected, it proves to be lower than that of the partly selected larger group, only 13 per cent, whether calculated on the basis of nests or of eggs, since each successful nest produced two fledglings.

This is certainly surprisingly low success for a nest which one might suppose would be overlooked by predators because of its small size and the protective coloration of the single diminutive parent who cautiously attends it. Yet the even smaller nests of hummingbirds are also subject to heavy losses. Of 62 nests of all kinds that I found in the lowland forest on Barro Colorado Island and in the small clearing surrounding the island laboratory, only 13, or 21 per cent, produced at least one fledgling. Some of these nests were not found until after the set was complete. Other areas in the lowlands of Central America, with a greater proportion of cleared and cultivated land than Barro Colorado, have given me a higher percentage of successful nests. However, nesting success has rarely exceeded 40 per cent. Even for birds of tropical lowlands, Orange-collared Manakins have high losses and rear few young; yet the species is abundant in the valley of El General. It appears, therefore, that the adults must enjoy fairly long lives.

SUMMARY

The Orange-collared Manakin has a restricted range on the Pacific side of southern Costa Rica and western Panamá, where it occurs from sea level up to at least 3500 feet. It inhabits the primary forest, light second-growth woods, neighboring coffee plantations, shady pastures, and dooryards with abundant shrubbery. With the shrinking of the original forest, it has shown an increasing tendency to establish its courtship assemblies and to nest beyond the forest.

This manakin's food consists of a variety of small fruits, arillate seeds, insects, and the like, which it plucks or catches by darting up, seizing the object in its bill, and carrying it away without alighting beside it. Frequently a manakin joins the mixed company of small birds which follow the army ants to prey on fugitive insects and spiders.

Males, which take no interest in the nests, establish a courtship assembly in parts of the primary forest where the undergrowth is dense, or in second-growth woodland and thickets. Here each adult male clears away all the fallen leaves and other removable debris from a roughly circular or elliptical area from one to about two and a half feet in diameter. These "courts" are always situated amid the slender, upright stems of saplings or shrubs, one or more of which adjoin the area of bare ground, while others stand a few inches beyond its edge. At the height of the courtship season, any light object placed on a court is soon removed by the attendant manakin.

The largest assembly that was discovered contained 14 courts scattered over about half an acre of tall second-growth woodland. The distance from a court to its nearest neighbor ranged from eight to 102 feet, but those closer together than 30 feet were rare and were found chiefly where the intervening undergrowth was dense. When the manakins tried to establish two courts only eight or ten feet apart, one was usually abandoned.

The courts are maintained chiefly from December or January to June or July,

after which they become covered with falling leaves and other litter. One court, however, was kept more or less clean throughout the year. A few others were, after an interval of neglect, rehabilitated during the nonbreeding season, and a new court was made in the nonbreeding season.

Both sexes have a very limited vocabulary, and all their calls appear to be variants of a single basic note, *cheeu*. The female is generally a silent bird; but, to compensate for the poor development of his voice, the male produces a variety of sounds that appear to be mechanical, made with his highly modified remiges. His ordinary flight is accompanied by a low rustle or *whirr*. Near his court, he often makes a deeper, reedy *whirr*. A loud *grrrt* is produced as he rises almost vertically from his court in the midst of a display. A rapid series of sharp *snap*'s is often made with raised, rapidly beating wings while he perches, and an explosive, staccato *snap* rings out while he jumps across his court.

The male's principal display consists in springing with a sharp *snap* across the bare court, from an upright stem on one side to a stem on the opposite side. A single performance may consist of from two to about 14 jumps. It usually also includes a single descent to the bare court, followed by an upward spring to the accompaniment of the growling *grrrt*. Activity at the courts is greatest in the first hour after sunrise, but it occurs sporadically through much of the day.

Although the male often "dances" alone, he frequently has a partner, a manakin in the greenish plumage of the females and young males. The two participants then jump simultaneously, crossing each other above the court. Often it appears that the green bird pursues the adult male. That the green partner is sometimes an immature male was revealed by the transitional plumage of one dancer. In another instance, the dance was followed by coition, which occurred while the female clung to one of the upright stems beside the court.

In the intervals when green birds are absent, neighboring males often perch close together on a twig that is usually nearer the smaller of their two courts. At these times, the manakins often give a display which consists of turning the head from side to side, twitching the folded wings, and making the whole body quiver. The display of the bird that seems to be dominant is less pronounced and briefer than that of his subordinate.

Although in the breeding season adult males were not seen dancing together over a court, in the nonbreeding season two, three, or possibly four sometimes jump together, either over a court or more often in the undergrowth where there is no court. Abnormal displays are sometimes given by adult males high in trees, even in the breeding season.

Immature males in green plumage not only dance with adult males at their courts but they also jump with two or three others in similar attire, and sometimes they perform alone. These performances of the green birds occur at all seasons, at times at a court made by an adult but often at a distance from a court.

Male Orange-collared Manakins appear to distinguish females of the Blue-crowned Manakin from those of their own species.

The female Orange-collared Manakin builds the nest and rears the young with no help from a male. In El General, building may begin in late February in wet years, but usually it does not become widespread before mid-March. Breeding is at its height in April and May, but a few occupied nests are found until September.

Rarely, a nest is built in the midst of a courtship assembly, but most are beyond

the assemblies. Some nests are up to a quarter of a mile from the nearest assembly. Nests have been found from 19 inches to 18 feet above the ground, but the great majority are between 2 and 6 feet up. The slight, shallow, open nest is suspended between two diverging horizontal twigs, to which its rim is fastened. Built of fibrous materials that are usually light in color and bound to its supports with cobweb, it typically lacks the pieces of moss or dead leaves on the bottom which distinguish nests of *Pipra*. A nest is sometimes built in a day, but more often three or four days are devoted to its construction.

The first egg may be laid less than a day after the completion of the nest; but usually the interval is from four to eight days, and once it was 14 days. The set nearly always consists of two eggs and larger sets have not been found. The eggs are laid around noon or in the early afternoon; the second egg is laid about 48 hours after the first.

The female is sometimes found incubating in the interval between the laying of the first and second egg. After the set is complete, she sits very steadfastly, permitting a man almost to touch her. Her sessions are often short in the morning but long in the afternoon, when they may continue for four hours or more. Some females incubate with a constancy of 80 to 85 per cent, but others are less patient.

At eight nests, the incubation period varied from a little over 18 to nearly 20 days. The average incubation period was about 19 days.

The nestlings hatch with pink skin, sparse gray down, tightly closed eyes, and mouths lined with yellow. The female nourishes them with insects and many small berries. These are brought to the nest in her mouth or bulging throat, which may contain up to nine articles. Feeding rates varied from 1.2 times per capita per hour for nestlings two days old to 1.7 times per capita per hour for nestlings 13 days old.

The nestlings' droppings are at first removed by the parent but later they are voided over the nest's rim and accumulate on the foliage or ground below.

In addition to brooding, the parent spends much time resting motionless beside her nestlings, continuing this even after they are feathered. If closely approached by a human being, she may drop almost to the ground and skim or flutter over it in a rudimentary distraction display.

Nestlings are clothed with olive-green feathers at the age of 11 or 12 days, but they may be brooded at night until they are 14 days old. Thirteen young manakins left their nests at ages ranging from 13 to 17 or 18 days, but the single one that remained longer than 15 days was retarded in development.

In one instance, a second set of eggs was laid in a nest which the first brood had left about six weeks earlier.

Of 54 nests found before the eggs hatched, 11, or 20.3 per cent, yielded at least one fledgling. Twenty-three of these nests were found before the set was complete; of these only three, or 13.0 per cent, were successful. Calculated on the basis of eggs rather than of nests, the reproductive success of these two groups was 16.2 and 13.0 per cent.

THRUSH-LIKE MANAKIN

Schiffornis turdinus

The Thrush-like Manakin is a rather stout bird about six inches in length. In both sexes, the head and upper plumage are deep olive-brown; the wings and tail are more russet, the throat and chest are light bistre-brown, and the rest of the under parts are olive. The black bill is short, broad at the base, and slightly hooked at the end. The deep brown eyes are large and the legs and feet are blackish.

This manakin ranges through the tropical forests from southeastern México to Perú and Brazil. In southern México and northern Central America, it is confined to the rainier Caribbean side; but in Costa Rica and Panamá, it occurs on both sides of the Cordillera. On the Pacific slope of southern Costa Rica, it extends from sea level up to at least 5000 feet, and on the eastern slopes of the Ecuadorian Andes, I found another race of this species at 4000 feet above sea level. Everywhere it is an inhabitant of the primary rain forest, where, dark in plumage and deliberate in its movements, it lurks so obscurely in the lowest and darkest stratum of the undergrowth that few ornithologists become well acquainted with it. Although it has been called a terrestrial bird, I have never seen it walking or hopping on the ground; its home is among the shrubbery within a yard or two of the ground. At times it may rise in search of food into the tops of the taller shrubs or the lower boughs of the trees, but it seems not to stay long so high above the earth. It is at all times solitary. Of the five kinds of manakins in the forests of El General, this largest and dullest species stays closest to the ground.

The Thrush-like Manakin has little in common with the smaller members of the family. The sexes are both dull in plumage, and the male displays none of the contrasting patches of bright color which adorn many of its smaller relatives. It makes no mechanical sounds with its wings, but, as compensation for this deficiency, it has a voice sweeter than that of any other member of the family which I have heard. Its manner of foraging is rather similar to that of other manakins, but its movements are slow and staid whereas theirs are sudden and brisk. Its nest and eggs are like those of no other manakin that I know; but in its failure to pair and in the male's lack of interest in the nest while he advertises his daily presence in a certain part of the forest, *Schiffornis* is a true manakin. Although somewhat thrush-like in form and coloration, and with a song which Peters (1929:453) has compared to that of a solitaire, this manakin bears no resemblance at all to the thrushes either in manner of foraging, nidification, or the parts taken by the sexes in attending the nest. In general appearance, voice, and solitary habits, the Thrush-like Manakin shows a certain similarity to some of the cotingas; but cotingas are birds of the treetops and none that I know dwells so low in the forest.

FOOD

Like other members of the family, the Thrush-like Manakin includes both fruits and insects in its diet. It plucks fruits by darting up and seizing one in its bill and pulling it from the stem without alighting. Then it carries the fruit to a convenient perch where it is swallowed. In its manner of fruit-plucking, it reminds one of a big, relatively sluggish *Pipra* or *Manacus*, or a small trogon. It snatches insects from the foliage in much the same fashion. Much of its hunting is done as it flits in a

leisurely fashion through the herbage and low bushes within a yard or two of the forest floor. Sometimes a fruiting shrub or small tree will tempt it to ascend higher, at times to a height of 20 feet. Its feast over, it drops down to the lower undergrowth where it is at home.

VOICE

I had not been long in the foothill region of the Costa Rican mountains before I became familiar with the voice of the Thrush-like Manakin. Wandering through the hill forests along narrow, muddy trails, I heard again and again a tripartite whistle of exquisite beauty. Once or twice I succeeded in glimpsing the songster among the boughs overhead, but I could not see it well enough to distinguish essential characters of a bird whose plumage offered no outstanding features to aid in identification. For six years, I knew it only as "the voice of the Costa Rican forests." I spent more hours than I like to recall, gazing up into the tops of the great forest trees until my neck ached, striving vainly for a better view of the elusive creature. My first sight of the brown bird above me had produced the erroneous notion that it was an inhabitant of the trees. When, after scrutinizing countless times the boughs whence its voice seemed to descend, I consistently failed to see it again, I concluded that it dwelt in the high upper levels of the rain forest, like the Bright-rumped Attila and the Rufous Piha, two cotingas whose voices were familiar sounds in these forests, but whose forms I glimpsed only on the rare occasions when they descended somewhat below the lofty regions where they appeared to pass most of their lives. The highly ventriloquial character of the "voice of the Costa Rican forests" quite failed to set me right, once I had fallen into the error of believing that it emanated from the highest boughs of the trees. Finally, I all but abandoned the unprofitable effort to behold the author of the mellifluous whistles.

Actually, the Thrush-like Manakin is not, like the attila and the piha, an inhabitant of the treetops that sometimes comes down; it is a dweller in the undergrowth and at times goes up to a level where it is more likely to catch the human eye. One morning in June of 1939, while walking along a woodland path in the valley of El General, I heard the "voice of the forests" arising from a point so close to me that there could be no doubt that it proceeded from no great height. I pushed through the undergrowth beside the trail and after a little searching I found the bird I sought. It was perched only a yard from the ground and was repeating at intervals the well-known song. Far from being an unapproachable creature, it was a plain, companionable bird resting intimately in my own humble stratum, and one which permitted me to come agreeably near. When I approached too closely, it merely flitted to a somewhat more distant perch in the undergrowth, whence it continued to send forth the beautiful whistles that permeated the whole forest.

After this encounter, I had no difficulty in watching the "voice" whenever I wished. At least two individuals sang daily in a level area of tall forest near my cabin, and I repeatedly saw them deliver their whistles. They were not shy. They perched on a fallen dead branch or some other convenient, nearly horizontal support, often within a yard of the ground, rarely as much as head-high, and sent forth their notes at their leisure. When approached too closely, they flitted off through the underwood. Numerous other Thrush-like Manakins that I have watched preferred to sing while clinging to a slender upright stem.

It is beyond my power to convey, by means of the printed word, an adequate

conception of the beauty of the Thrush-like Manakin's unique song. To me, it never suggests syllables of human speech; and musical notation, were I able to employ it, would give the pitch but not the essential tone-quality of the notes. The exquisitely modulated whistle, pensive and restrained, consists of three parts. The first is long and ascending; the second is very short; the third part is longer than the second but considerably shorter than the first part and like it ascending. The entire song occupies an interval of about two to two and a half seconds. One manakin delivered his song twice or thrice in a minute. Another sang three or four times per minute. Still another, less miserly with his golden notes, sang regularly from five to seven times per minute. This manakin proclaims his presence day after day in the same part of the forest.

In Costa Rica, the season of song of the Thrush-like Manakin begins early in December, when the wettest months are past and the afternoon rains are becoming lighter and the days sunnier. In the delightful weather of the early part of the dry season, when balmy air, brilliant skies, and an abundance of blossoms seem to invite every bird to sing, the foothill forests are strangely silent. The monotonous chirring of innumerable cicadas serves merely to draw attention to the absence of melodious voices. But two small birds that dwell obscurely in the undergrowth do what they can to relieve the monotony of silence and to fill the whole great height of the forest with sweet notes. Neither is a voluble songster. Each sends forth at intervals its clear, commanding song, then becomes mute. The pure tones of the brief musical phrase are enhanced by the wide margin of silence. One of these musicians is the Lowland Wood Wren; the other is the Thrush-like Manakin.

Toward the end of February and in March, when the air is hot, dry, heavy, and oppressive with the smoke from countless fires set to burn the newly cleared forest land, the Thrush-like Manakin enters a period of relative silence. But after the showers of late March or April have quenched the fires, cleansed and refreshed the atmosphere, and brought new life to vegetation and insects, he sings freely again until July or August. There may even be a fair amount of song in September in favorable years. In the wet months of October and November, the manakin's song is heard more rarely.

The female Thrush-like Manakin delivers a song much like that of the male in form, but it is weaker and less melodious.

The song of the Thrush-like Manakin that I heard on the eastern slopes of the equatorial Andes was sufficiently similar to that of its Costa Rican relatives to be recognized as the utterance of the same species; yet it was somewhat different in form. The last note seemed to fall instead of rise. The voice was clear and sweet, but it was not quite equal to that of the Costa Rican Thrush-like Manakin at its best. The Ecuadorian manakin that I watched sang from the undergrowth of the forest like its northern relatives. When it rose into the trees to forage, it did not sing.

THE NEST

In twenty-seven seasons spent in the forests where the Thrush-like Manakins dwell, I have seen only four occupied nests and a few similar structures that had been abandoned. The first nest was discovered on May 8, 1940. This nest was complete but no eggs had been laid in it. It was in the forest, on a ridge above the Río Pacuar in the basin of El General, at an altitude of about 2400 feet above sea level. The site of the nest was 4½ feet above the ground, in the angle between

a slender palm trunk and a thin stiff vine, which crossed each other and were bound together by the loops of a cord-like twining creeper. The palm trunk and the vine passed, on opposite sides, within two inches of the upright trunk of a small tree, against which one side of the nest rested. The structure was composed almost entirely of whole leaves, some of which were partly decayed while others were reduced to a delicate transparent lacework. These leaves, apparently from a single species of plant, were mostly from 6 to 7 inches long and from 2 to 2½ inches in width. They formed a bulky pile 5½ inches high, the top of which was deeply cupped. This hollow was lined on the bottom with a thick pad of fine, black fungal filaments. The spreading tip of a brown, dry palm frond, caught up between the crossed stems, formed a fluted hood that sheltered the whole nest.

The second nest was discovered near my home in El General on March 5, 1942. It was in a low, somewhat moister area in upland forest, 45 inches above the ground in a crooked sapling overgrown with an assortment of epiphytic and scandent vegetation, including an aroid with ample cordate leaves, a species of *Carludovica*, the twining fern *Salpichlaena volubilis*, small epiphytic ferns, and mosses. The nest was supported among the epiphytes, close against the thick stem of the sapling, which was covered with roots and moss. The nest was a rather bulky mass of fairly large, light-colored, dead leaves, many of them whole or nearly so. It was lined with broad pieces of lacy leaf skeletons, and in the bottom was a mat of fine, dark brown rootlets. The overall measurements of the nest were about 4 inches high by 4½ inches in diameter, not including the leaves projecting beyond the main bulk of the structure. The cavity measured 1¾ inches in depth by 2½ inches in diameter.

The third nest, found in the same locality as the second on May 22, 1949, was 4½ feet up in a clump of small palms that bristled with long, black, needle-like spines. Supported between two of the thorny stems just below the fronds which sprang from their summits, it was built upon an old nest of another bird, apparently that of the Blue-black Grosbeak. After the manakin had abandoned this nest, the grosbeaks returned, lined it with tendrils, fungal strands, and other fibrous materials, and incubated two eggs in it.

The fourth nest, discovered in the same tract of forest as the second on April 24, 1958, was built 43 inches above the ground in a tangle of the climbing fern *Salpichlaena volubilis* growing over a small spiny palm, beneath a giant tree of *Brosimum utilis*. This bulkiest of all the nests had a loose foundation composed of twigs, old inflorescences, semi-decayed vines, tendrils, and other coarse pieces, many of which were branched. Within this was a thick middle layer consisting of leaves in all stages of decay, many of them reduced to lacy skeletons. The largest of these leaves was 9 inches long by 3½ inches wide. In the bottom of the cup was a thick pad of rootlets and other fibrous vegetable material, mostly blackish in color, although there were a few light strands. This nest was about 5½ inches high by 6 inches in diameter. The interior was 2½ inches deep by 3 inches in diameter.

The Thrush-like Manakin's coarse, bulky nest contrasts strongly with the delicately wrought structures of species of *Manacus*, which are about the slightest fabrics that could hold the small eggs.

THE EGGS

As in many birds of the tropical rain forest, a considerable interval separates the completion of the Thrush-like Manakin's nest and the laying of the first egg. My

first nest seemed to be finished when found on May 8, but I did not see an egg until May 14; none had been present on May 12. The fourth nest likewise appeared to be finished when I discovered it on April 24, but the first egg was not laid until May 3, nine days later. This egg was warm, and apparently had just been laid when I first saw it at 10:35 a.m. on May 3. On a number of visits during the next 48 hours, I found the egg unattended, although at 9:50 a.m. on May 4 it was warm, as though the manakin had left it a short while before my visit. On other visits I found it quite cold. At 11:00 a.m. on May 5, the nest still contained the single egg. At 12:23 p.m., I found the manakin in her nest, evidently laying. When I returned at 1:25 p.m. there were two eggs, already cold. The second egg had been laid between 11:00 a.m. and 1:00 p.m., two days after the first was laid.

At nest 3, the first egg was laid between 1:30 p.m. on May 24 and 8:50 a.m. on May 25. At 10:00 a.m. on May 25 there was still one egg, unattended. At 1:50 p.m. on the same day I found the manakin sitting on the nest, and she was still present at 2:20, when it began to rain. Returning at 3:40 p.m., I found two eggs. Thus, it appears that the eggs, at least the second eggs in sets, are deposited around the middle of the day or in the early afternoon, as in certain smaller manakins, rather than early in the morning as in many passerine birds.

Three nests contained sets of two eggs, and in one nest a single egg was laid. The eggs are oval in shape and have a high gloss. On a pale buffy ground, they are marked with large and small blotches and roundish spots of black and dark brown, or black and pale lilac, which are concentrated in a wreath around the thick end, with a few scattered over the remaining surface. They contrast with the bed of dark fibers on which they lie. The measurements of seven eggs average 24.3 by 17.9 millimeters. Those showing the four extremes measured 25.4 by 19.1, 23.0 by 17.5, and 24.2 by 15.9 mm.

In one nest the eggs were laid about February 22, and in the other three nests they were laid in May.

INCUBATION

The first nest of the Thrush-like Manakin was found by my helper. For some days after the exciting discovery of this curious nest, it was always unattended at the time of my visits, and I could not conjecture to what bird it belonged. But on May 14, while I stood admiring the egg that had recently been laid, I was elated by the approach of the big, olive-brown manakin, who whistled once in the undergrowth. This was my first intimation of the identity of the nest.

On my next three visits to the nest, I found the manakin covering the egg. She did not budge when I came very near, and I did not deem it prudent to put her off in order to learn whether a second egg had been laid. At last, at noon on May 17, I found the nest unattended and still with the single egg. I was at the nest many minutes, writing a description of the structure and its contents. While I was so engaged, I heard a call composed of a long ascending whistle followed by two shorter ones, much like that of the male Thrush-like Manakin. This was repeated many times. Presently the bird approached fairly near me and clung to upright slender stems of saplings within a yard of the ground. She watched me with large eyes, while she repeated over and over her exquisite call. Once she pivoted quite around the vertical stem to which she clung.

As incubation progressed, the manakin became even more confiding in my

presence, and she would continue to cover her egg while I advanced slowly and stood within arm's length. She was quite as steadfast as many individuals of the smaller Orange-collared Manakin, Blue-crowned Manakin, and Yellow-thighed Manakin whose nests I have studied. One morning, after I had stood for a minute looking at her intently from a distance of two feet, she suddenly jumped from the nest, although I had made no further movement. Alighting upon a small, prostrate log six or eight feet from me, she stood there for a few seconds. Thence she flitted to a thin stem to which she clung at a point a foot or so above the ground, depressing her head and swelling out her throat, eyeing me intently. She moved to neighboring stems and continued her scrutiny, and twice she gladdened me with her beautiful song. On another of my visits, she fell almost at my feet while I stood close beside her nest.

I allowed the manakin to incubate for a week, then set up a small blind to command a view of her nest. In this I watched from 12:20 to 5:30 p.m. on May 23 and from 5:40 to 11:40 a.m. the following day. The manakin was sitting quietly when I arrived early in the afternoon of the first day, and she did not become frightened as I entered the blind. The sky was clear. A Black-throated Trogon off in the forest called *cow cow cow* in a low, mellow voice, the notes always in trios. A Long-billed Gnatwren was singing his beautiful clear trill. A Black-hooded Antshrike sounded a loud wooden rattle. At the forest's edge, a pair of Buff-throated Saltators called back and forth with sweet, soft notes. Orange-collared Manakins whistled *cheeu* and made explosive noises with their wings in the neighboring undergrowth, where they had cleared little circles of bare ground for their courtship rites. Above me in the trees, a few cicadas buzzed loudly. After a while, an agouti came silently over the ground. When behind the brown wigwam that concealed me, four yards away, it wrinkled up its broad nose and sniffed the air suspiciously. Then it bolted away, emitting low grunts as of labored breathing, interrupted by louder notes like harsh sneezes. Through all this small stir of forest life, the brown manakin continued to sit calmly beneath the fluted palm leaf that formed a hood above her.

At 12:50 p.m., I began to hear the whistles of another Thrush-like Manakin in the distance; but what relation, if any, this bird bore to the one before me I could not discover. At 2:07 the manakin ended her long session by jumping from the nest and dropping almost to the ground before flying away. I heard a call from the direction in which she had vanished. She was absent for a long while; but at 3:44 she returned alone, clinging to upright saplings at points near the ground, and peering carefully from side to side as she approached her nest. Then, clinging to the vine which formed one of the supports of the nest, she voiced her beautiful song. Next she settled on the egg, and while sitting there she preened. At 4:15 a hard shower began to fall, but at 4:28 the manakin left her nest in the rain. At 4:50, as the shower ended, I examined the nest and found it perfectly dry beneath its palm-leaf shelter. At 5:02, after an absence of 34 minutes, the manakin returned silently and alone. At 5:30 I stole away in the failing light, leaving her on the nest.

The next morning I returned at 5:40 a.m. to resume my watch at the manakin's nest. When there was sufficient light, I saw that it was unoccupied, but at 6:15 the brown bird returned alone and in silence. At 8:00 I heard the song of another Thrush-like Manakin in the distance, but it soon ceased. At 8:29 the bird left the nest and stayed away until 10:03, when again she returned silently; but after

settling on the egg she sang once. At 11:40 she dropped from the nest nearly to the ground and flew away.

This manakin's rhythm of coming and going was very slow. The sequence of her sessions and recesses on the afternoon of May 23 was as follows: on nest 107+ minutes, off 97, on 44, off 34, then on for the night. On the morning of May 24 the sequence was: off before I could see in the dawn, on 134 minutes, off 94, on 97 minutes. The average of the manakin's four sessions was 95.5+ minutes; that of her three recesses was 75 minutes. She covered the nest for 56 per cent of the day. Although her sessions were long, they were not as long as those of certain Yellow-thighed, Blue-crowned, and Orange-collared manakins that I have watched; whereas her recesses were far longer than those taken by these species. She devoted much less time to incubation than these far smaller manakins, which often cover their eggs for more than 80 per cent of the day. While incubating, the Thrush-like Manakin always sat with her head toward the palm leaf that arched over her nest and her tail extending outward on the other side. I found no evidence that she had a mate who took an interest in the nest; she was as solitary as I have invariably found nesting manakins of other species.

This Thrush-like Manakin continued to incubate for at least 21 days after her single egg was laid. I found her covering it as late as June 4. That evening a violent storm of wind and rain blew down many dead limbs and trees in the forest. Next day I found the egg lying on the fallen leaves beneath the nest, cold and wet but unbroken. Perhaps the noises of the storm had frightened the bird from her shallow nest so suddenly that she threw out the egg, as I have seen happen at nests of the smaller manakins. I replaced the egg; but it lay neglected in the nest for a week, after which I opened it and found that it had been infertile.

When I visited the second nest, found with two eggs on March 5, 1942, the owner would also cling near the ground to upright stems and utter the trisyllabic whistle, but in a subdued voice. As I returned to the nest late in the morning on which it was discovered, I heard the manakin's low whistle. A small venomous snake, green with dull red marks on its back, was coiled on the nest, with one of the eggs in its widely distended mouth. This snake, a species of *Bothrops*, was only about a foot in length; its neck was scarcely thicker than a lead pencil and it was having difficulty in swallowing the egg, which was of greater diameter than its own body. When I lifted the serpent from the nest with the point of my machete, the egg came with it and dropped to the ground, followed by the snake, which struck at me viciously. Although the egg was only slightly cracked, doubtless from its fall, I did not return it to the nest. Cracked eggs attract ants which may cause the abandonment of a nest, and they usually dry out and fail to hatch unless they already contain a large embryo. Opening this egg, I found a very small embryo, still many days from hatching. The manakin continued to incubate the single egg that remained in the nest.

At nest 3 the manakin also permitted me to come very near, sometimes almost to touch her, before she jumped from her eggs and fell almost vertically, then flew rapidly out of sight. As incubation advanced, she stayed closer after dropping from the nest, and sometimes she sang while watching me from the neighboring undergrowth. Then one day, when her eggs were almost ready to hatch, she clung low on a vertical stem only a yard from my legs and uttered a note which I can best describe as a scream of protest at my intrusion. After lingering beside me for a good

fraction of a minute, she flew to more distant stems and repeated the scream, which seemed to be a modification of the trisyllabic song. On the day her nestling hatched, she permitted me to touch her tail before she jumped from the nest.

On June 1, while incubation was in progress, a dawn-to-dusk watch was made at this nest by Barbara Norby, Darwin Norby, and me. As at the first nest, this manakin left her eggs at daybreak, before there was enough light in the forest undergrowth to see her. At 6:30 a.m., she returned to resume incubation. Throughout the day, no more than one manakin was ever seen at a time, although the song of a second manakin sometimes sounded in the distance while this bird sat. When leaving her nest, she dropped to near the ground before she flew away. Returning, she would cling low on a slender, upright stem some distance from the nest and stretch out her neck as she peered around. Then she might advance to a stem nearer the nest and repeat her survey. Sometimes, while so engaged, she sang in a voice weaker than the male's. Finally, by means of successive advances, she reached her nest and settled down on the eggs. Late in the morning, she closed her eyes while sitting, taking numerous brief naps, which rarely lasted as long as a minute.

The sun shone a little soon after it rose, but the remainder of the morning was cloudy. Before noon, rain began and continued to fall intermittently until nightfall. In the course of the day, the manakin took four sessions, ranging from 97 to 151 minutes and averaging 113.5 minutes. Her five absences varied from 14 to 82 minutes in length and averaged 51.4 minutes. She covered her eggs for 68.8 per cent of the day, which is a record considerably better than that made by the manakin I had watched nine years earlier. She had the same slow rhythm of coming and going, but her sessions were somewhat longer and her recesses were, on the average, very much shorter.

At this nest, the second egg was laid between 10:00 a.m. and 3:40 p.m. on May 25. At 1:30 p.m. on June 13, I found this egg slightly pipped. Twenty-four hours later, the shell was well pipped but still unpierced, and at 7:15 a.m. on June 15 there was a single nestling, so recently hatched that its down had not yet spread out. The empty shell had already been removed. From these dates, it is evident that the incubation period could not have been shorter than 19 days and 21 hours nor longer than 20 days and 21 hours. Probably it was closer to the latter, or nearly 21 days.

Four days after this nestling hatched, it vanished; but the other egg remained in the nest and the manakin continued to incubate it. She was last seen covering it nine days after the first egg hatched and five days after the nestling disappeared. For a few days longer, the unhatched egg remained in the nest, but it was always cold when I visited it. By the end of June it had vanished.

THE NESTLINGS

When I approached nest 2 on March 16, the manakin sat until I came within a foot of her, then jumped down to a position close to the ground on an upright stem, uttered her sweet whistle, then vanished amid the undergrowth. She left a newly hatched nestling, which had pink skin shaded by copious, long, brownish gray down more abundant than that on the nestlings of the majority of passerine birds. Its legs and toes were blue-black.

On the afternoon of March 20, I set my blind near the nest. Before I had completed the adjustments, the female returned with food. As she approached I hid

myself inside, and with little hesitation she fed the nestling. The next morning I watched for the first three hours after daybreak. In this period, the five-day-old nestling was fed only three times, or once per hour, but the meals were generous. The first was a very big green caterpillar, the second a large green caterpillar or mature insect, the third a smaller insect. Although I found the early morning air cool in the deep shade of the forest, the nestling was brooded only once, for 19 minutes. It was now several times as big as when it was newly hatched, and when resting motionless in the nest, with its head doubled beneath its body, it was a fluffy, featureless ball of dark gray down. Its skin had become much darker than when it was newly hatched; the eyes remained closed; and the pinfeathers were not yet evident.

When the nestling was nine days old, its pinfeathers were prominent and those of the remiges were very long. Despite its infrequent meals, the young manakin never gave evidence of hunger by lifting its gaping mouth when I shook the nest or held a hand above it, as many young nestlings do. It never exposed the inside of its mouth to my view. By March 31 it had vanished from the nest, but I am not sure that it had left spontaneously at the normal age. At no time did I see two parents come near this nest and take an interest in it. As in other species of manakins, the nestling Thrush-like Manakin is apparently reared by the female alone.

SUMMARY

The Thrush-like Manakin dwells in the undergrowth of heavy forest, from sea level up to at least 5000 feet in Costa Rica and to 4000 feet on the eastern slopes of the equatorial Andes. It is usually seen within a yard or two of the ground, clinging to upright stems or at times to horizontal branches. Although it may rise as high as 20 feet to forage, it soon returns to a lower level. It seems rarely to alight on the ground. Its movements are slow and deliberate, and it is always solitary.

This manakin's diet includes insects and many berries. In plucking a berry from a bush or a low tree or an insect from a leaf, it flies up, seizes the object in its bill without alighting, and carries it to a convenient perch, where it is swallowed.

Males utter a beautifully modulated tripartite whistle, which proclaims their presence in the same small area of forest undergrowth day after day. The song occupies about two seconds and is delivered from about two to seven times per minute from a perch near the ground. In El General, the season of song is from December to August or, in some years, September. When disturbed at their nests, females protest with a similar but weaker whistle, which at times is modified into a scream.

The nest is built in a spiny palm, in a tangle of vines, or in an epiphyte-burdened sapling, from 3½ to 4½ feet above the ground in the forest. It is a bulky open cup, composed chiefly of whole leaves or leaf-skeletons, some of which are surprisingly large. Sometimes there is a loose foundation of sticks, vines, and other coarse materials. The bottom is lined with a thick pad of blackish fibers.

Each of three nests contained two eggs, but in another nest only a single egg was laid. In two instances, the last egg in a set was laid around midday or in the early afternoon. The glossy eggs are pale buff, with blotches and roundish spots of black, dark brown, and pale lilac, chiefly in a wreath around the thick end. In El General, one set was laid in late February, and three sets were laid in May.

Only the female takes an interest in the nest. While sitting, she permits a very

close approach by a man. Whether she is frightened from the nest or leaves spontaneously, she drops almost straight down to near the ground before she flies off. Her sessions on the eggs are rarely shorter than an hour and sometimes last two and one-half hours, but her absences are also long, frequently exceeding an hour. A female which was watched from dawn to nightfall covered her eggs for 68.8 per cent of the day. Another female, watched for most of the day, incubated with a constancy of only 56 per cent. In one instance, the incubation period was between 20 and 21 days.

Nestlings are hatched with copious, long, brownish gray down, which after it spreads out completely covers their pink skin. A five-day-old nestling was fed about once an hour, but each meal consisted of a very large insect or caterpillar. One nestling disappeared from the nest 15 days after it hatched, but it is uncertain whether its departure was spontaneous.

GENERAL SUMMARY OF INFORMATION ON THE PIPRIDAE

The manakins are a family of very small or, exceptionally, medium-sized passeriform birds numbering about 60 species. They are confined to the wooded portions of tropical continental America, including Trinidad and Tobago. Closely allied to the American flycatchers and the cotingas, some of the intermediate genera have been shifted back and forth between these families. But with the exception of a few marginal forms, the manakins are a compact, easily recognizable group, in this respect contrasting sharply with such vast and heterogeneous assemblages as the ovenbirds and the flycatchers. Typical manakins have very small, stout bodies, usually short tails, and short, broad bills. Black is the prevailing color of the males, but nearly always it is relieved by sharply contrasting areas of intense red, orange, yellow, blue, or white, sometimes in the form of a cap or hood, sometimes as a broad collar encircling the neck, or else more extensively spread over the body. In a few species the males are crested; in some species the central tail feathers are greatly elongated; in other species the shafts of the rectrices protrude as long, curving filaments. The females of these typical manakins, far less ornate than the males, are usually clad wholly in shades of olive or olive-green. In the less typical members of the family, male and female alike wear olive-green, brown, or rufous plumage.

Manakins are rather solitary in their habits, apparently never moving in unified flocks. The males, however, congregate in courtship assemblies, and often a number of individuals of both sexes are drawn together by an attractive source of food. They appear never to migrate. The manakins are more nearly restricted to the warm lowlands than any other of the larger passeriform families of tropical America.

The food of manakins consists of both fruits and insects in liberal quantities. They are fond of small berries, which they pluck by darting up to the cluster, seizing one with the bill, and pulling it away without alighting, the whole action being performed with the vigor and dash characteristic of nearly everything these brisk little birds do. Insects are snatched from the foliage in much the same fashion. At times manakins, in company with numerous birds of other families, gather about the swarming army ants to prey on the fugitives. They give attention particularly to the smaller insects which escape the hunting ants by crawling up the stems and foliage of the low vegetation. Manakins forage chiefly in the lower half of the forest, but at times they ascend into the tops of tall trees the berries of which attract them.

The voices of manakins are less likely to attract attention than the bright colors and odd antics of the males. Long-drawn dry whistles, staccato monosyllables, and twanging and buzzing sounds are their most characteristic utterances. But the Blue-crowned Manakin voices an appealing little clear trill, and the Thrush-like Manakin has a truly beautiful and arresting whistled song that is one of the unforgettable sounds of the forests where it dwells. In both of these species, the female delivers notes scarcely inferior in quality to those of the male. In addition to vocal sounds, manakins produce a variety of noises which appear to be mechanical. The males, and less often the females, of a number of species make in flight a rustling or whirring sound, which on occasions, especially in the courtship assembly, is intensified

to a reedy or growling *whirr*. Explosive noises, resembling the detonation of a small firecracker or the sudden breaking of a tough, dry twig, may be given either singly or in series. The single explosive *snap* is often produced in flight, whereas the rolling *snap* is usually heard while a perching manakin rapidly beats his raised and expanded wings. According to Sick (1959:300) the true *snap* (*Knacken*) is restricted to *Manacus* and *Pipra mentalis*, although a wide variety of other wing sounds are made by other species. This author attributes certain clapping sounds, as those of *Neopelma pallescens* and *Pipra fasciicauda*, to the striking together of the wings, evidently above the bird's back (*op. cit.*:273, 277). Most of the wing sounds of manakins, however, appear to be produced by the passage of air through the variously modified remiges or, in the case of the explosive *snap*'s of *Manacus* and *Pipra mentalis*, by the striking together of the thickened shafts of the secondaries of each wing separately, although the mechanics of this process have not been adequately clarified.

The courtship activities of manakins are of special interest. As far as we know, no species of manakin forms enduring pairs; the females attend the nest without help, while the males take up stations where they advertise their presence to the other sex. The females come to these stations, are fertilized by the males, then go off alone to lay their eggs and rear their offspring. Our knowledge of the courtship habits of manakins is still far from complete; for a number of species and even genera, no information is available. But we have extended studies of a few species and scattered observations on a number more, and these permit us to trace a series from courtship habits that are relatively simple and apparently primitive to those which are extremely varied and complex. At the same time, we notice an increase in cooperation among the courting males. Those with the simplest modes of courtship are solitary. With increasing complication of sounds and antics, there is a tendency for a number of males to form a courtship assembly. The members of this assembly collectively attract the females to a certain part of the woodland, where each male performs alone in an effort to draw the females to himself from neighbors which are simultaneously cooperators and competitors. Finally, in *Chiroxiphia*, several males dance in closest concert in the presence of a female.

Manakins with the simplest courtship attract the females chiefly, if not wholly, by vocal means. Among them are the Thrush-like Manakin, whose beautiful song we have already noticed, and, according to Sick (1959:271-272), the Brazilian manakins *Piprites chloris*, *Tyrannetes stolzmanni*, and *Neopelma aurifrons*, whose voices are far less melodious. In their plain attire, no less than in the apparent simplicity of their courtship habits, these manakins resemble cotingas or American flycatchers. Their systematic attribution to the Pipridae is perhaps open to question.

The Orange-crested Manakin adds to vocal advertisement a simple visual display. From a perch in the lower part of the forest, this small olive-green bird springs upward for about a foot, hangs in the air a moment, then descends to the same perch. While performing so, he spreads his brilliant yellow crest and with each jump gives from three to five twanging notes, apparently a vocalization. This phrase may be sounded while the bird rests motionless, and the dance may be performed without the song (Davis, 1949b). A congeneric species, *Neopelma pallescens*, likewise jumps up and down, sometimes making a note like the hammering of a small woodpecker by striking its wings together, once as it ascends and once as it descends (Sick, 1959:272-273). *Schiffornis*, *Piprites*, *Tyrannetes*, and *Neopelma* usually call or perform

in solitude; other individuals of the same kind may be audible in the distance but they are seldom visible.

The simple display of the White-throated Manakin, consisting chiefly of showing off the snowy gorget and an area of glossy steel blue on each wing, is given when other males are present. Apparently, however, their courtship activities lack organization (Davis, 1949a). White-ruffed Manakins use as a communal display ground a mossy, prostrate log in the midst of the forest. To this the males fly with a slow, strongly undulatory flight, their tails turned up and their plumage fluffed out until each resembles a tiny black balloon with a gleaming white patch on its forward side. Although several males may engage simultaneously in this beautiful display, their movements are not coordinated (Skutch, 1967).

The courtship habits of certain species of *Pipra* are more varied and complex than those of the foregoing genera. Here we meet well-organized assemblies, with each member occupying a definite position within the group. One of the less specialized species of this genus is the Blue-crowned Manakin, of which each courting male occupies a poorly defined area, 20 or 30 feet in diameter, in the undergrowth of the forest, where he is 75 or more feet from his nearest neighbor. Here he advertises his presence by combinations of a soft, clear trill and a peculiar harsh *k'wek*, flights of various sorts, and wing-flapping without the production of snapping sounds. The nuptial perch, where the female receives the male, is an obscure twig near the ground, some distance from the higher perches where the manakin spends most of his time.

In other species of *Pipra*, the more compact assembly is the scene of more varied and spectacular displays. An assembly of the Golden-headed Manakin may contain from four to 12 males, whose stations are from 10 to 30 feet apart (Snow, 1956, 1962b). Assemblies of the Yellow-thighed Manakin consisted of four or five males, whose display perches were from 20 to 125 feet apart. Among the displays of these species of *Pipra* are rapid about-faces and sliding backward along the perch, with legs stretched up to show off the brightly colored thighs, darting between twigs a few feet apart, and a swiftly circling flight, all to the accompaniment of various vocal and mechanical sounds. Unlike that of the Blue-crowned Manakin, the principal display perch is also the nuptial perch, where the female accepts the male.

Manacus appears to be the only genus of manakin in which each male removes fallen leaves and other debris from a small, roughly circular or elliptical area of ground, forming a "court," above and around which his displays center. In the Golden-collared Manakin these courts are usually from 30 to 40 feet apart, with extremes of 12 and 200 feet (Chapman, 1935:483-484). In the Orange-collared Manakin, they are rarely as close as eight feet apart, but usually their separation is 30 feet or more. A far higher degree of sociability is exhibited by the Black-and-White Manakin, whose crowded courts are only three to six feet apart and at times almost in contact, with possibly a hundred males occupying a small area (Snow, 1956, 1962a; Darnton, 1958). Beside each court are several slender, upright stems, between which the manakin jumps back and forth, over and around the bare area, usually making a loud, explosive *snap* each time he leaps. Sometimes he drops on the bare ground, then shoots upward to the accompaniment of a harsh *grrrt*. A minor element in the display is the protrusion of the elongated feathers of chin and throat to form a "beard," which reaches to or beyond the tip of the bill. When a female arrives, she dances with the male, the two jumping back and forth in opposite

directions, crossing each other above the court. Coition occurs on one of the upright stems beside the court that serve as turning points in this dance.

In some of the foregoing species, two adult males sometimes display to or with each other, usually at a point somewhat removed from their principal display stations, and in a more or less subdued manner. But at the critical moment when a female arrives, each goes to his own station and intensifies his activities in an effort to win her for himself. In *Chiroxiphia*, however, several of the adult males join in a single elaborate performance, not only in the absence of a female, but likewise when she visits them. Moreover, young males in transitional plumage, which are rarely seen in some other manakins but frequently noticed in this genus, often dance with the adult males. In the Blue-backed Manakin, the "bower" or display perch is a slender stem or branch close to the ground, from around which the manakins pluck away green leaves, thereby increasing visibility. Four such bowers, situated 15 to 21 paces apart in open bushy forest, belonged to a single clan or assembly, the members of which used them in common, with no indication of territorial defense. There are two main forms of display: (1) a cartwheel dance, performed by two males who simultaneously move backward through a vertical orbit, successively occupying the same positions in space; and (2) a "bouncing" dance, in which from one to four males bounce up and down and back and forth, often passing over each other, on a nearly horizontal limb (Gilliard, 1959*b*). Snow (1956, 1963*a*) watched two males give both types of performance, from a horizontal perch, in the presence of a female. Lamm (1948:273) saw two males of this species perform the bouncing dance before a female. They persisted until one dropped out, apparently spontaneously rather than driven by his partner; whereupon the other, after some additional displays, mounted the waiting female.

For the Long-tailed Manakin of Central America, Slud (1957) described both the bouncing and the cartwheel displays, with two participants performing from a horizontal perch near the ground. Young males in transitional plumage dance with each other, just as the adults do. A quite different display was described by Sick (1959:284-285) for *Chiroxiphia caudata*, the Dansador of southern Brazil. Three adult males line up on an inclined twig; all are pressed close together, facing in the same direction with body horizontal and head stretched forward. Beside the uppermost of the three is a motionless female or young male, perching upright. The lowest of the three adult males rises a few inches into the air, hovers facing the group on the twig, then settles next to the motionless spectator, in the space which the other two adults have made for him by sliding down the twig. After alighting, he turns about to face in the same direction as his companions, the lower and outermost of which now rises in the air and repeats the movements of the one that preceded him. To the accompaniment of animated sounds, the three performers continue this circular dance with machine-like regularity.

On the Río Napo, I watched a male Striped Manakin emit a sharp, buzzing sound, with widely opened mouth, in the presence of a female. Then he made his body revolve rapidly under and over a slender, horizontal twig, to which he clung with his feet. Although our knowledge of the habits of manakins is still fragmentary, an almost bewildering variety of courtship arrangements and bizarre antics has come to light. Others, not mentioned here, are described in Sick's paper, in which 25 species are treated in more or less detail. The evolution of manakin displays has recently been discussed by Snow (1963*b*), who gives a useful synopsis of the various types.

The nest of most members of the Pipridae is placed in trees or bushes near the ground. The highest nest of which I have information was that of a Yellow-thighed Manakin which was situated 30 feet up, an elevation unusual even in this species. The more typical structures are among the slightest of birds' nests: thin-walled, shallow hammocks, suspended between the arms of a slender, horizontally forked branch or between two diverging branches of a sapling. In *Manacus* the nest, attached by its rim to the supporting twigs, is composed of fine but often stiff materials, such as bast fibers or the slenderest divisions of the inflorescences of grasses. These often form so thin and open a fabric that the eggs can be seen through the meshes of the bottom. In *Pipra* and *Chiroxiptia* the nest is essentially similar, differing chiefly in having few or many pieces of dead leaf, pinnae of ferns, and at times also tufts of moss, loosely attached to the bottom. Often the silk of spiders or caterpillars is employed to strengthen the rim's attachment to the supporting twigs. The depth of these nests scarcely exceeds the transverse diameter of the eggs they hold; and the bird sits upon rather than in them, with practically all of her body visible from the side. Very different are the nests of the relatively huge Thrush-like Manakin. These are high, bulky piles of fairly large dead leaves, some reduced by decay to skeletons. The deep depression in the top of the mass is lined on the bottom with a mat of fibrous rootlets, fungal filaments, or similar materials.

The nest is built by the female alone. I have watched the construction of nests by the Yellow-thighed, White-ruffed, Golden-collared, and Orange-collared manakins without ever seeing a male in attendance.

The eggs are usually laid in the middle of the day, either shortly before noon or in the early afternoon, at least in the Thrush-like, Blue-crowned, and Orange-collared manakins. An interval of two days separates the laying of successive eggs. In *Manacus*, *Pipra*, and *Chiroxiptia*, the eggs are dull white, cream, buff, or pale gray. They are usually quite heavily marked over most or all of the surface with shades of brown; the markings on the sides are often elongated in the direction of the long axis of the egg. The eggs of the Thrush-like Manakin are dull or buffy white, spotted and blotched with black, pale lilac, and dark brown, chiefly in a wreath around the thicker end. Manakins normally lay two eggs; I have no knowledge of larger sets. In the few instances where a single egg was being incubated, there was a possibility that its companion had been lost.

Incubation is performed by the female alone. Although at times she attempts to steal unobtrusively away as a man approaches her nest, usually she sits very closely, relying on her minute size and neutral color to escape detection. She allows a person to come within a few feet or even inches of the nest, and sometimes she actually permits the person to touch her. Most steadfast on the nest of all the manakins that I have studied are the Yellow-thighed Manakins, which in several instances have sat firm while I touched them. One exceptionally brave individual continued on her eggs while I felt beneath her breast to learn whether they had hatched; I photographed her at close range, even pushing her with a finger into the desired pose. This steadfastness in sitting is associated with long sessions and relatively short recesses, so that manakins devote a greater proportion of the day to incubation than do most small birds. In the Thrush-like, Blue-crowned, Yellow-thighed, and Orange-collared manakins sessions of over an hour are frequent, and sometimes they continue for three or four hours. In the three last-mentioned species, recesses tend to be short, with the result that a constancy in incubation of from 80

to 85 per cent is often achieved by these diminutive birds. The larger Thrush-like Manakin has been found to sit less constantly, often taking recesses that exceed an hour in length. In two instances, females covered the eggs for only 56 and 69 per cent of the day.

The incubation period is 17½ to 19 days in the Blue-crowned Manakin, 18 to nearly 20 days in the Orange-collared Manakin, and, in one instance, between 20 and 21 days in the Thrush-like Manakin.

The nestlings, when newly hatched, bear gray down which is fairly copious in *Schiffornis* but sparse in *Manacus* and *Pipra*. Their eyes are tightly closed, and in the latter two genera, at least, the interior of the mouth is yellow. The young are attended by the female alone. Their food, consisting of small insects and many berries, is brought to the nest chiefly in the parent's throat, although a few additional articles may be carried in her mouth and bill. At times seven or eight berries, large in proportion to the tiny bird, are brought at one time, and delivered to the nestlings either whole or slightly mashed. These are never comminuted or pre-digested, so that it is doubtful whether this mode of feeding should be termed "regurgitation." Nestlings are fed infrequently, once or twice per young per hour for older nestlings, rarely somewhat more often. At first the parent removes the droppings from the nest; but older nestlings eject the droppings over the rim of the nest, with the result that the foliage or the ground beneath the nest becomes heavily soiled before the young are fledged. Thus manakins of the genera *Pipra* and *Manacus*, at least, are less careful of the sanitation of the nest than are most passerine birds.

After permitting a close approach by her human visitor, the incubating or brooding manakin often drops more or less abruptly from the nest and flies away close to the ground. A female Orange-collared Manakin with nestlings may at times skim or even flutter rather rapidly over the ground, in an unconvincing display of injury simulation. The female Blue-crowned Manakin is a better actor. Alighting on a branch near the ground, she quivers her spread wings as though in pain, then flits ahead, repeating this little act again and again if she can induce her visitor to follow her away from her nestlings. Parents of fledglings which have flown a distance from the nest sometimes display in the same fashion.

The nestling period of both the Blue-crowned and the Orange-collared manakins is normally from 13 to 15 days, but one abnormal nestling of the latter lingered in the nest for at least 17 days. At the time of departure from the nest, the young are fairly well clad in dull olivaceous plumage resembling that of the female, and they can fly a little. Scarcely anything is known about the age at which the males of the strongly dimorphic species acquire their distinctive colors and ornaments. Often they perform many of the adults' courtship antics while they still wear the dull colors of females and young males.

FAMILY FORMICARIIDAE

GREAT ANTSHRIKE

Taraba major

The Great Antshrike is one of the largest of the Central American antbirds, although it is not nearly as big as the giant *Batara* of southern Brazil and Paraguay. The Great Antshrike is a long-tailed, stout bird about eight inches in length, with a thick, strong, black bill terminated by a little notched hook at the end of the upper mandible. As in many other antbirds, the sexes contrast strongly in plumage. The male is black on all the upper parts, including the sides of his head and neck, but there are conspicuous white tips on all the wing-coverts. The concealed basal portions of the feathers in the center of his back are extensively white. The under plumage is nearly everywhere pure white. The female's upper plumage is bright chestnut instead of black. Her under parts are white, becoming cinnamon on the flanks and light chestnut on the under tail-coverts. In both sexes, the eyes are brilliant red. So penetrating an eye is sure to catch and hold attention and is perhaps the outstanding feature of this strikingly attired bird.

The species extends through the humid tropical lowlands from southern México to northern Argentina. In Central America it is confined to the Caribbean side, except in central and southern Costa Rica and parts of Panamá, where humid conditions occur on the opposite coast. On the Pacific slope of southern Costa Rica, the Great Antshrike ranges upward to no less than 3000 feet above sea level, and it extends about as high in the Mexican state of Veracruz, which is near its northern limit (Ridgway, 1911:31). On Mount Duida in Venezuela, this generally lowland species has established itself in the Subtropical Zone and occurs as high as 6700 feet above sea level, where it is represented by a distinct, dark-colored race, *duidae* (Chapman, 1931:83).

Throughout Central America, the Great Antshrike inhabits low and very dense second-growth thickets, often where tall, rank grasses grow beneath the bushes and add to the impenetrability of the vegetation. Clumps of bamboo along the banks of streams (Richmond, 1893:500) and patches of tall wild cane or great-leafed wild plantains (Carriker, 1910:601) also provide favorable habitats. In Central America, the antshrike appears not to enter the primary forest and it rarely even penetrates the heavier secondgrowth, but in northern Colombia a related race, *granadensis*, is said to frequent low, swampy forest (Todd and Carriker, 1922:319).

When a female Great Antshrike visited my dooryard one May, she was followed by a noisy crowd of suspicious Song Tanagers. Possibly she was the first Great Antshrike they had seen—she was the first that I had seen in the vicinity of my house—and the strangeness of the visitor may have caused the excitement among the resident birds. The antshrike flew into a dense hedge at the back of the yard and was not seen again.

FOOD

The food of the Great Antshrike appears to consist almost wholly of insects and their larvae, varied by an occasional small lizard. The antshrikes hunt through the thickets near the ground, and sometimes they loudly rustle the dry, dead leaves of

banana plants in deserted plantations choked with bushes, as they ransack the folds for prey. Richmond (*loc. cit.*) states that the Great Antshrike often hunts on the ground, but I have not seen it do so. Although it is not particularly shy in the presence of man, the density of the low vegetation in which the antshrike lives makes observation of its habits extremely difficult.

VOICE

The song of the Great Antshrike is a long-continued, loud roll, uttered with increasing speed and often becoming so rapid at the end as to defy transcription: *took took too to to to t' t' t' rrrrr*. This verse is often, but by no means invariably, terminated by a nasal *wahh*, a sort of buzzing growl of most peculiar intonation which does not carry as far as the notes that precede it. Although somewhat harsh when heard near its source, this powerful song carries far and is distinctly melodious when softened by distance. From March to June or July, the peculiar song sounds far and wide over the low, impenetrable thickets where the antshrikes lurk. Often they perform unseen in the dense vegetation, but at times the male may rise to sing from a conspicuous perch about 20 or 30 feet up in an isolated tree standing in or at the edge of the tangled thicket. Sometimes he has continued to sing unperturbed while I stood watching in plain view below him.

The female has a song very similar to that of the male, but her voice is less full and resonant. The song that I have paraphrased is subject to many variations in both form and pitch. Sometimes the speed of delivery is almost uniform throughout, and again it may begin with the usual slow tempo, be accelerated, then slow down toward the end. Deep, throaty, often long-continued rattles are uttered by both sexes. When their nest or young appear to be in danger, the distressed parents complain with a full, throaty, churring note, *kerrr*.

NEST AND EGGS

In El General, the Great Antshrike begins to nest in April, if not earlier, and continues until at least July. Twelve years after I began to hunt for the nest of this elusive bird, my search was rewarded. On May 26, 1942, while passing along a narrow, little-used path that traversed a low, entangled thicket near a rivulet on my farm in El General, I discovered an antshrike sitting in its nest close in front of me. The nest was an ample structure, attached basket-like by its rim in typical antbird fashion, but about twice as bulky as that of any other antbird that I had seen. Two slender, diverging green stems of the scrambling composite *Eupatorium vitalbae* formed the supporting arms. From these, in the center of a low bush, six feet above the ground and close beside the pathway, hung the deep, open cup. The outer framework was of long, slender, dry, herbaceous vines, many of them looped over the supporting arms, forming a wide-meshed basket that served to hold in place the very thick layer of dry leaves that made up the bulk of the structure. These leaves were largely from monocotyledonous herbs and included strips of the huge foliage of *Heliconia*, *Calathea*, and related plants. Some of the pieces, broad and long, were curled and twisted into the nest. A mat of curled, slender, dry, herbaceous vines formed the lining in the bottom. The nest measured 6 inches in height by 5 inches in overall diameter. The cavity was $4\frac{3}{4}$ inches deep by $4\frac{1}{2}$ inches in diameter.

On April 20 of the following year, I found a nearly completed nest near the site of the first, but it was on the opposite side of the rivulet. This second nest was just within the low, dense thicket which had grown up on a field that had been planted with maize in the preceding year. The antshrikes apparently liked this younger growth better than the thicket where they had nested a year earlier, for the latter was now two years old and much taller than when they had made their home in it. The new nest was five feet above the ground, supported between the stems of saplings growing close together, and it resembled the first nest in construction.

Each of the nests contained two eggs, curiously marked and of great beauty. They were broad and blunt, dull creamy white in ground color, and marked with heavy, widely scattered dark chocolate and blackish blotches and spots which were most numerous on the broader end, and they were covered all over with indistinct spots and crooked criss-cross streaks of purplish brown and pale lilac. One egg in the first nest had a heavy, diffuse pigmentation of brown on the broader end, and those of the second set were suffused with pale lilac. The eggs of the first set measured 29.4 by 23.0 and 30.2 by 22.2 mm; those of the second set measured 28.2 by 23.0 and 29.4 by 22.2 mm.

I am aware of no additional Central American records of the nest of this species. Belcher and Smooker (1936:803) state that in Trinidad the Great Antshrike (*T. m. semifasciatus*) breeds from May to July, inclusive. The nest, as described by them, is rather similar to those that I found in Costa Rica, except that it contains no distinct lining. They mention one set of three eggs, although two is the usual number. Six eggs of this race averaged 27.8 by 21.7 mm.

INCUBATION

While I examined my newly found first nest and its two eggs, the antshrikes were loud in their protests. The black-backed male appeared to be the more perturbed, for he ventured far nearer than his brown-backed mate, flitting through the bushes with his long black crest raised, and repeating a loud note that sounded like *kerrr*, which must have warned all the neighborhood, friend and foe alike, that a nest was being molested. At times he approached within two or three yards of me, still voicing his complaints. His mate was equally vociferous but less obvious, keeping herself well hidden in the undergrowth while she scolded me. The cries of anger and distress of this pair followed me for a long while after I had finished writing my notes and started away.

When I returned in the middle of that same afternoon to set up the blind for further studies of the nest, I found the male sitting. On my arrival, he left the eggs and hopped through some neighboring bushes, again protesting loudly. Soon, however, he returned to the nest and covered the eggs, while I worked only four or five yards away. It was necessary to clear a space in the thicket for the blind and to level off a little platform on the steep slope where I could sit. While I chopped and dug, the male antshrike continued to cover the eggs. The nest was so deep that he was quite invisible to me even when I stood with my eyes on his own level, and doubtless he felt a degree of security in concealment.

On the following day, May 27, I entered the blind at dawn. For 50 minutes I neither saw nor heard the antshrikes. At 5:55 a.m., I first heard the voice of the male off in the thicket—a long-drawn, throaty, rolling call, beginning loudly and gradually dying away. He repeated this call and soon appeared near the nest, but

the female, which had passed the night in the nest, continued to sit low until the male alighted on the rim. Then, at 5:58 a.m., she silently went off, and the male took his place on the eggs.

For more than two hours, the male antshrike sat in silence. At 8:10 a.m., the female gave a very long rolling call. It began slowly, rapidly accelerated, and then gradually became slower toward the end. She approached the nest, then drifted away, from time to time calling in the bushes, now with a shorter roll and in a lower voice. At 8:24 a.m., she came to the nest and stood on the rim. The male was slow to leave but finally made way for her. She looked carefully around, then settled on the eggs.

For the next four hours, the female incubated. Like the male, she sat very low, so that, with my eye at the level of the nest, she was invisible, although at times I could see the tip of her tail. Sometimes, too, an intensely red eye gleamed through the meshes in the side of the nest. By 9:21 a.m. the sun was beating down on the blind so hotly that I slipped out behind it to cut some leafy boughs to cover the top. The rustling of the foliage caused the female to leave the nest and call in the bushes nearby. She repeated again and again the long, accelerated roll, terminated by the peculiar, growling note, then, after seven minutes, she returned to the nest. For the next two hours she incubated in silence. At 11:32 a.m., hearing the voice of another of her kind sounding faintly in the distance, she hopped from the nest and called again and again. After 17 minutes of this, she went back to her eggs. At 12:23 p.m. the male came at last, uttered once a rapid, harsh, clicking call, stood on the nest's rim, and relieved his mate of her long spell of incubation. Thereupon, I ended my watch.

My vigil was resumed at 1:25 p.m. on May 29, during a lull in the heavy rain which had begun before noon. The female was then sitting. At 1:38 I heard the male's long, accelerated roll, repeated over and over, each time sounding closer. At 1:44 he emerged from the bushes and hopped upon the rim of the nest above his mate, who promptly left. He looked carefully into the nest, bending his head far down into the cup, then settled down to incubate. He continued quietly to cover the eggs all afternoon, while rain fell steadily. At 5:42 p.m. a long-drawn, throaty rattle announced the female's approach. She promptly replaced the male; and at 6:00, when the light was failing, I left her sitting in the rain.

As in all other antbirds that I have studied, male and female shared the task of incubation by day, but the female attended the nest through the night. Their diurnal sessions were somewhat longer than those of smaller antbirds. On the morning of May 27, the male sat for 2 hours and 26 minutes; then the female was in charge for 4 hours less one minute. On the rainy afternoon of May 29, the male incubated for 4 hours less 2 minutes. The day appeared to be taken up by two long sessions by the male, separated by one of the female, much as in the Quetzal. The eggs were covered for 96.4 per cent of the 11.5 hours of observation.

At this nest, as at the one that I found the following year, both parents sat very closely, allowing me to approach to within a foot or two, then suddenly dropped off, diving into the low, dense vegetation, where they raised their peculiar, loud outcries of alarm. Sometimes it was necessary to shake the first nest in order to make the male leave it; then, if I disappeared into the blind, he would return to the eggs in two or three minutes.

The nest that I found when nearly completed on April 20, 1943, contained two

eggs on April 23. Both of them were pipped on May 9 and one had hatched by the afternoon of May 10, but the chick failed to emerge from the other. Thus the incubation period was 17 or 18 days.

THE NESTLINGS

When I approached the first nest at 10:30 a.m. on June 5, 1942, I found the female antshrike sitting. She allowed me to come within a foot of touching her, and then she fluttered to the ground and vanished promptly in the bushes. When out of sight, she began to voice her loud, harsh complaints. Her departure left a single nestling exposed to view. Its skin was dark flesh-color and, as in most newly hatched antbirds, perfectly naked. But the buds of the feather sheaths of both the remiges and the rectrices and of the contour feathers along the center of the back were visible through the transparent skin. The eyes were tightly closed, and the interior of the mouth was yellow. The second egg failed to hatch and when opened was found to be without any trace of an embryo.

Two days after the first egg hatched, I found the male antshrike covering the single nestling and the unhatched egg. He permitted me almost to touch him, then fluttered to the ground, seeming to fall, and at once began his loud complaints. He stayed very close to me, sometimes advancing to within three or four feet. Almost as soon as I withdrew from the nest, and while I watched unconcealed about 15 feet away, he returned to cover the nestling. This difference in the behavior of the male and the female was constant. The female scolded just as earnestly as her mate, but she stayed out of sight; he, on the contrary, regularly came close to express his displeasure at my intrusion. As they scolded, both parents raised the long feathers of their crown, which were black on the male, rich brown on the female. The male at times spread the feathers in the middle of his back to reveal the usually hidden basal portions which formed a conspicuous white patch.

On June 9, when the nestling was four days old and covered with sprouting pinfeathers, I watched the nest from 5:50 to 10:50 a.m. In the five hours, the young antshrike was fed only five times, thrice by the male and twice by the female. The meals, however, were usually big and substantial. A whole small lizard formed one meal, while the rest, as far as I could see, consisted of insects or their larvae, including a smooth caterpillar about an inch long, and the abdomen of a big, green, cricket-like insect. The male brooded the nestling for a total of 127 minutes, most of which was accounted for by a long session of 92 minutes and another of 26 minutes. The female brooded for a total of 84 minutes, and her longest session lasted 35 minutes. Thus the nestling was covered for 211 minutes and left exposed for 89 minutes during the five hours. The female was consistently far more cautious in approaching the nest than her mate. Sometimes, while she stood on the rim looking down at her nestling, she uttered a long-drawn, low, throaty roll or rattle.

After the nestling was six days old and bristled with long pinfeathers, the parents no longer brooded it so constantly. Yet even when absent they seemed to keep a watchful eye on the nest. Whenever I passed that way, I heard one or the other parent scolding loudly, unseen in the bushes and rank vines of the thicket. If the male were present when I visited the nest, he would now come within half a yard of my upraised hand, always crying loudly. The female still protested from a greater distance, usually keeping herself screened by the low vegetation.

On the morning of June 14, when the nestling was nine days old and its feathers

were beginning to expand, I watched again for five hours, from 5:10 to 10:10 a.m. The young antshrike was now fed more frequently, a total of 13 times. Seven of these meals were brought by the male and six by the female. Again, nearly all of the objects brought to the nestling were quite substantial. All appeared to be insects, adult or larval. Big caterpillars were a favorite article of food.

The partly feathered nestling was brooded three times by the male, for a total of 64 minutes, and twice by the female (after her first morning departure from the nest), for a total of 40 minutes. Both parents also spent brief periods, up to nine minutes, perching on the nest's rim, in the attitude of "on guard" or "inspection"—as one also sees in other antbirds, including the Slaty Antshrike and the Tyrannine Antbird, after their nestlings no longer require much brooding. At the conclusion of a period of standing on the nest's rim, the parent either jumped down into the deep cup to cover the nestling, or else it flew away through the thicket. As the morning grew warmer, the latter course became more frequent.

The parents were exceedingly noisy while attending their nest on this sunny morning. They called or sang frequently while they hunted through the surrounding thicket, and sometimes they continued their loud utterances while they approached the nest with a large object in the bill. The female voiced her long, throaty rattle while standing on the nest's rim, and while brooding she answered her mate's calls in an undertone. Once, when there was a commotion in the thicket, a sharp call of alarm from the male sent the female from the nest; and then the excited notes continued to emanate from the depths of the tangled growth. An Orange-billed Nightingale-Thrush also gave a mewling call, but I could not discover the cause of the disturbance. During the last half-hour of my watch, the pair of antshrikes neglected their nest while they sang back and forth almost constantly, the female in some bushes within view of the blind, the male out of sight in the thicket. They seemed not to work hard to keep their nestling supplied with food.

The development of the young antshrike was rapid. Its eyes, tightly closed when it hatched, began to open when it was two days old. At this age, the sheaths of the remiges already projected an eighth of an inch from the skin, and the dark buds of the feathers on head and body could be seen beneath the skin. When the nestling was six days old, the pinfeathers on its wings and back had become very long. By its eighth day, these pinfeathers, leaden in color, formed a horny panoply over the nestling. The feathers were just then beginning to escape from the tips of these conspicuous sheaths.

When ten days old, the nestling was nearly clothed with expanded plumage, which on the upper parts was dark brown, with fine, distinct, dusky, transverse bars. This barring in the juvenal plumage suggested closer kinship to the barred species of *Thamnophilus* than is revealed by the uniform expanses of color in the adult *Taraba*. The young bird clung so tightly to the bottom of its nest that I desisted from my attempt to lift it out for a view of its ventral plumage, knowing that too forceful pulling might result in bloody, cut toes. At the same time, it voiced loud cries of distress. All the while that I was at the nest, the male flitted around very close, at times advancing within my reach, uttering his loud, churring complaints.

As I passed through the thicket on my way to visit the nest on the morning of June 17, the female antshrike began to scold while I was still a good distance away. As I suspected, on reaching the nest I found that the young bird had departed, at the age of 12 or at most 13 days. While I looked into the empty basket, the male

came very close and protested as energetically as though the nest still contained something to be defended. It seemed useless to search for the fledgling in the tangled, impenetrable growth; thus ended a most satisfyingly intimate study of a retiring bird of the thickets.

The single nestling that hatched in the nest which I found the following year disappeared before it was feathered, the victim of some unknown predator. But on the morning of August 15, 1941, at the edge of a thicket beside a pasture on my farm, I had met a female Great Antshrike with an insect in her bill. She peered out through the bushes and seemed ill at ease. Searching for a nest, I found a stubby-tailed fledgling resting low in a bush. The young bird perched, undisturbed by my scrutiny, but the parent protested vigorously. As the young antshrike flew deeper into the thicket, I saw that its brown back was barred, like that of the other young bird whose development I watched in the following year. These two brown-backed fledglings were probably both females, for Ridgway (1911:30) described a male nestling as being wholly black above, with very indistinct narrow vermiculations of rusty brown on the tips of some of the feathers. The throat and chest of this male nestling were dull grayish, broken by broad bars of black and more narrowly barred with light buffy brown, and the rest of the under parts were variously barred and vermiculated. The fledgling that I saw in mid-August must have hatched from an egg laid in the first half of July.

SUMMARY

The Great Antshrike inhabits low, dense, second-growth thickets, often where tall, rank grasses abound, in the humid lowlands. It ranges upward to about 3000 feet above sea level in southern Costa Rica. Its food includes insects and lizards.

The male's song is a loud, far-carrying, long-continued, accelerated roll, which is often terminated by a peculiar nasal *waah*. The female's song is similar but less full and resonant. Deep throaty rattles and churrs are uttered by both sexes.

In El General, the breeding season extends at least from April to July. Only two nests were found, in low, dense, second-growth thickets. Both were beside a pathway or near an opening; they were 5 and 6 feet above the ground. The bulky, open nests, suspended by their rims, were composed chiefly of large pieces of dead leaves, held together by herbaceous vines, which also formed the lining.

Each nest contained two eggs marked with chocolate, purplish brown, blackish, and pale lilac on a creamy ground.

The female incubated through the night, and by day she alternated with her mate. Diurnal sessions were long, and each parent took charge of the nest for four hours continuously. In 11.5 hours of observation, the eggs were covered for 96.4 per cent of the time. In one instance, the incubation period was 17 or 18 days.

Both parents brooded and fed the nestling, bringing it adult and larval insects and rarely a lizard. A single four-day-old nestling was fed only five times in as many hours. When nine days old, it was fed 13 times in five hours, but its meals were substantial. The parents were very noisy while attending the nestling.

The parents were watchful, and even when they were not brooding, a man could rarely approach the nest without being seen by them. They raised a loud outcry, and the male came within reach of the intruder, at times displaying a usually concealed white patch in the middle of his black back. The parents never attacked or simulated injury.

When newly hatched, the dark-skinned nestling was devoid of down and the interior of its mouth was yellow. Its pinfeathers grew very long before the plumage began to expand. At ten days of age the juvenal was nearly covered with expanded feathers. The barred juvenal plumage suggests affinity with *Thamnophilus*. The nestling left the nest when 12 or 13 days old.

SLATY ANTSHRIKE

Thamnophilus punctatus

This small antshrike, about five and a half inches in length, lacks the prominent bars of many of its congeners. In the male, the top of the head is largely black, mixed with slate-gray on the forehead. The feathers of the hindneck and back are black and slate-gray, and those in the center of the back have pure white basal portions, which are revealed only on special occasions. The wings are black with white tips on all the coverts and white or light gray margins on the remiges. The superciliary region, the sides of the head and neck, and the under parts are gray. The female is largely olive-brown above. The feathers in the center of her back have concealed white bases, and the dull chestnut-brown upper tail-coverts have buffy tips. The dark chestnut-brown tail feathers have white or buffy ends. The wings are dusky with pale buffy tips on all the coverts and lighter margins on the remiges. The chin and the throat are olive-buff and the remaining under parts are buffy olive, which becomes more yellowish in the middle of the abdomen and more rufous on the under tail-coverts. In both sexes, the eyes, bill, and feet are dark.

The Slaty Antshrike ranges from British Honduras to southern Brazil. North of Panamá, it is confined to the Caribbean side of Central America, at low altitudes. According to Carriker (1910:603), it is scarcely ever found in Costa Rica more than 1500 feet above sea level. In the Santa Marta region of Colombia, it extends occasionally as high as 3000 feet, but it is of irregular occurrence above 1500 feet (Todd and Carriker, 1922:314). It lives not only in the rain forest but also in second growth, and it even inhabits semi-arid regions, especially in South America.

In the forests of Barro Colorado Island on the Isthmus of Panamá, where alone I have watched this antshrike, it forages in the lower strata of the vegetation, hopping and flitting deliberately through the foliage and vine tangles as it searches for insects and other small creatures. It rarely ascends high in the great trees, nor does it often alight on the ground. Johnson (1954:50) found the Slaty Antshrike frequent in the "social aggregations" of which White-flanked Antwrens and Velvety Antwrens were the leaders. One sex or the other, and sometimes both members of a pair of Slaty Antshrikes, was "invariably present" in these social flocks as they roamed through the lower levels of the forest. Along with other members of these flocks, the Slaty Antshrike foraged with army ants for short periods, when the path of the raiding ants and their attendant birds happened to cross that of the social flock. On several occasions, Johnson (*op. cit.*:60) saw an antshrike forage among the ants on the ground. But it is far from being a regular or constant associate of the ants, and in my experience it often goes its own way, apart from any flock. Almost fearless of man, it is easy to approach and to watch.

Slaty Antshrikes are usually solitary or in pairs, and they probably remain mated throughout the year. They seem never to form flocks of their own kind, and it is rare to see two adults of the same sex together. When two adult males approached each other among some vines on March 7, 1935, they postured with their tails fanned out, displaying the white tips of the black feathers, and with the plumage of the back spread to reveal a patch of pure white in its center.

VOICE

The song of the Slaty Antshrike is a long wooden roll, which becomes faster and slightly higher in pitch as it proceeds and ends with an emphasized note of peculiar and characteristic quality: *r-r-r-r-r-r-wánk*. The song is heard chiefly as the antshrike roams through the woodland. At its nest, it uses another note, in a sense the reverse of this, for the emphasized, staccato note introduces the long, ascending rattle or roll: *wánk-r-r-r-r-r*. Both sexes deliver these calls with throat distended and vibrating and tail shaking rapidly up and down—movements which suggest that they throw all their energy into their utterances. At times the antshrikes give a simple *churr*, without the emphasized note at the beginning or end. A number of shorter phrases and monosyllables are used to express varying emotions, especially at the nest.

NEST AND EGGS

In the Canal Zone, breeding begins early, and I found a nearly completed nest on December 22, 1930. The nest is hung in the horizontal fork of a small tree or a shrub in the undergrowth of the forest, from 3 feet (Harrower, MS) to 12 feet (Stone, 1918) above the ground. Of the six nests which I saw on Barro Colorado Island, two were 6 feet high, three were at 8 feet, and one was 9 feet above the ground. These nests were open cups, attached by their rims to the supporting arms of the fork. Composed of fine, blackish fibers and rootlets, they were so thin that the eggs could be seen through the meshes of the bottom. A variable amount of green moss was attached to the outer surface of these nests. On some it covered almost the whole exterior of the cup and hung in graceful tufts below it, whereas on others it was sparingly applied and left much of the surface exposed. One of the nests had much moss on one side but very little on the other side. A typical nest measured $2\frac{1}{2}$ by $2\frac{1}{4}$ inches in internal diameter by $2\frac{3}{8}$ inches in depth.

On December 22, 1930, I saw both the male and the female bring a few contributions to a nest which already appeared to be nearly finished. On February 13, 1935, I watched a nest in an early stage of construction. It was then a thin, open weft of fine fibers with tufts of green moss attached to the outer side. Both sexes came with material and each sat in the delicate meshwork and arranged with care the fibers it had brought. Once the male churred softly while he rested in the nest. After arranging the last contribution that he brought while I watched, the male perched beside the structure and quietly inspected it for a minute or more. The slow, deliberate movements of these antshrikes contrasted strongly with the rapid, sprightly motions of a pair of Fulvous-bellied Antwrens that I had watched building their nest earlier on the same morning.

Building proceeds slowly, and a considerable interval may separate the virtual completion of the nest and the laying of the first egg. The nest which on December 22 appeared to be practically finished was still without an egg on the following January 5; but when I revisited it on January 13, there were two eggs. The nest which I found at an early stage of construction on February 13 seemed to be completed a few days later, but there were no eggs in it at noon on March 2. By the evening of March 5, it held two eggs. Many birds of the tropical forest allow a number of days to pass after the completion of their nest before they begin to lay, but in the Slaty Antshrike this interval is surprisingly long.

Each of my six nests on Barro Colorado contained two eggs or nestlings, and



Fig. 9. Nest and eggs of Slaty Antshrike. Barro Colorado Island, Canal Zone, January 12, 1931.

this is the number reported in three additional nests in Panamá and Costa Rica by Carriker (1910:603), Harrower (MS), and Johnson (1953). The eggs are white, heavily spotted and blotched, especially on the thick end, with chocolate or umber. The measurements of six eggs average 23.9 by 16.6 mm. Those showing the four extremes measured 25.4 by 16.7, 22.6 by 16.7, and 24.2 by 16.3 mm.

In the Canal Zone, laying has been recorded from the end of December well into July. The dates of 12 occupied nests (including five of the six which I found) are given by Eisenmann (1952:34). Six of these nests were discovered in July, but the concentration of records in this month probably reflects the frequency of ornithologists on Barro Colorado rather than a peak of breeding activity by the antshrikes. Carriker found a set of eggs, well advanced in incubation, on the Río Sixaola in the Caribbean lowlands of Costa Rica on August 6, 1904.

INCUBATION

Male and female share incubation by day and the female covers the eggs through the night. The parents sit steadfastly and frequently remain at their post until their human visitor shakes the branch that supports the nest, advances his hand to



Fig. 10. Male Slaty Antshrike incubating eggs. Barro Colorado Island, Canal Zone, January 12, 1931.

within a few inches of them, or sometimes until he touches them. When I found my first occupied nest of the Slaty Antshrike—which was also my first nest of any kind of antbird—the male happened to be covering the eggs. When I shook his nest he jumped off and, perching close by, called *wánk-r-r-r-r-r-r* over and over while keeping his eyes on me, until finally his mate approached through the forest and joined him. When I had finished making measurements and taking notes, I retired behind a neighboring tree to watch. It was then nearly 1:00 p.m. At 1:01 the female flew up to the nest, repeated several times a call like that which I had heard from her mate, then settled down to incubate. She sat for 34 minutes, after which the nest was neglected until, 32 minutes later, the male entered it after calling many times. He incubated for 43 minutes, then left with a sudden jump as the female silently approached. She settled on the nest ten minutes later and then sat quietly for the next hour, or until 4:00 p.m., when I left.

On the following morning, the male was sitting when I arrived at 8:09 a.m., and he continued to incubate until 10:20, when he departed in response to a call, probably that of his mate, coming from the distance. The female entered the nest at 10:37 and sat until 11:19, when I also left. Both parents habitually approached the nest from the center of the sapling that held it, by means of a series of rapid sideward hops along the supporting branch. They entered the nest facing outward, and usually they continued to sit with this orientation, although rarely they turned to face into the crotch.

A few days later, in order to learn which parent slept in the nest, I watched as night approached. The male was sitting when I arrived at 5:00 p.m., but he left as I gently lowered the branch that supported the nest in order to make certain of his identity. He flew away in silence, and a few minutes later the female came silently to settle on the eggs. She remained quietly at her post, while daylight faded from the forest and a distant Great Tinamou heralded the approach of night with whistles of incomparable beauty. At 6:45, when the undergrowth around me was in deep dusk, I approached the nest for a final close inspection, to make certain that I had not mistaken the sex of the bird that sat in it. As I turned to leave, a stick broke with a sharp report beneath my foot, frightening the female from her nest. Repenting the blunder, which I feared would cause the eggs to remain unwarmed through the night, if not to be permanently abandoned, I retreated a few steps and watched. After a few minutes, the bird came hopping back to the nest that she could hardly see. After another interval, I switched on my flashlight and saw her white-tipped tail sticking up above the nest's mossy rim. This experience demonstrated the Slaty Antshrike's extraordinary attachment to her nest, and it also taught me to make visits of this sort at the night's end, not at its beginning.

As I went into the forest at daybreak on May 7, 1935, I found a nest that I had not previously seen. In the open cup was a loose, disordered mass of brownish feathers, some of which spilled over the rim. From one side of this mass some tail feathers stuck out, but in the dim light of a wet dawn I could distinguish neither head nor bill. I thought that some bird had died and disintegrated in its nest. Approaching closer, I touched the nest's bottom: the heap of loose feathers drew together immediately and darted away so swiftly that, in the obscurity, I could not distinguish what bird I had seen. Returning later in the morning, I found a female Slaty Antshrike sitting in this nest with her contour feathers laid flat in their usual diurnal position. A few nights later, I again found the female sleeping in this nest with her feathers so widely and loosely spread that they seemed not to be attached to a bird. This, then, was the Slaty Antshrike's normal manner of sleeping in the nest, as I have since found it to be in other antbirds.

The Slaty Antshrikes' great attachment to their nest and eggs was vividly demonstrated when I took some photographs of my first nest. While I set up and adjusted the camera, the male flitted close around me, coming at times within six feet, and calling almost constantly as long as I was occupied there. The more timid female stayed a little farther away. After the camera was ready, I retired into a blind of palm leaves which I had built against the buttresses of a neighboring great tree. Hardly had I entered this nook when the male took his place on the nest, a yard from the camera, and I pulled the thread that released the shutter. After each change of film, one parent or the other promptly returned to the nest, with the result that in little over an hour I obtained five exposures, three of the male and two of his mate.

Because of the loss of eggs to predators, I was unable to learn the length of the incubation period, but at one nest Johnson (1953) found this period to be about 14 days.

THE NESTLINGS

When I revisited my first nest on January 16, the male antshrike was sitting. When my finger touched his breast, he flitted to a perch a foot away and stood there,



Fig. 11. Female Slaty Antshrike incubating eggs. Barro Colorado Island, Canal Zone, January 12, 1931.

spreading and closing his tail feathers, while he silently watched me feel the contents of the cup. My fingers encountered two nestlings, which had not been present on my last visit, three days earlier. Removing one, I found that it was quite naked, with no trace of down on its dark flesh-colored skin, and its eyes were tightly closed. As I lifted it out, the parent called a few times. After examining the nestling, I returned it to the nest and withdrew a few paces to watch. Almost immediately, the antshrike resumed brooding.

On my next visit, four days later, I found the female resting beside the nest and looking down at her nestlings, guarding or inspecting them. Here she stayed motionless until I was only a yard from her, when she jumped to the ground and beat her wings against the carpet of dead leaves, as she fluttered slowly and apparently painfully away. I followed, and after she had lured me onward about 20 feet she rose into the nearest bush and called. Almost immediately her mate appeared, uttering a nasal *churr*, and ventured closer to me than the female had dared. When I returned to the nest, he perched on a twig less than a foot from it in a belligerent attitude, wings spread and fluttering, tail expanded into a fan bordered with white spots, black crown feathers erect and bristling, and the plumage of his back turned outward to reveal a broad central patch of snowy white, the existence of which I had not suspected. When I tried to lift a nestling from its pensile cup, the male lunged forward and bit my finger. Doubtless all his strength went into that nip, yet

it was so gentle that I hardly felt it. Two more swift attacks on my fingers were followed by equally swift retreats, before the antshrike withdrew a short distance. Meanwhile the female, less courageous than her mate, perched in a neighboring bush and complained with a nervous rattle, the while displaying a hitherto concealed white patch in the middle of her olive-brown back.

Many other antbirds have simulated injury when I visited their nestlings, and one other, a Bicolored Antbird, has bitten my hand while I held its nestlings. But at no other of the thousands of nests of many species in diverse families that I have examined have the parents cooperated in this manner, one trying to lure me away while the other attempted to repel me by force. Very rarely has more than one parent been present to use whatever means of protecting its nest it possessed. The nearest approach to the behavior of these antshrikes was exhibited by a pair of Catbirds whose nest in a barberry hedge in Maryland I watched some years later. When I examined the contents of this nest, the female nipped my fingers while her mate buffeted the back of my head. This double attack was repeated many times, and I am sure that it was always the female that bit me, because her bill was conspicuously deformed.

I found the nestling antshrikes, now five or six days old, bristling with blackish pinfeathers, Their eyes were beginning to open. After I replaced the young birds, the male took his stand above them, like a sentinel on guard. Here he stood motionless, while I cut fresh palm fronds to replace the withered ones that formed my blind. Even the loud noise of chopping with my bush knife did not drive him off. When my blind had been made thick enough to conceal me, I entered and watched from 8:50 to 11:30 a.m. In the afternoon I returned and watched from 1:50 to 4:30 p.m., and on the following morning I was present from 8:00 to 10:00 a.m. During these three watches, the two nestlings were fed 11 times by the male and 7 times by the female, making 18 meals in 7 hours and 20 minutes, or 1.2 meals per nestling per hour. Their food included a spider, two larvae, a green insect, a roach, and other insects. A single item was brought in the bill at each visit, and I recognized no vegetable matter. The parent always approached the nest by alighting on the supporting branch between the main stem and the fork in which it hung, then hopping outward to it. While the bird approached, the other parent, if it happened to be brooding, flew away. Each parent always delivered its offering directly to the nestlings. Both parents carried away droppings.

On these two days, the male alone was seen to brood the nestlings, which were still without expanded plumage. He did so for five periods, which ranged from 1 to 92 minutes and totalled 128 minutes. In addition to this, he guarded them for five periods that ranged from two to seven minutes and totalled 27 minutes. Often after standing guard he jumped down into the nest to brood. The female guarded only twice, for 18 minutes and later for 2 minutes. While guarding, the parent stood on the supporting branch just below the fork in which the nest was hung, and often it cocked its head to one side while it intently regarded its offspring. In the depth of the forest, the high canopy of which was penetrated only here and there by a round spot of sunshine, the nestlings needed no shading.

Even when not visible from the nest, the parents were alert to what happened there. After the nestlings' eyes were open, their squeak when I touched them promptly drew a parent from the surrounding undergrowth; and the calls of the

parent who first arrived usually brought the other. Then both scolded me with a nasal *krrr* of most peculiar tone.

The nest that I found on May 7, 1935, would have broken from its support on one side and spilled out the eggs if I had not sewed it up. Both eggs hatched on May 17, and by May 25 the nestlings were well covered with plumage which resembled that of the female. The following night, their last in the nest, she brooded them. Early in the morning of May 26, one young antshrike had left the nest and was perching beside it. Later in the day, both had departed, at the age of only nine days. At this nest, as at the earlier one, the parents often stood motionless at the base of the supporting fork, guarding the nestlings.

SUMMARY

The Slaty Antshrike inhabits rain forest and lighter types of woodland at low altitudes. It forages among foliage and vine tangles in the lower strata of the forest, and it seems to subsist wholly on insects, spiders, and other invertebrates. It is found in pairs at all seasons. When two adult males met, they threatened each other by displaying the white areas in their plumage.

The song is a wooden roll with an emphasized final syllable. A variant, used chiefly at the nest, has the stressed note at the beginning rather than at the end of the series.

In the Panamá Canal Zone, nesting begins in December and continues until at least July or August. The nest is hung in a horizontal fork of a small tree or a bush in the undergrowth of the forest, at heights ranging from 3 to 12 feet. It is a thin-walled cup of dark fibers, with varying amounts of green moss on the outside, and it is attached by its rim to the arms of the fork. Both sexes build.

Two weeks or more may intervene between the virtual completion of the nest and the start of laying. The set regularly consists of two eggs, which are white, heavily spotted and blotched with reddish brown and chocolate. Both sexes incubate by day and the female covers the nest at night. She sleeps with her feathers so loosely spread that they seem not to be attached to a living bird, but if disturbed she promptly pulls herself together. In one instance, the incubation period was 14 days.

Newly hatched nestlings have dark flesh-colored skin devoid of down. Both parents nourish them with insects, spiders, and the like; at one nest the male brought more food than the female. He continued to brood by day after the female had ceased to do so. Both parents often stood beside the nest, guarding its occupants.

Both members of the pair show exceptionally strong attachment to their eggs and nestlings. Often, a sitting bird will permit a human hand to touch it. When driven from the nest, the parent remains close by and calls, bringing the other parent from the surrounding forest. They return to their nest, even in the dusk, while a human stands only a few paces away. A female with nestlings tried to lure me away by simulating injury, while her mate bit my hand which I had placed on the nest. While simulating injury or attacking an intruder, both sexes spread the feathers of the back to reveal the usually concealed white bases.

The nestlings are feathered when eight days old, and a day later they leave the nest.

BLACK-HOODED ANTSHRIKE

Thamnophilus bridgesi

In the antbird family, the sexes often differ strikingly in coloration. The male and female of the Black-hooded Antshrike are so distinct in appearance that they were for a long while classified as separate species, the female being called *Thamnophilus bridgesi*, the male *T. punctatus*. The error was corrected by Cherrie (1893:279), whose extensive field work in southern Costa Rica enabled him to point out the true relationship of these birds. Since the female had been described earlier than the male, the name *bridgesi* became the designation of the species. One may see the two supposed species figured side by side on plate 49 of Salvin and Godman (1879-1904).

This fairly big, heavy-set antbird is about six and a quarter inches in length. The male is nearly everywhere black, with conspicuous white terminal spots on the wing-coverts and narrow white tips on the outer feathers of the graduated tail. His bill and feet are black, his eyes brown. The female, which alone appears to be hooded, has the head and neck black all around, conspicuously streaked with white. Her wing-coverts are blackish with terminal white spots somewhat larger than those on the male. The remainder of her upper plumage is dull dark brown, without spots. Her tail is marked like the male's. Her breast, abdomen, sides, and flanks are slate-gray or olive-drab. The breast has broad whitish streaks which become narrower and fainter posteriorly. She has brown eyes, black upper mandible, and blackish lower mandible and feet.

The Black-hooded Antshrike is confined to the Pacific side of Costa Rica and western Panamá. In Costa Rica, it ranges as far north as the Volcán Tenorio in the Province of Guanacaste, but it is more abundant in the wetter and more heavily forested region to the south of the Gulf of Nicoya. It is common in the lowlands around the Golfo Dulce and the mouth of the Río Térraba, and it is not rare in El General, where it extends upward to about 3500 feet above sea level. Carriker (1910:602) stated that these antshrikes are "usually found in heavy forest, frequenting the undergrowth and low limbs of the trees." My own experience in the upper reaches of the Térraba Valley is somewhat at variance with this. Although the Black-hooded Antshrike is at times seen in the undergrowth of heavy, unbroken forest, it is far more commonly met along the edges of the forest, where there is an exceedingly close stand of bushes and vines, or in woodland from which trees have been cut, leaving light-flooded gaps which become filled with similarly dense vegetation, or in the older second growth, where slender young trees stand close together and are entangled with vines and scrambling shrubs. It is not often found in the lower second-growth thickets where the Barred Antshrike and the Great Antshrike are at home, but in transitional forms of vegetation the three species sometimes mingle.

The birds appear to remain mated throughout the year. Unless they are accompanied by dependent young, they rarely keep company with others of their kind, but sometimes they associate loosely with other small birds of the forest edge and the heavier second growth. They subsist on various insects, spiders, and other small

creatures which they find as they hunt deliberately through the undergrowth. Rarely, they vary their diet with small fruits.

VOICE

Through much of the year, Black-hooded Antshrikes are noisy birds, but after the close of the nesting season, they become quiet and retiring. They have a considerable variety of utterances, the loudest of which is a strong, harsh, rapidly repeated *cack cack cack* that carries a long distance. A somewhat different call is almost equally loud but less harsh, and it sounds like the syllable *wak* deliberately reiterated. A lower, more rolling call may be written *cow cow cow cow k' k' k' cow*. As the antshrikes deliver these diverse phrases, they move their tails emphatically up and down. Their voice is wooden like that of the Barred Antshrike and the Slaty Antshrike.

NEST BUILDING

In El General, nesting may begin early, for on March 26, 1942, I found a pair of antshrikes feeding young as large as themselves. The nest in which these young antshrikes were reared could hardly have been begun later than the first week of February. Another nest, newly completed and still without eggs, was discovered on March 17 of the following year. The nest is placed amid the shrubs and vines at the forest's edge, or in the growth that chokes a small opening in the woodland. More rarely it is situated in the deep shade of unbroken forest. Six nests ranged in height from 22 inches to 12 feet above ground. The lowest was in the forest and, as far as I could ascertain, it never held an egg.

The nest is built by the male and female together, as I have seen in three pairs. They work in an irregular and desultory fashion, arriving together, each bringing material a few times, then drifting away and staying out of sight for a long while. At one nest, I watched for several hours on two mornings without seeing the birds, but in the middle of both afternoons I found them at work. They took nearly equal shares in bringing material, and each sat in the nest to arrange the fibers and give it shape. The female devoted slightly longer periods to this occupation than did the male. He was fairly noisy, calling loudly *weck weck weck weck* as he approached the nest with fibers in his bill. The female usually did no more than answer in nasal monosyllables. This nest, found when newly begun on April 24, appeared to be completed by April 28, although I saw the female antshrike bring an additional strand of material on the following day. Thus five or six days were required for construction.

The completed structure is a typical antshrike's nest, a roomy, open cup suspended by its rim from a horizontal fork at the end of a slender branch. The fabric is composed of fine, dark-colored fibers, including rootlets and fungal filaments, and it is so thin that much light passes through its meshes. Cobweb is employed for binding the nest to its support, and there are usually a few tufts of green moss loosely attached to the lower side.

THE EGGS

In four nests, the complete set consisted of two eggs. In one instance, the second egg was laid two days after the first. The eggs are dull white, with a wreath of bright brown and pale lilac blotches and spots around the large end and a few

speckles scattered elsewhere over the surface. The eggs in one set measured 23.8 by 16.7 and 22.2 by 16.7 mm.

INCUBATION

As in other kinds of antbirds, both sexes incubate. They replace each other on the eggs several times a day, but the female occupies the nest through the night. As a rule, both male and female sit with great steadfastness when approached by a human visitor. Often the sitter will not quit the nest until it, or at least the surrounding foliage, has been sharply shaken. Some antshrikes will almost allow themselves to be touched. I generally used a mirror to examine the contents of nests situated above my head, and more often than not the parent bird remained sitting until the mirror reached the nest. Sometimes it was necessary to strike the supporting branch once or twice to make the bird leave and permit me to see what the nest contained. One female remained covering her eggs while an assistant and I set up a blind only 15 feet from her. The noisy chopping of undergrowth, clearing away of fallen litter, and all the moving around and talking which accompanied the work, failed to make her desert her post.

On jumping from the nest in the face of an intrusion, the antshrike usually drops almost straight down to the lowest vegetation, into which it may vanish before it raises its loud, rattling cry of alarm. Or it may return and look on from a convenient perch while its nest is being examined. One male antshrike, whose nest was ten feet up, came within a foot of the mirror which I raised on a long stick to look into the nest. Beneath the nests that I have studied, the vegetation was too dense and entangled to permit the antshrikes to perform the "broken wing" act; but twice I have seen a male, when driven from newly hatched nestlings, drop to a perch near the ground and only a few feet distant from me, where he relaxed and quivered his wings, repeating this performance in various positions and in plain sight, as though trying to lure me away from his progeny.

At one nest, both eggs hatched 14 days after the last egg was laid. At another nest, the incubation period was 14 or 15 days. At a third nest, there was one nestling and one pipped egg 15 days after the set was complete. When I returned on the following day, the nest was empty. The second egg, if it hatched, required about 16 days of incubation.

THE NESTLINGS

Hatching.—The newly hatched antshrike has pink skin, devoid of any trace of feathers or down, and tightly closed eyes. The interior of its mouth is orange-yellow. At the first nest of the Black-hooded Antshrike that I found, I had the good fortune to be watching from a blind when the first egg unexpectedly hatched. Since the nest had been discovered only on the preceding day and was above reach, I had no notion, when I began my vigil at dawn on June 2, 1937, that incubation was so far advanced. As it grew light enough to distinguish details in the dense, entangled undergrowth of the forest, I saw that the nest was unattended, but at 5:45 a.m. the female antshrike returned to cover the eggs. She sat in silence for the next 74 minutes, then called in a subdued voice from the nest. She was becoming restless and doubtless also hungry. At 7:15 she called again, and this time she was answered by the male. A minute later she flew away, after sitting continuously for an hour and a half. Then the male alighted on a twig a few yards from the nest and called

wak wak wak wak wak wak in a loud voice all in the same key, moving his tail up and down as he delivered the notes. Next he flew to one of the twigs that supported the nest and called a few times more in the same incautious fashion. Finally, at 7:17 a.m., he settled in the nest.

After the male had been incubating for an hour and a half, the female came quietly and rested on the supporting branch about a yard from him. With the feathers of her crown raised to form a low crest, she called in subdued notes. But her mate did not budge from the nest. After a minute, the female flew off to chase some trespassing bird that I did not see well. She called a few times in a low voice, then vanished.

The sitting male had become restless, often rising up to look down into the nest. At 8:56 a.m., a few minutes after his mate's departure, he picked up the cap of an eggshell and carried it away. I took advantage of his absence to slip from the blind and hold above the nest a mirror, which revealed a newly hatched nestling, but the male antshrike returned so promptly that he caught me in the act and protested loudly. I hurried back to concealment, and he soon returned to carry away the large part of the empty shell. Within 3 minutes, he was at the nest once more, looked intently down into it while standing on the rim, then brooded.

At 9:24 a.m., the female called softly from a nearby point, and the male answered in very low tones. Five minutes later, she called from a nearer position, and he left the nest. Continuing to call softly, she approached the nest by flitting from twig to twig. On reaching the rim, she delayed there for several minutes, silently contemplating her first nestling, which she now saw for the first time. Then she settled down to brood. After she had been sitting for only 7 minutes, the male, at 9:42, returned with a particle of food in his bill. He perched near the nest, but the female neither offered to take it from him nor made way for him to deliver it directly to the nestling. He lingered near the nest, continuing to hold the morsel in his bill. Then, at 9:47, he came to stand directly behind the female and she left. He promptly gave the nestling its first meal, 51 minutes after he had removed the shell from which it escaped. Then he sat in the nest.

At 11:10 a.m., the female antshrike called at no great distance. The male answered with low notes and jumped from the nest to fly in her direction. Soon she appeared, calling rather loudly, although she held something in her bill. At 11:15 she gave the nestling its second meal, delayed about 2 minutes looking down into the nest, then brooded. At 11:28 the male again returned, this time bringing a green insect. The female did not leave in response to his subdued notes, so he approached the nest and perched directly behind her, where he remained for several minutes. At 11:33 the female suddenly jumped from the nest, and at the same instant the male swallowed the insect that he had been holding, evidently quite unintentionally, probably because of the jarring of his perch. Since he no longer had anything to give the nestling, he simply settled down to brood it. He remained there for an hour and 24 minutes before the female returned and called him from the nest. She gave the nestling a green insect, then swallowed the nestling's first dropping, at 12:59 p.m., 3 hours and 12 minutes after the young bird had received its first meal. At this point I ended my long watch.

It is of interest that the male antshrike, although he had been sitting continuously for more than an hour and a half, refused to make way for his mate when she came in the usual manner to replace him in the nest while the first egg was

Table 5
Care of Two Nestling Black-hooded Antshrikes

Date in June, 1937 ¹	Brooding (minutes)			Left uncovered	Feedings (no. of times)		
	Male	Female	Total		Male	Female	Total
2 ²	289	121	410	39	2	2	4
3	212	122	334	61	4	3	7
6	193	106	299	96	5	5	10
9	8	135	143	252	19	12	31
12 ³	0	0	0	395	9	11	20
Totals	702	484	1186	843	39	33 ⁴	72

¹ The observation periods extended from 5:30 a.m. to 12:05 p.m., except on June 2, when the period extended to 12:59 p.m.

² One nestling hatched at 8:56 a.m., the other in the afternoon, of June 2.

³ One nestling left the nest at 6:51 a.m. on June 12, the other stayed until the next day.

⁴ This includes eight meals brought by the female after the male had gone away with the first fledgling.

hatching, or had just hatched, beneath him. Nor did he make any move or utterance, perceptible to me, to acquaint her with what was happening. Hence she went away in ignorance of what had transpired at the nest; her behavior when she returned, without food, 40 minutes later, is evidence that she was unaware that a nestling had hatched. The male antshrike's failure to inform his mate that an egg had hatched accords with the behavior of female songbirds of numerous species, whose nests I have watched at this critical period. Either they cannot, or will not, convey to their mates the information that a nestling has hatched. The latter must make the discovery for themselves, which they often do in less than an hour, but in other instances they do not learn about the nestlings until several days have elapsed (Skutch, 1953).

The second egg hatched in the afternoon of the same day, June 2.

Brooding.—I watched this nest from dawn until noon, or slightly after, on June 2, 3, 6, 9, and 12, on the morning of which the first young bird departed. On the afternoon of June 12, I watched from 2:40 to 5:40 p.m., and I resumed my vigil at dawn the next morning, continuing until the departure of the second nestling at 6:27 a.m. on June 13. Some of the data gathered in these watches is presented in table 5, which covers events up to noon on June 12.

On the day the nestlings hatched, the nest was almost constantly covered. Thereafter, the parents brooded less on each succeeding day for which I made a record. At first, they regularly brooded the nestlings after feeding one of them. Late in the morning of June 3, the day after the nestlings hatched, I witnessed the first departure from this routine, when the male, after delivering food, flew away instead of settling in the nest. Henceforth, with increasing frequency, the parents left after feeding. Associated with the decrease in the amount of brooding was a change in the manner of disposing of the droppings. At first, the parents swallowed the fecal sacs after they delivered food and before they settled in the nest to brood. Early in the morning of June 6, when the nestlings were four days old, the male carried away a dropping after he delivered a meal; then he promptly returned to brood. In the middle of the same morning, the female, after feeding a nestling, flew off with a dropping and stayed away for more than an hour, but later in the morning she carried off a dropping and returned after four minutes to brood. After this, droppings were regularly carried away instead of being swallowed.

The male brooded far more than the female. At first, when each parent as a rule remained sitting until relieved by the other, the length of each period of brooding

was determined by the absent partner rather than by the brooder's willingness to continue at its post. Since the female usually remained away longer than her mate, he covered the nest for longer periods than she took; because the male was quicker to return, the female brooded less. He continued to take the larger share in covering the nestlings by day at least until they were four days old. But when they were seven days old and bristled with long pinfeathers, the male had practically ceased to brood, although the female continued to do so, and now she brooded more than he did. And the female, of course, was responsible for keeping the nestlings warm through the night. The male's longest periods of continuous brooding were as follows: June 2, 122 minutes; June 3, 73 minutes; June 6, 92 minutes; June 9, 8 minutes. The female's longest periods of uninterrupted brooding were: June 2, 91 minutes; June 3, 42 minutes; June 6, 33 minutes; June 9, 42 minutes. The totals are given in table 5.

On arriving, each parent always alighted on the supporting branch some distance inward from the nest. The bowing down of the branch and nest under the weight of the newcomer was the signal for the departure of the sitting partner, if it had not already left. The antshrike entered the nest from the base of the fork in which it was suspended. Thus, when the bird first settled in the nest, it faced the extremity of the branch, and it invariably preserved this original orientation as long as it sat, never turning to face inward toward the stem of the nest tree. I have noticed at other nests of the Black-hooded Antshrike, and also at the nests of other species of antbirds which build similar vireo-like structures, that they nearly always sit facing outward. Plain Antvireos, however, are less constant in their orientation while sitting in the nest. The Yellow-green Vireo, on the contrary, habitually sits facing the crotch to which her nest is attached, with her tail rather than her head outward.

Feeding.—As long as the parents continued to alternate their visits to the nest, each remaining to sit until relieved by the other, each brought food approximately an equal number of times. After the nestlings required little warming by day and the parents became quite independent in their comings and goings, the male brought food more often than did the female. The difference in their rates of feeding was especially pronounced on the morning of June 9, when the male brought food 19 times and the female only 12 times. In the first 1 $\frac{3}{4}$ hours of June 12, the male brought food 9 times and the female only 3 times. After that, the first fledgling, which had already dropped from the nest, vanished amid the foliage. Subsequently, the male, apparently giving his attention wholly to the fledgling, was not seen again at the nest, which until the exit of the second fledgling was attended solely by the female. Until the first fledgling's disappearance, I had seen the male bring food 39 times and the female 25 times, in about 25 hours of watching.

Although the rate of bringing food increased until the young left the nest, it was at best rather slow compared with that of many small insectivorous birds. When the two nestlings were seven days old, they received food only 31 times in 6 $\frac{1}{2}$ hours, or at the rate of 2.4 feedings per capita per hour. But substantial portions compensated for infrequent feedings. This was especially true during the nestlings' first days, when they were still brooded for long periods. Then it seemed to be the parents' practice to bring to the nest the largest insects that they could find, or at least the biggest that the little birds would be able to swallow. Usually the insects were so bulky that the young antshrikes struggled to gulp them down.

The infrequent feedings seemed to be correlated with the parents' habit of

coming to the nest only at long intervals and remaining a long while. As they did less brooding, the parents brought food more often, and the articles which they delivered were not so consistently large as before, especially when the nestlings' increased capacity is taken into account. The young birds' diet consisted almost wholly of mature and larval insects, spiders, and the like. A large proportion of the insects were green, suggesting that they had been caught on foliage, but a few were brown and had apparently been hiding on the bark of trees. The wings and legs had been removed from the biggest insects before they were brought to the nest, and on several occasions an enormous green abdomen alone was presented to a nestling. Once I saw the male bring what appeared to be fruit pulp, and once the female came with a round object that resembled a berry.

Defense of the nest.—Although the male antshrike was the more faithful attendant of the nest, the female was the more furtive. With rare exceptions, she came in discreet silence, but the male's loud, not unpleasant *cow cow cow cow k' k' k' k' cow* usually gave warning of his approach before he emerged from the undergrowth. If he did not sing, he might call loudly as he drew near the nest, and sometimes he both sang and called. As they grew older, the nestlings learned to recognize his voice, and on hearing it they lifted up their open mouths in anticipation of food, before they could see him.

The parent antshrikes defended their nest with zeal. One morning, while the female brooded, a Squirrel Cuckoo, foraging through the bushes, happened to alight on the base of the branch that supported the nest. Quick as a flash, the female antshrike pounced upon the long-tailed trespasser, far larger than herself, and it fled with all speed, driven almost to the ground by its assailant. After the cuckoo's departure, the antshrike perched below her nest and called a few times in a full, low voice, then flew away. I noticed indications of antagonism between the Black-hooded Antshrikes and a pair of Great Antshrikes, which sang loudly in the vicinity. Both the male and the female Black-hooded Antshrikes pursued a female of the larger species, which passed by the nest bearing a strip of leaf in her bill. On another occasion, I heard sounds, out of sight in the bushes, which told of an altercation between the two kinds of antshrikes.

Departure from the nest.—When the nestlings were four days old, their pinfeathers were becoming prominent. These feather-sheaths continued to elongate without opening until, at the age of eight days, the nestlings bristled with very long, dark pinfeathers. The horny sheaths now began to ravel off with surprising rapidity, and in the course of about 24 hours the nestlings, now nine days old, were clad in blackish feathers, which on the preceding day had been tightly enclosed in their protective wrappings. The shedding of the feather-sheaths and the expansion of the plumage was as rapid as in anis and Citreoline Trogons. On the morning of the day following that on which it became clothed with feathers, each young antshrike in turn left the nest.

When I entered the blind in front of the nest at dawn on June 12, the sky was overcast and a slight drizzle fell. If the female antshrike had brooded through the night, she had slipped from the nest before the light was strong enough to reveal her. At 5:47 a.m., as the light increased, the male came, singing in an undertone. The nestlings, hearing his voice, lifted up their gaping mouths while he was still at a distance. He gave food to one of them and went off. Then the young birds began to preen their newly acquired plumage. The male brought food three times more,

and twice carried away droppings, before the female appeared, at 6:20, bringing a large green insect. The nestling which became feathered first (doubtless the one that was older by half a day) had become very restless, standing up and moving around in the nest. At 6:28, it climbed out and perched on the supporting limb close beside the nest, called in a small voice, and preened much. It greatly resembled the male in plumage, but its tail was very stubby. After three minutes, it hopped back into the nest. In the next 20 minutes, the male brought food twice and the female, once. At 6:51, the older nestling again hopped from the nest and perched beside it. Coming once more with food, the male parent alighted beside the nest, and the sudden shaking of the branch caused the little bird to lose its balance. It fell almost straight downward into the tangled vegetation of low bushes and vines beneath the nest, and the male instantly followed it there. The latter's response was so rapid that the two seemed to fall together, the parent slightly above the fledgling. The two were at once engulfed in the foliage. After a few minutes the parent reappeared, but I did not again see the young bird.

Soon the female came with a green insect of medium size, wings and legs still attached, and gave it to the young antshrike that remained in the nest. The latter had considerable difficulty in gulping down the insect. The female lingered beside the nest for three minutes, then flew away. At 7:13 a.m., the male brought an insect and took it into the bushes where the first fledgling was hiding. This was the last time but once that I glimpsed him. The fledgling was apparently led off through the undergrowth so silently that it was a long time before I was aware that it had gone, although the spot where it had fallen was only 10 feet distant from the blind where I sat. The young bird must have moved away keeping quite close to the ground, where the screen of foliage was most complete, because if it had ascended higher I should have seen it. The male apparently devoted himself for the rest of the day wholly to the departed fledgling, and he did not again come near the nest in the 9 hours that I watched it between the exit of the first and second fledglings.

During the next 23 hours, the remaining nestling was attended by the female alone. She was out of sight for long periods and may possibly have given a few meals to her other chick. However, it is not at all unlikely that after the departure of the first fledgling the parents divided the brood between them, each now making itself solely responsible for a single young bird, at least until the second fledgling left the nest. A similar division of the family has been observed in other species of birds.

Through the rest of the morning of June 12 (from 7:15 a.m. to 12:05 p.m.), the female antshrike fed the single remaining nestling eight times, and she carried away droppings four times. Although she did not brood after delivering an insect to the nestling, she sometimes lingered beside the nest, guarding it, once for 9, once for 8, and once for 3 minutes. At midday the nestling, which had lain very still in the nest since the departure of the other fledgling 5 hours earlier, became more active and began to preen. Except for its face, it was now completely clothed with feathers which had begun to unsheath only 24 hours earlier. There were a few white shaft stripes on the feathers of its crown and upper back and conspicuous white spots on its wing-coverts.

That afternoon I watched the nest for 3 hours more. At 3:00 p.m. the nestling was hungry and cried weakly *tit tit tit tit*. . . . The female fed it six times between 2:40 and 5:40 p.m. The nestling always made a low, buzzing sound when it stretched up to take food. Once when removing a dropping, the female carelessly

allowed it to slip from her bill, and it fell to the ground. She darted down in pursuit and spent several minutes among the low bushes and vines, apparently seeking the lost white object to carry away. The afternoon was rainy, with intermittent showers, during the hardest of which the female covered the nestling. After the rain stopped, she continued to sit in the nest while the foliage dripped, brooding for 45 minutes continuously. She had not, I believe, brooded the nestlings through the preceding night, and she left the single nestling uncovered during the night which followed, although at this season nocturnal rains were frequent. Nor had she sat in the nest in the morning, which was cloudy but rainless. But rain actually falling often stimulates parent birds to brood their nestlings when they have otherwise ceased to cover them.

The following morning, June 13, I witnessed the departure of the second nestling, whose manner of leaving the nest was almost identical with that of the first. The female, who had spent the night elsewhere, approached through the undergrowth before sunrise, calling loudly *wek wek wek wek*. The nestling replied with a soft, rapidly repeated *tow tow tow*, and 2 minutes later it received its breakfast. In the next half-hour, it was fed twice more, and again it voiced its soft *tow tow tow*. At 6:20 a.m., it hopped from the nest to an arm of the supporting fork. Here it called, preened vigorously, and stretched its wings sideways and above its back. After a few minutes, it sidled along the twig to the main branch, where it turned to face in the opposite direction. But soon it lost its balance, fell from the branch, caught hold of a leaf to which it clung precariously, then lost its grasp and tumbled into the tangle of vines and bushes below the nest. The female, which was perching close by when it fell, immediately followed it to the ground, as the male had followed the first fledgling. The female led the fledgling silently away through the undergrowth. I had a single fleeting glimpse of it as it crossed the path about 50 feet from the nest, then I saw it no more. But I heard both parents calling in the distance, which suggested that the family was reunited.

I can give the nestling period of the first young antshrike far more exactly than is possible in most instances. It had hatched at about 8:50 a.m. on June 2, and it hopped from the nest for the last time at 6:51 a.m. on June 12, when it was 9 days and 22 hours old. The second young bird left the nest when between 10½ and 10¾ days of age. Antbirds of other species may abandon the nest when as young or younger. Two Slaty Antshrikes left when nine days old.

Some years later, a curious thing happened at a Black-hooded Antshrikes' nest that I periodically visited. On the morning after the two nestlings hatched, I found one of them on the ground beneath the nest. Probably it has been brushed out accidentally by one of the parents on leaving the nest, a not infrequent occurrence with newly hatched nestlings. It was already moribund, but thinking that if warmed it might revive, I returned it to the nest beside the other nestling. Then I watched for the next hour. The male was in attendance, but he brooded inconstantly, spending much time on the rim, poking down into the nest, and going off for fairly long intervals. Apparently, the presence of the dying nestling so upset his routine that he failed to brood in the normal manner; yet the nestling's only chance of survival lay in protracted brooding. Returning to the nest in the afternoon, I found it to contain only a single nestling, doubtless the one that had not fallen, and it appeared to be very hungry. The parents were nowhere to be found. The following morning

there was one dead nestling in the nest. It appeared that the return of the moribund nestling to the nest so disturbed the adults that they permitted the other to die of neglect. Yet they had always appeared most devoted to their nest.

In the upper T rraba Valley, between 2000 and 3000 feet above sea level, the breeding season of the Black-hooded Antshrike is long. It may begin, as we have seen, in February. One pair hatched their eggs on August 3, and another pair were building a nest as late as August 22. I do not know how many broods a single pair may produce in a year.

SUMMARY

The Black-hooded Antshrike inhabits the edges of the rain forest, or openings within it, and taller second growth. In southern Costa Rica, it is found from sea level up to about 3500 feet. It appears to be mated throughout the year, and it rarely accompanies birds of other kinds.

Its notes are loud and harsh or wooden, never liquid. Its song is an accelerated roll, with an upward inflection at the end.

In El General, this antshrike breeds at least from February to August. The nest is placed from two to 12 feet up at the forest's edge or in an opening in the woodland. Attached by its rim to the arms of a horizontal fork, the ample cup is composed of dark fibrous materials, which form a fabric so thin that much light passes through. A little green moss is usually fastened to the outside of the nest. Both male and female build in a desultory fashion, sometimes taking five or six days to complete the structure.

The set regularly consists of two eggs, which are dull white with a wreath of bright brown and pale lilac blotches and spots.

Incubation is performed by both parents, who sit closely. When driven from the nest the parent birds tend to fall straight downward. They may quiver their relaxed wings in front of the intruder, but convincing injury simulation was not witnessed. The incubation period is from 14 to 16 days.

When an egg was hatching beneath him, the male parent refused to relinquish the nest to his mate when she came to take her usual turn at incubation. Fifty-one minutes after the male removed the empty shell, he gave the first nestling its first meal.

Until the nestlings were at least seven days old, they were brooded by both parents, for periods which at first often exceeded an hour. Until the nestlings were at least four days old, the male brooded more than the female, but the female continued to brood in the daytime after the male had ceased to do so. The female also brooded at night.

The nestlings were fed by both parents, but the male brought food more often than the female. The meals, substantial but infrequent, consisted of larval and adult insects, spiders, and apparently a little fruit.

The parents drove away larger birds, including a Squirrel Cuckoo and a Great Antshrike.

The two nestlings left the nest in the same manner, early on consecutive mornings. Each became restless, hopped from the nest to the supporting branch, then fell into the low vegetation beneath it, closely followed in its descent by the parent which happened to be present at the time. The male was present when the first fledgling

fell from the nest, and the female was present when the second young bird fell from the nest. The male led off the first young bird, and the female alone took charge of the nestling that remained in the nest for nearly 24 hours longer. The first fledgling left 9 days and 22 hours after it hatched, and the second fledgling left when it was from 10½ to 10¾ days old.

BARRED ANTSHRIKE

Thamnophilus doliatus

This widespread, easily recognized antbird is about six inches in length. Except on the head, the male is nearly everywhere transversely barred with black and white. On the upper parts and the tail, the black bars are far wider than the white ones, whereas on the under parts, the bars of the two colors are about equal in width, or, in some races, the white ones are broader. The elongated feathers of the crown are white with black tips and form a low crest, which is black when folded but largely white when the feathers are raised and their basal parts are revealed. The sides of the head, the chin, and the throat are streaked, rather than barred, with black and white. In contrast to her boldly marked mate, the female is almost uniformly colored, being cinnamon-rufous above and ochraceous-buff below. The black streaks on her buffy cheeks, neck, and throat, and sometimes faint dusky bars on her breast, alone suggest her relationship to the barred and streaked male. In both sexes, the eyes are pale yellow, the upper mandible is blackish, the lower mandible is bluish gray, and the legs and feet are plumbeous.

The Barred Antshrike ranges from northern Argentina to the State of Tamaulipas in northeastern México, and it seems to be the only member of the multitudinous antbird family to be found as far north as the Tropic of Cancer. Although many heat-loving birds are found at considerably higher elevations in Costa Rica than in Guatemala and México, the reverse is true of the Barred Antshrike. It ranges upward to 5000 feet in Guatemala (Griscom, 1932:234) and to 6000 feet in México (Griscom, 1957:55), but it is rarely seen as high as 4000 feet in Costa Rica. Perhaps this difference is to be ascribed to the greater dryness of the Guatemalan and Mexican highlands, for this antshrike thrives best in regions where the rainfall is moderate. Hence it is more widespread and abundant on the Pacific side than it is on the Caribbean side of Central America.

In southwestern Costa Rica, the Barred Antshrike's distribution is irregular and puzzling. In 1936 and 1937, I found it fairly common at Rivas, near the lower end of the valley of the Río Buena Vista, and here all of my nests were discovered. But in other parts of El General, at slightly lower altitudes, I have seen it seldom, although seemingly suitable thickets are not lacking. Lower in the Térraba Valley, as around Buenos Aires de Osa, it is not uncommon. In the Canal Zone and many parts of South America, it frequents dooryards and gardens with abundant shrubbery.

In the regions where I know it best, the Barred Antshrike inhabits low, dense, second-growth thickets. How reluctant it is to abandon such sheltering vegetation was vividly demonstrated to me long ago, when, at the end of a dry March, an area of such vegetation was burned to clear the ground for planting, without the usual preliminary slashing down. As with loud crackling and clouds of smoke the flames advanced across the acre or so of thicket, the flycatchers and tanagers of several species fled well in advance of the blaze. Next came the pigeons and doves. Finally even a secretive Chinchirigüí Wren could endure it no longer and rushed forth, flying slowly and laboriously over the adjoining open field. But a pair of Barred Antshrikes and three Chisel-billed Caciques clung to the burning thicket as though their lives

depended on it. Retreating reluctantly, close in front of the advancing conflagration, they were finally driven into a corner, where they defied the heat and smoke. Fortunately for them, this small patch of bushes, only a few yards in extent, failed to burn; here the two antbirds stayed with the three black caciques.

Barred Antshrikes apparently never flock but live in pairs amid their sheltering thickets, where they are heard far more often than they are seen. The notes of this wide-ranging bird have often been described, and it is difficult to decide whether the divergences in the published descriptions are due to actual variations in the repertoires of the antshrikes in distant regions or whether they must be ascribed to the writers' sensitivity to sounds and choice of words. The utterance that I have most frequently heard from the Barred Antshrike in Costa Rica is a loud, dry roll or rattle, slightly accelerated as it proceeds, with an emphasized *wank* at the end. This unmelodious but not unpleasant performance, which probably should be regarded as the antshrike's song, may last as long as 4 seconds and is similar in the male and female, although the voice of the latter is slightly weaker, and they often sing responsively. A singing male, which I watched from close at hand, stretched out his neck and raised the long feathers of his crown, revealing that they were snowy white except the black tips, which alone were visible when his crest was completely folded. His outstretched neck shook and his tail vibrated rapidly up and down. The utterance of this rattling song seemed to demand no slight exertion.

Haverschmidt (1947:358) described the "strange rhythmical duet" of a pair of Barred Antshrikes that visited his garden in Paramaribo, Surinam, and performed in the early morning. The birds sang either simultaneously or the male started to sing his few rhythmical notes, after which the female answered with exactly the same strophe, although often in a somewhat higher pitch. They performed with their crown feathers erect and their slightly spread tails vibrating with the notes, just as I have seen in Costa Rica.

I never realized how varied the Barred Antshrike's vocabulary can be until my visit to north-central Venezuela in 1966. In this region the antshrike is less retiring than I have found it in Central America, for it sometimes ventures forth from light woodland to hunt through dooryard shrubbery, and it even visits feeding trays (Gilliard, 1959a:20). A pair frequently foraged close beside the large farmhouse that we occupied near Pirapira in the State of Carabobo, usually coming early on warm afternoons, when the house was quiet and nobody was in sight. These antshrikes often repeated the wooden roll ending in a nasal *wank*, long familiar to me. They also uttered a crow-like *carw* and a guttural croak. It was easy to confuse their notes with those of other birds and even of the frogs nearby. Often these antshrikes announced their arrival with a few soft, mellow notes that so closely resembled the *cow cow* of the Collared Trogon or the Black-throated Trogon that I searched for a trogon in the surrounding trees until I was convinced that none was present.

On the island of Tobago, Barred Antshrikes come to houses for bread, a surprising choice of food for a member of an almost exclusively insectivorous family (Hundley and Mason, 1965).

NESTING

Probably no other antbird's nest has been so frequently found and described as that of the present species. At Caicara, on the Orinoco River in Venezuela, Cherrie (1916:278) found an empty nest on July 4 and a nest with feathered young

on June 21. In Trinidad, Belcher and Smooker (1936:805) found single sets of eggs in January, February, July, and December; in June, two nests were recorded. In the Canal Zone, Harrower (MS) discovered nests with eggs in July and August. The same writer mentions a set of eggs found in Chiapas, México, in May, and another in June, as reported by Skinner in a paper unavailable to me. On the Pacific slope of Guatemala, at about 3500 feet above sea level, A. W. Anthony (*in* Griscom, 1932:234) found a nest with fresh eggs on May 11.

At about 2900 feet in the basin of El General, Costa Rica, I discovered a nest with eggs on April 15, 1936, a nest with a nestling beginning to be feathered on January 25, 1937, two nests with eggs in early April of the same year, and one with eggs at the end of May. These five nests were situated in or beside dense, tangled thickets, at heights of 3, 5, 7, 7, and 10 feet. One of these nests was 7 feet up in an orange tree growing in a field which had been neglected until it became choked with tall weeds; the others were in native bushes and trees, including *Piper*, *Solanum*, *Heliocarpus*, and *Nectandra*. Each of the nests was a deep, thin-walled, but well-made cup attached by its rim to the arms of a horizontal fork, between which it hung. One nest was composed of fine brown fibers. Another was constructed of thin herbaceous vines, tendrils, and coarse vegetable fibers. Most of these nests were adorned on the exterior with a few tufts of green moss, applied too sparingly to conceal the generally brownish color. A nest which lacked moss bore on its outer surface a few sprigs of the delicate inflorescence of a weedy *Iresine*, which had apparently been plucked by the antshrikes while they were still green, although when I found the nest they were withered and dry. A nest made of rather coarse materials was lined with fine fibers. Although most of the nests reported by other writers fall within the range of 3 to 10 feet above the ground, Belcher and Smooker (1936:805) found that in Trinidad this antshrike occasionally built as high as 30 feet.

Three of my five nests contained sets of two eggs. One held a single egg and the other a single nestling. The eggs of one set were white, marked everywhere, but most densely on the thick end, with innumerable scratches of chocolate and a few heavier flecks of the same color. The eggs of another set were white, rather sparingly speckled and blotched with purplish brown, with somewhat heavier pigmentation on the thick end. Another egg had a wreath of purplish brown spots around the wider end and a few spots of the same color scattered elsewhere. Four eggs measured 23.8 by 17.1, 23.8 by 17.5, 23.0 by 17.5, and 22.6 by 16.7 mm. The measurements of seven eggs found in Trinidad by Belcher and Smooker (1936:805) averaged 22.8 by 16.9 mm. They remarked that there are "endless variations to be found in size, shape, ground-colour, and markings; yet the eggs are unmistakable." Although in Trinidad most nests contained only two eggs, very rarely these authors found sets of three, which is most unusual in the antbird family.

Although I have found antbirds in general, and especially species of *Thamnophilus*, so strongly attached to their nests that it was not difficult to approach them closely, sometimes even to touch them while they sat, the Barred Antshrikes that I studied were exceptionally wary. The attendants of my first nest would slip from it and vanish into the bushes the moment that I came in view, which was at a point about 25 feet distant from them. Sometimes, as I approached, I would catch a glimpse of the black and white male covering the eggs; sometimes I saw his red-brown mate. To make more detailed observations, I set my blind in the thicket about 20 feet

from the nest. However, even after it had been there for three or four hours the antshrikes would not return to their eggs, and therefore I removed it. Only while covering newly hatched nestlings did the female of this pair remain at her post until I came close to her. Two days later, these parents were as wary as they had been before their eggs hatched.

A year later, I set my blind before a nest with two eggs. The nest hung ten feet up in a young burío tree at the edge of a low, dense thicket, beside a bean field. I began to watch as the eastern sky brightened, and when the light grew stronger I could see no bird in the nest. After half an hour, the female rose above the rim of the deep cup; while she slept, she had been so deeply ensconced in it that she was invisible to me. Another 15 minutes passed before, at 5:45 a.m., the male delivered his loud, dry, rolling song in the neighboring thicket. Rising higher in the nest, the female replied with a song that was similar but more subdued. Then she jumped from the nest and flew in the direction of his voice. Two minutes later, the male alighted on the side of the tree opposite the nest and sang twice, then he went to sit on the eggs. After incubating for only 19 minutes, he suddenly flew back into the thicket. The eggs were neglected for a quarter of an hour, after which the female came and sat for 25 minutes. When her mate called from a point near the nest, she flew toward him and they sang together.

For the next hour and a half, there was far more calling and singing by both parents than steady incubation. The female took another session of 18 minutes, which she ended in order to chase away a Chisel-billed Cacique that had come into the nest tree. Later, the male sat for 37 minutes without interruption. Antbirds nearly always incubate far more constantly than this. Perhaps the presence of my blind, coupled with the loud sound of hammering that came from the neighboring rustic church, had made these antshrikes restless. Accordingly, I removed the blind. My three-hour watch had shown that the female incubates through the night, that both sexes share incubation, that the male and female sing responsively with very similar songs, and that the female often sings in the nest.

When newly hatched, the nestlings are quite devoid of down and the interior of the mouth is yellow. Their pinfeathers sprout rapidly and become long before the feathers begin to escape from their tips at an age of eight days. The expansion of the feathers is thenceforth rapid, and at the age of ten days the nestlings are well covered with plumage.

Although distraction displays are widespread in the antbird family, and a male Slaty Antshrike repeatedly bit the finger that I placed on his nest, the parent Barred Antshrikes stayed discreetly out of sight whenever I visited their nestlings; yet their voices revealed that they were not far away in the thicket.

One of the young left the first nest at the age of 12 days. After these nestlings were feathered, I had refrained from touching them, in order to avoid causing their premature departure. But when I found that one had gone, I decided to lift up the other to examine its ventral plumage. When I placed my hand over it, the nestling squirmed with a violence that amazed me, and it uttered such distressing cries that I regretted having disturbed it. Taken in hand, it raised the black-and-brown barred feathers of its crown and continued to struggle and to cry. Its calls drew the female out of the depths of the surrounding thicket. With her long, rufous-brown crest erect, and uttering at short intervals a somewhat liquid, mournful call that I had not previously heard, she circled all around me through the bushes, keeping at a

distance of 5 to 10 feet. Her calls, added to those of the nestling, brought her mate, who came with his loose black-and-white crest standing straight up and he likewise hopped in a circle around me, uttering a harsh, nasal, long-drawn complaint. This was the best view I ever obtained of the bold and strikingly different coloration of this antshrike. A Striped Brush-finch, which evidently had a nest hidden in the denser part of the thicket, far from assisting the distressed parents, tried to chase them away.

I had already seen that the upper plumage of both nestlings was barred. On one, the alternating, narrow, transverse bars were brown and blackish, and on the other they were buffy and dusky. The latter was the first to depart, and I held in my hand the nestling with brown and blackish bars on its back. Turning it over, I found that the feathers of its throat and breast were buffy with dusky bars. The sides and flanks were pale buff with indistinct dusky lines, and the abdomen was whitish. Of a sudden, the young antshrike jumped, slipped through my fingers, and hopped off through the densely entangled vegetation with an alacrity which assured me that its period of helpless infancy had come to an end. Since if undisturbed it would probably have stayed in the nest until the following morning, we may place its nestling period at 13 days.

Another nestling that I examined also had barred plumage. Although in most species in which the sexes differ strongly in coloration the juvenal plumage resembles that of the adult female rather than that of the adult male, the reverse is true of the Barred Antshrike. The young differ from the adult male chiefly in their lack of a white, black-tipped crest and in having the lighter bars on the dorsal surface buff or brown rather than white. Possibly the fledgling with buffy bars was a male and the one with brown bars was a female. Cherrie (1916:279), however, noticed no difference in coloration between a male and a female fledgling from the same nest.

SUMMARY

The Barred Antshrike inhabits low, dense thickets, and is more abundant in regions of moderate rainfall than in those which are very wet. In contrast to many other birds of the Tropical Zone, it ranges to somewhat higher elevations in northern than in southern Central America, being found occasionally at 5000 feet in Guatemala but seldom as high as 4000 feet in Costa Rica. It is paired at all seasons.

The song of both sexes is a loud, long-continued, dry rattle or roll, accelerated as it proceeds, and ending in an emphasized *wank*. Male and female sing responsively and sometimes one performs while sitting in the nest. Other utterances include a harsh, nasal scold and a liquid, mournful note of complaint.

In El General, at an altitude of about 2900 feet, five nests were found, in January, April, and May. They were placed at heights of from 3 to 10 feet, in or beside dense, tangled thickets. The nest is a deep cup attached by its rim to the arms of a horizontal fork. It is composed of fine fibers, thin vines, tendrils, and the like, and it is adorned on the outside with a few tufts of green moss, or with sprigs of inflorescences.

Two eggs are usually laid, but in other regions sets of three have occasionally been found. The eggs are white, variously marked with shades of brown.

The female covers the eggs by night, and by day the sexes sit alternately. The incubation period appears not to be known.

Newly hatched nestlings are devoid of down, and the interior of the mouth is

yellow. When they are eight days old, their feathers begin to escape their long sheaths, and at the age of ten days they are fully feathered. Fledglings of both sexes have barred plumage and resemble the adult male more closely than the adult female. The nestling period is 12 or 13 days.

Except when they had newly hatched nestlings, the parents were most wary and difficult to see on the nest. Unlike many other antbirds, they never gave a distraction display.

RUSSET ANTSHRIKE

Thamnistes anabatinus

In this plainly colored antbird, about five and a quarter inches long, there is little difference between the sexes. The upper parts are brownish, more olivaceous on the back, brighter and more rufous on the crown and wings, and brightest on the upper tail coverts and tail, which are deep cinnamon-rufous. There is a buffy superciliary stripe set off by a dark streak behind the eye. The ventral plumage is grayish, with a yellowish tinge on the throat and breast. On the center of the male's back is a concealed patch of cinnamon-rufous, which the female lacks. The heavy bill with a small terminal hook is dusky on the upper mandible and grayish on the lower.

The Russet Antshrike ranges from southern México to Bolivia. In Central America it is largely confined to the Caribbean rain forests, except in southern Costa Rica and adjacent parts of Panamá, where it occurs in the heavy forests of the Pacific slope. In this region I found it from sea level up to 4000 feet in the Cañas Gordas district, and Slud (1964:213) has recorded its presence 500 feet higher.

Of all the antbirds that I know, this species consistently forages highest in the trees, generally keeping above the level where the Velvety Antwren is usually seen. Occasionally, however, it may descend as low as 15 or 20 feet at the forest's border or in an adjoining clearing with scattered trees; Slud has even seen it on the ground. Throughout the year, I have found Russet Antshrikes in pairs, one of which often forms part of the mixed flocks of small birds that roam through the forest. In the lowlands near the Golfo Dulce in November and December, I found pairs of these antbirds flocking with the Gray-headed Greenlet, Tawny-crowned Greenlet, White-throated Shrike-Tanager, Green Shrike-Vireo, Scarlet-rumped Cacique, Black-striped Woodcreeper, Wedge-billed Woodcreeper, Rufous-winged Woodpecker, and wintering Chestnut-sided Warblers.

An active, restless bird, seldom delaying long in one spot, the Russet Antshrike searches through the foliage of the trees like a stout brown vireo, clinging in all attitudes while it plucks insects from the leaves. Its whole aspect and manner of life are so different from those of typical antbirds that I never attributed it to this family until one day, years after I had become familiar with it, I came close enough to a low-foraging individual to detect the revealing hook at the tip of its upper mandible. Until then, I had tried fruitlessly to find its description among the ovenbirds in Ridgway's catalogue. Its plumage, with brownish body and contrasting rufous tail, is of a type common enough in the Furnariidae but unusual in the Formicariidae. By its stout bill and manner of foraging high in the trees, this bird reminds me of a shrike-vireo, although its coloration is quite different.

The call, or song, of the Russet Antshrike is a rapid series of almost identical notes, delivered in a full, soft, rather plaintive, but far-carrying voice: *cheep cheep cheep cheep*. There are usually from three to five notes in a series. It is most difficult to trace these notes to their source in the foliage overhead in the forest, and I was long in discovering their author.

NESTING

Early in the morning of April 9, 1965, I found a pair of Russet Antshrikes just starting a nest, about 50 feet up in a slender tree of *Goethalsia meiantha* that grew a short distance within the edge of the forest, beside the riverside pasture on our farm in El General. The site they had chosen was the roughly triangular space between a slender horizontal twig and two curving lateral twiglets that met a few inches out from their point of attachment. The nest site was screened above by the foliage of taller trees, but visible from the neighboring pasture, and quite inaccessible to a man. While I stood watching, the antshrikes gathered cobwebs or cocoon silk and wrapped this material around the twigs that enclosed the chosen space. From 7:45 to 8:30 a.m., the two together brought material 12 times, and on three occasions they were at the nest site together.

By 6:30 next morning, some fragments of dead leaves had been fastened to the cobweb in a strand across the nest space. The birds continued to bring material, and by 7:00 the nest space was loosely covered with pieces of leaf. Then, for the first time, I saw one of the builders try to sit in the nest space and shape the structure, spreading its wings over the twigs at the sides. Most of the addition and arrangement of materials, however, continued to be done while the birds rested on the supporting twigs. Again and again the loose fabric over the nest space broke away, to hang precariously from one side, and the birds spent much time pulling up the web of cobweb and leaf fragments, spreading it over the central space, and fastening it to the surrounding twigs. They also brought some long, thin vegetable strands and laboriously worked them into the fabric to strengthen it.

Building proceeded slowly. From 6:30 to 7:30 a.m., the two antshrikes made 18 visits to the nest and from 7:30 to 8:30, only 10 visits. On arriving, the builders habitually alighted near the base of the slender supporting twig and rapidly hopped out along it to the nest. On most visits, they spent considerable time arranging the materials. To leave, they flew directly from beside the nest. Usually, one left as the other arrived. Sometimes they were together at the nest for a few seconds, but as far as I could see, each nearly always arranged what it had brought. Only once did one seem to pass its contribution to its mate. When I left at 8:30 a.m., the central space of the nest was open, with a rim of material around it. To start this nest was not easy.

On the following morning, April 11, the antshrikes worked somewhat faster, bringing material 23 times from 6:30 to 7:30 a.m. On most visits they spent much less time arranging the nest than they had done on the preceding day, but sometimes they sat in it. By 7:30 that morning, the nest seemed to be acquiring its final shape. After this, however, the work languished. By the morning of April 12, it appeared much the same as when I left it on the preceding morning. At least one bird continued to build, but by evening I could detect little progress. On the following days I failed to find the antshrikes at work, and I sadly concluded that the only nest of the Russet Antshrike that I—and perhaps any ornithologist—had ever found had been abandoned unfinished.

On the afternoon of April 16, a good shower ended a fortnight of unseasonably dry weather. By 7:00 a.m. next day, the birds were building again and had at last completely closed the bottom and sides of their nest. Evidently their materials had proved too refractory when dry, and like many other birds the antshrikes preferred

to work with damp materials that are more easily molded into the desired shape. In the half hour from 7:00 to 7:30, they brought material 16 times, but after that they stayed away until I grew tired of waiting for them. However, the structure was now promptly finished, or at least so it seemed from a distance. It was a rather deep, vireo-like nest, attached by its rim to the supporting twigs. It was brown, from the fragments of dead leaves that made up most of its bulk. There were a few large pieces of dead leaves attached loosely to the outside.

After the nest appeared finished, it seemed to hang deserted for over two weeks. Only once in this interval did I find an antshrike present; it stayed in the nest for four minutes, moving around too much to be incubating. Then, on May 4, I at last saw one of the birds sitting motionless in the nest as though covering eggs. It was difficult, even through binoculars, to detect an antshrike in its deep brown pouch so high above my head, except when, in hot sunshine, it sat higher than usual, panting with open bill. Sometimes I would watch for over an hour without detecting a sign of life at the nest. But as I passed by on May 19, I noticed a parent perching beside it and lowering its head into the cup, as though feeding nestlings, although I could not detect any food in its bill. After continuing this for a minute or two, the parent jumped into the nest. It brooded for a little over an hour, then flew away as its mate approached. The newcomer stood on the supporting twig and lowered its head into the nest just as the first had done, continuing this for 2 or 3 minutes. Finally, apparently having delivered food that I could not see, it entered the nest to brood. Undoubtedly there were newly hatched nestlings which needed to be coaxed to take their food. This observation made it clear that both parents fed and brooded the young, as in other antbirds.

On the morning of May 27, I watched the nest from 6:10 to 9:10 a.m. The nestling(s), of unknown number, were fed only five times in the 3 hours. Once they received an insect with very long antennae; otherwise I could not recognize the food, as the parents approached rapidly and on reaching the nest immediately lowered their heads into it. Only one dropping was carried away. The nestlings were brooded only once, for 44 minutes. As far as I could see, while sitting in the nest the parents always faced outward, as is usual in antbirds, instead of toward the center of the nest tree, as in vireos.

At daybreak on May 29, I found the nest hanging well below the supporting twigs, from which it had been almost torn away. Presently an adult came out of the forest with a green insect in its bill. It peered into and around the nest for the nestlings, then descended to a lower branch, from which it returned to the nest, all the while holding the food. When finally it flew up from the branch to which the nest was attached, the jar shook off the precariously hanging structure. As the parent vanished into the forest, the ill-fated nest fell into the vine tangle below, where I could not find it.

From the time of its arrival, the parent uttered no note audible to me. Indeed, while building and attending their nest, these antshrikes were very silent. On the second day of construction, one of the builders called *cheep cheep cheep cheep cheep*, repeating this phrase until its mate came. Thereafter, I heard only an occasional low note while building was in progress, and none while the antshrikes incubated and attended their young.

After the loss of their nest, the antshrikes became more vocal, and I often heard their soft, plaintive call at the edge of the forest, and even from the dense crowns

of some rose-apple trees in the adjoining pasture. I looked hopefully for a replacement nest, but in vain.

SUMMARY

The Russet Antshrike inhabits heavy forest from sea level up to about 4500 feet. Throughout the year it lives in pairs, which often roam through the woodland in mixed flocks of small birds. It remains higher above the ground than most antbirds. It subsists on insects which it gleans from the foliage much in the manner of a vireo or a shrike-vireo.

Its call, or song, is a rapid series of three to five full, soft, rather plaintive, but far-carrying notes.

A pair was found beginning a nest in early April in El General, at about 2500 feet above sea level. The site was a slender horizontal twig about 50 feet up in a tree just within the forest edge. Both sexes built; when working most rapidly, they brought material 23 times in an hour. The completed structure was a vireo-like cup or pouch, attached by its rim to the supporting twigs, and composed largely of pieces of brown dead leaves, bound together and to the support by cobweb.

It was not possible to see inside the nest, but both parents fed and brooded the young, sometimes sitting for over an hour at a stretch.

PLAIN ANTVIREO

Dysithamnus mentalis

In size and plainness of attire, this small arboreal antbird resembles a stout vireo, but it differs from the vireos in that the sexes are readily distinguishable. In the male, the top and back of the head are slate-color. An elongated patch of darker slate, broadening backward, covers the orbital and auricular regions and is separated from the dark crown by a band of lighter gray. The rest of the upper parts are dark grayish olive. The wing-coverts are darker, deep gray to black, with two white wing bars and some small white spots on the lesser coverts. The throat is white or pale gray. The chest and the sides of the breast are gray, whereas the center of the breast is yellowish, passing into pale yellow on the abdomen and under tail-coverts. The female differs from the male chiefly in having the pileum chestnut instead of slate-color, and the upper plumage is more brownish. Both sexes are slightly over four inches in length and have brown eyes, blackish bills, and blackish legs and toes.

The Plain Antvireo ranges from northern Argentina to extreme southern México. However, it has seldom been recorded north of Costa Rica where it occurs in the rain forest on both the Caribbean and Pacific slopes, chiefly in the upper levels of the Tropical Zone, from about 2000 to at least 5000 feet above sea level on the Pacific slope of the Cordillera de Talamanca. On this slope, I found it very abundant between 3500 and 5000 feet in extreme southern Costa Rica. In northern South America, races of this species occur in both the Tropical and Subtropical zones. At the northern extremity of its range in northern Guatemala and southern México, it is found in the lowland forests.

Although this forest-dweller is not shy, its dull plumage and quiet ways make it difficult to detect in the dimly lighted underwood. One morning, after spending many minutes trying to see an antvireo whose song I heard, I finally found it perching not 10 feet from me, where, to judge by its voice, it had been all the while. Avoiding both the crowns of the great trees and the lowest undergrowth, the Plain Antvireo forages chiefly in tall bushes and smaller trees, from about 6 to 20 feet up. Although I lack a convincing number of observations, it seems to live in pairs throughout the year, and it rarely accompanies the mixed flocks of small birds. It hunts through the foliage and vine tangles in a deliberate, vireo-like manner, and it appears to subsist largely on insects and spiders, which at times it plucks from leaf or twig while hovering on the wing. Occasionally the gray-capped male presents a morsel to his chestnut-capped mate while they forage through the woodland. Once in December, however, I saw a male twice refuse to give the female a large spider, which he ate.

VOICE

The antvireo's song, given by both sexes, is a dry, long-drawn rattle or roll, which becomes more rapid and wooden toward the end. This roll is at times so low as to be scarcely audible at a distance of 20 feet. The call note is a questioning *how*. A pair which I watched attend their nestlings kept up a low conversation as they hunted through the bushes for insects to give them. Sometimes their notes reminded

me of the Slaty Antshrike, sometimes of the Tawny-crowned Greenlet, and again of the scolding of a small squirrel, but they were always more subdued. The antvireo's scold or complaint, given when the nest appears to be in peril, is a low, mournful, not unmelodious *cher, cher, cher* which may be continued with scarcely a pause for several minutes.

Another utterance, which I often heard in the forests near Cañas Gordas in extreme southern Costa Rica, consists of from five to seven soft, melodious notes rising rapidly in the scale, forming a delightful liquid ripple of sound. Once, at day-break, I heard this softer call mingled with the oft-repeated rattle. Although I could not see the birds, I surmised that a mated pair were singing responsively, and that the more liquid notes were the female's. Later I watched a female give this pleasing song while she held food in her bill.

NEST BUILDING

At an altitude of 3500 feet on the slopes above the valley of El General, I found a nest which on February 26 already contained a naked nestling. Another nest at 4000 feet in the same region held two eggs on April 21. On my farm at 2500 feet, the two earliest of six nests had eggs which hatched at the end of May; hence, they must have been laid about the middle of the month. Here three nests with eggs were found in June, and in the latest of the six nests the eggs were laid about July 11. In this locality, the antvireo breeds early in the rainy season.

The antvireo's nest is suspended, vireo-like, between two diverging twigs, which may be the arms of a horizontal fork, or it may be suspended from two thin branches springing from the same point on an upright stem. Sometimes, the nest hangs from a false crotch formed by the crossing of two separate twigs. The 12 nests which I have seen were placed from 22 inches to 6½ feet above the ground, in the undergrowth of the rain forest.

At about 10:30 a.m. on June 10, 1943, I found a pair of antvireos building what appeared to be a newly begun nest in heavy forest. Between two slender, diverging branches of a sapling, the birds had loosely stretched black fungal filaments and fine rootlets, the ends of which were wrapped around the supporting twigs. A number of tufts of green moss were entangled among the strands which looped between the supports. While I stood watching beneath a huge candela tree, with only sparse undergrowth between me and the nest, the diminutive antbirds continued their building, heedless of their spectator. In the next hour, the male took material to the nest eight times. He brought tufts of moss and fine fibers, which he wrapped carefully around the supporting twigs, resting on one of them while he worked. I saw the female bring material only three times. While they worked, the two communicated in low tones, with an occasional dry rattle or roll, of typical antbird form, but much more subdued than the calls of most antbirds. At times, perching beside the incipient nest and looking down at what he had done with a little help from his mate, the male voiced a rapid roll, so very low that I probably would not have become aware of it had I not noticed the vibrations of his tail and strained to catch the sound.

Returning at 9:40 next morning, I found the nest nearing completion. No work was done in the next hour and a half. By 7:00 a.m. on June 12, the nest appeared to be finished, and by 2:00 p.m. of the same day, the thin fabric had grown no thicker. This nest, or by far the greater part of it, was built in less than two days,

and most of the work was probably done within an interval of 24 hours. The deep, open cup hung beneath the supporting twigs and was composed chiefly of dark fibrous rootlets. It was lined with black fungal hyphae or "vegetable horsehair," and decorated on the outside with green moss, festoons of which hung gracefully beneath it. The open meshwork of the bottom permitted much light to pass. It was rather similar to other nests of the Plain Antvireo that I have seen, except that some had less moss on the exterior. One of these nests measured $2\frac{3}{4}$ inches in outside diameter by $2\frac{1}{2}$ inches in height. Another nest was 3 inches in outside diameter by 2 inches high, and the cavity measured 2 inches in diameter by $1\frac{3}{4}$ inches deep.

THE EGGS

In the nest which appeared to be completed on June 11, the first egg was found in the afternoon of June 14 and the second egg two days later. Eleven of my nests contained two eggs; the twelfth contained a single nestling. In southern Brazil, Euler (1867:402) found sets of two eggs in nests which resembled those of the Costa Rican representatives of the species. The antvireo's eggs are dull white, flecked and blotched all over, but most heavily on the thick end, with purplish brown. The measurements of 12 eggs average 20.0 by 14.8 mm. Those showing the four extremes measured 21.4 by 15.5, 19.1 by 14.7, and 19.8 by 14.3 mm.

In 12 nests on the Pacific slope of Costa Rica (El General and Cañas Gordas), eggs were laid as follows: February, 1; March, 1; April, 1; May, 5; June, 3; and July, 1.

INCUBATION

In late May of 1949, Mr. and Mrs. Darwin Norby and I spent 17 hours taking turns watching a nest in which the two eggs were almost ready to hatch. The female slept on the eggs, and by day she and her mate replaced each other. Usually one sat until its partner arrived, but sometimes the bird that had been incubating went off before the mate appeared, leaving the eggs exposed for a short while. The male's sessions lasted for 120, 137, 103, 126, and 100+ minutes. The female's diurnal sessions lasted for 41, 66, 75, and 79 minutes. Eight intervals when the eggs were exposed ranged from 1 to 18 minutes and totalled 45 minutes. The eggs were covered for 95 per cent of the period of diurnal activity and were left exposed for 5 per cent of this period. The antvireos sat facing either into or out from the crotch in which their nest hung, and more rarely they sat sideways, with the head over one of the supporting arms and the tail over the other. Once, when he came to take his turn at incubation, the male brought a fiber for the nest. Early one morning, a black tayra walked deliberately between the blind and the nest. When about three yards from the blind, the mustelid stopped and looked suspiciously at it, sniffing the air. Then it resumed its walk at the same pace. The female antvireo was then sitting, and she remained at her post on the eggs.

At one nest, the incubation period was 15 days.

THE NESTLINGS

At the nest where we watched the parent birds incubating, the female sat restlessly early in the afternoon of May 29. Presently, at 2:52 p.m., she carried away a piece of shell. Taking advantage of her absence, I went up to the nest and saw that one egg had hatched. The naked nestling already stretched up its yellow-



Fig. 12. *Above.* Nest of Plain Antvireo, with male incubating. He sat motionless while the camera was set on a tripod only three feet away and the unconcealed photographer made four time-exposures. Cañas Gordas, Costa Rica, 3800 feet, May, 1964. *Below.* Male Plain Antvireo incubating. A detail from the above photograph.

lined mouth for food. After eight minutes the female returned, alighted beside the nest, lowered her head into it, flitted her wings nervously, then settled down to brood. As far as I could see, she brought no food on this visit. After sitting for 34 minutes, she went off, only to return in 2 minutes and perch on the nest's rim, again without any food that I could detect. But she promptly flew off and a minute later reappeared with a small object, which she beat against a twig. Proceeding then to the nest, she quickly delivered the insect to the nestling—undoubtedly its first meal. After brooding for 6 minutes, she again left, and 9 minutes later she returned to feed the nestling again. Then she entered the nest and brooded continuously until her mate arrived at 4:01 p.m.

The male antvireo spent about 15 seconds perching on the nest's rim and looking down at the newly hatched nestling. Not having seen it before, he had brought no food for it. The female, whose absences had previously lasted well over an hour while her mate incubated, now returned after 11 minutes to feed and brood the nestling. After an absence of only 3 minutes, the male came back with his first offering for the nestling, and after giving it the food he brooded it. Between its first meal at 3:37 and its last meal for the day at 5:55, the newly hatched nestling received seven objects from the female and three from the male. With so much activity, periods of brooding were mostly short; the longest period, taken by the male in the late afternoon, lasted 37 minutes. After the female had settled on the nest for the night, two Little Tinamous walked slowly beneath her in the dusk, but she paid no attention to them.

I sat before this nest through the following morning, which was showery with brief gleams of sunshine. The second egg had not hatched by midday, and accordingly I watched the parents attend a single nestling. From 6:06 a.m., when the female ended her night session, until I left at 11:09, the male brooded for nine periods, ranging from 3 to 52 minutes and totalling 172 minutes. The female brooded for eight periods, varying from 2 to 24 minutes and totalling 114 minutes. The nestling and unhatched egg were exposed for six periods, ranging from 1 to 6 minutes and totalling 17 minutes. The nestling, less than one day old, was fed 8 times by the male and 9 times by the female, about 3.4 meals per hour. Usually as one parent approached the other left the nest, and the newcomer fed the nestling and afterward brooded it. Most of the articles of food were too small for me to recognize, but once the male came with a moderately large insect. As he stood on the nest's rim, presenting it to the nestling, the female returned, took it from his bill, and she herself offered it to the nestling, who was slow to take it. As she repeatedly presented it over an interval of one minute, she voiced low *churr*'s. Finally, she ate the insect herself and then brooded. On another occasion, she jumped from the nest, caught a passing insect, gave it to the nestling, and resumed brooding.

This nest was pillaged a few days later, and for observations on the care of older nestlings we turn to an earlier nest, which I watched when the nestlings were on the point of leaving. In the three hours from 6:10 to 9:10 a.m. on July 10, 1943, the two nine-day-old nestlings were fed 8 times by each of their parents. This was only 2.7 feedings per capita per hour, considerably fewer than the newly hatched nestling received, but the meals were now much more substantial. By 7:55, the young antvireos were so full that they failed to respond to a green insect that the female brought to them, and she ate it herself. At 8:40, when she came with another large insect, they did indeed lift up their open mouths, but their swallowing reaction was slow, and she moved the insect from one nestling to the other until at last one of them gulped it down. As far as I saw, the parents brought only a single article at a time, usually an insect, although once it was a brown spider with remarkably long legs, and once a worm-like object half as long as the nestlings.

Although I watched without concealment, these parents were almost fearless of me. After I took my post, the little birds hunted for many minutes through the foliage and vine tangles close around me, exchanging low, confidential notes. Presently the male found a small insect and started to take it to the nest. When almost there, he drew back, but then he approached again, and so, by little advances and withdrawals, he came at last to the nest and placed his offering in one of the



Fig. 13. Edge of Upper Tropical Zone forest near Cañas Gordas, Costa Rica, at about 3800 feet above sea level. In the lower levels of the forest lived Plain Antvireos, Slaty Antwrens, Bicolored Antbirds, and Black-faced Antthrushes. The treetops were frequented by Turquoise Cotingas, Rufous Pihas, Russet Antshrikes, Red-faced Spinetails, and Golden-naped Woodpeckers.

upraised yellow mouths. Emboldened by her mate's act, the chestnut-headed female now proceeded toward the nest with a small insect, voicing low, questioning notes as she went. After flitting back and forth a few times, she reached her destination and fed a nestling. Later, she rested only eight feet from me while she preened her plumage.

At this and other nests, both sexes frequently simulated injury in a most convincing fashion, both before and after their eggs hatched. One day a neighbor's boy led me up into the forest to see a Great Tinamou's nest. As we neared its site,

I stopped, while my guide went ahead to locate it more exactly. As I stood with my eyes fastened on the boy, I suddenly caught sight of a small brownish bird that appeared to spring up from my feet. It fluttered painfully over the leaf-strewn ground, here rather free of undergrowth, until lost to vision amid the foliage. My first surmise was that I had stepped on some ground-nesting bird and injured it. But examination of the ground where I stood failed to reveal a nest. Then I noticed, at the level of my head in the small sapling beside which I stood, and so close that I could touch it without moving a single step, a deeply cupped nest with a single naked nestling. The female had continued to cover the nestling until her courage failed, then she dropped straight to the ground in an attempt to entice me away. So well did she create the impression that her movement began at a point on the ground, that had she been dealing with an animal, or even with a human inexperienced in the ways of birds, her nest would doubtless have escaped detection.

At other nests where I was not taken so greatly by surprise, I noticed more details of this realistic act. The parent, of either sex, stuck to its eggs or nestlings until I came close, sometimes within arm's length. Then it fell straight down and began to display the moment it reached the ground. One female varied the procedure by clinging an inch or two above the ground to the sapling which supported her nest and slowly fluttering her spread wings. Then she crept slowly and apparently painfully over the ground, pausing frequently to beat her wings against it. A male antvireo, instead of following a straight course away from the nest, which would soon have taken him beyond my sight in the dense undergrowth, continued to double back and forth close by me, the more effectively holding my attention. Once this same male continued his display for about a minute. While groveling on the ground, males make themselves more conspicuous by revealing, on each shoulder, a band of white (the outer webs of the outermost scapulars), which is ordinarily concealed; whereas females display buffy patches in the same positions. After trying to lure the intruder away in this fashion, the antvireo sometimes rises to a perch above his head and protests with low, liquid, mournful notes, *cher, cher, cher, cher*, interminably repeated. Sometimes the other parent arrives and joins in this melodious complaint.

The newly hatched nestling antvireo has tightly closed eyes and pink skin devoid of down. The interior of its mouth is yellow. When five days old, the nestling bristles with unopened feather sheaths. A day or two later, the horny sheaths begin to ravel off, a rapid process which leaves the nestling fully feathered at the age of eight days. Its upper parts are now wholly dark olive; but if a fleck of sunshine falls upon it, the crown appears slightly more brownish than the back and wings. Thus in their first plumage the antvireos resemble neither parent in coloration. A day after becoming feathered, or at the age of nine days, the young birds leave the nest. At this age, five fledglings left three nests. At a late nest in very rainy weather, the nestling period was 10 days.

SUMMARY

In Costa Rica the Plain Antvireo inhabits heavy rain forest, chiefly from 2000 to 5000 feet above sea level. Alone or in pairs, or rarely in mixed groups of small birds, it hunts for insects among the foliage and vine tangles in the lower levels of the woodland. Usually it is seen about six feet above the ground. The male sometimes feeds his mate away from the nest.

The song is a long-drawn rattle or roll; the call, a questioning *how*; and the

scold or complaint, a low, mournful, not unmelodious *cher, cher, cher*, repeated many times. The antvireo has also a considerable variety of low, conversational notes.

Nests were found at altitudes above 3000 feet in February, but at lower elevations nests were not found until May. Breeding continues into July at the lower elevations. The open nest is suspended between two twigs, often the arms of a horizontal fork, at sites from about two to six feet above the ground, in the forest. The frail, open fabric of dark filamentous materials is adorned on the outside with variable amounts of green moss. At one nest, both sexes built, but the male did most of the work. The structure was completed in less than two days.

Two whitish eggs, blotched with purplish brown, are laid. The second egg is laid two days after the first. The female covers the eggs through the night, but by day she alternates with her mate. The male incubates the larger share of the diurnal hours often sitting for over 2 hours without interruption. At one nest, the eggs were covered, by both sexes, for 95 per cent of the diurnal period. The incubation period was, in one instance, 15 days.

The nestlings are fed and brooded by both parents, who give prolonged distraction displays, in which they reveal white or buffy shoulder stripes that are ordinarily invisible. The young are hatched without any trace of down; they are feathered when eight days old and leave the nest at the age of nine days.

SLATY ANTWREN

Myrmotherula schisticolor

This diminutive antbird, slightly less than four inches in length, is so inconspicuous, yet so distrustful of man, that I did not become aware of it until I found a nest, nearly six months after I began to study birds in the forests of El General, where it is not rare. Even then, the male was so shy, and the female, which alone permitted a close approach, was so lacking in distinguishing features, that it was necessary to watch from a blind in order to identify them. To make this more difficult, the male was breeding in a plumage intermediate between that of young birds and that of the fully adult males. From this it appears probable that the males sometimes, and perhaps always, take more than a year to acquire their definitive plumage. In adult plumage, the males are slate-colored on all the upper parts, except the wing-coverts, which are black with white spots. The chin, throat, and chest are black, forming a shield which contrasts with the slate-color of the remaining under parts. The under tail-coverts are spotted with white. The eyes are brown, the bill black, and the feet blackish. The dorsal plumage of the female is brownish olive, which is deepest on the crown and hindneck. The sides of her head and all her under parts are buff of varying shades.

The Slaty Antwren ranges from Perú and Venezuela to southern México, but it is rare north of Nicaragua. In Costa Rica, it occurs chiefly in the more elevated parts of the Tropical Zone and at the lower edge of the Subtropical Zone, between 1000 and 5200 feet above sea level. In the Santa Marta region of Colombia, it was found in the Subtropical Zone at elevations of from 4000 to 5000 feet (Todd and Carriker, 1922:311). In the Coastal Range of Venezuela, it occurs from 1300 to 5580 feet (400 to 1700 meters) above sea level and is most abundant between 1970 and 2950 feet (600 and 900 meters), according to Schäfer and Phelps (1954:99). This is likewise the altitudinal zone in which this antwren is abundant on the Pacific slope of southern Costa Rica. Twenty years ago, when there was still a good deal of primary forest in the vicinity of San Isidro del General, it seemed to be the most common antbird of the heavy woodland.

In El General, the Slaty Antwren is strictly confined to the forest, through the lower levels of which it wanders in company with other small birds, including the Red Ant-Tanager, Tawny-crowned Greenlet, Buff-throated Automolus, Sulphur-rumped Myiobius, and others. It is one of the most constant components of these mixed parties, and its incessantly reiterated whining notes, along with the harsh calls of the ant-tanagers and the deep little notes of the greenlets, do most to draw one's attention to them. These bands differ in species composition from those which follow the army ants, and the members move through the underwood much more rapidly, searching the leaves and tree trunks, or else snatching insects from the air. The Slaty Antwrens hunt, warbler fashion, through the foliage of the higher shrubs and the lower branches of middle-sized trees, often hanging inverted while they investigate curled dead leaves for the insects and spiders which hide in them. Restless, shy, and constantly flitting about, they are far from easy to keep in view. They seem to live in pairs at all seasons, but it is difficult to obtain satisfactory

evidence of this. There is usually a single pair of Slaty Antwrens in a mixed flock of small birds.

The male and female call to each other with low, whining, nasal notes. Rarely I have heard them deliver a little song, which runs *t'weet t'weet t'weet, t'weet weet weet weet*, in very low, soft tones. At times, the series is longer than this.

In early October, a male in adult plumage delivered a similar song over and over, while he rested about 20 feet up on a horizontal branch in second-growth woods. He sang with his back humped up and his tail depressed. Each song was introduced by a little squeak. An answering *cheer cheer* came from the neighboring woods, probably from a female which I did not see. After a few minutes, the male stopped singing; yet he continued to perch in the same spot, sometimes gaping or stretching a wing, for at least 20 minutes. It is most exceptional to see one of these restless birds remain stationary for such a long time, unless it is attached to a nest.

NEST AND EGGS

Near Cañas Gordas, at an altitude of 3600 feet, I found a nest with two eggs on March 21, 1964. The earliest of the five nests which I have found in El General, between 2400 and 3000 feet above sea level, held nestlings in pinfeathers on May 15, 1940, and it is evident that the egg had been laid in the second half of April. In the other four nests, the eggs were laid in May. All five were built in slender saplings in the forest, at heights ranging from 34 inches to 6 feet above the ground. The tiny, rather deep, open cups were attached by their rims to the arms of a horizontal fork, or to two diverging or nearly parallel branchlets, with the body of the nest hanging below its supports. The nests were composed almost wholly of blackish fungal strands and fine, dark-colored rootlets, which formed a fabric so open that the eggs could be seen through the sides and bottom of the delicate pensile structure. In some nests, cobweb had been applied to strengthen the attachments. No moss was used, but one nest contained a few bits of the green fronds of a filmy fern, which had apparently been chosen for its rootlets rather than for the fronds themselves. One nest measured $2\frac{1}{4}$ inches in diameter by $1\frac{3}{4}$ inches in height. All the nests were completed before I found them, and observations on building are lacking.

Each of the nests contained two eggs or nestlings. The ground color of the eggs varies from white to cream, and both colors may occur in the same set. The blotches, spots, and sometimes also scratches of reddish or purplish brown may be concentrated in a wreath about the thick end or spread over most of the surface, although they are lightest on the thin end. The measurements of seven eggs average 17.7 by 13.4 millimeters. Those showing the four extremes measured 18.3 by 13.5, 17.1 by 13.5, and 17.5 by 13.1 mm.

INCUBATION

On June 30, 1940, I spent the morning watching a nest with two eggs on the point of hatching. When I entered the blind at 6:00 a.m. the nest was unoccupied, but 11 minutes later the male arrived to incubate. Then he and his mate, sitting alternately, attended the eggs constantly until nearly midday. He took three sessions, lasting 33, 44, and 142 minutes and totalling 219 minutes. The female's two sessions lasted 53 and 66 minutes and totalled 119 minutes. At 11:49 the male, although undisturbed, left the nest, and the eggs remained exposed until I ended my watch

at 12:00. The changeover was usually accompanied by some calling in weak, clear notes. When he heard his mate approaching, the male called *weet weet weet*—from the nest, then flew off uttering the same notes more rapidly, while the female settled on the eggs. On returning to relieve her, he called *weet weet* over and over, and she flew off voicing similar notes.

At one nest, the incubation period was about 15 days.

THE NESTLINGS

The newly hatched nestlings have dark flesh-colored skin, devoid of down, and the interior of the mouth is yellow. On the morning of June 9, I spent 205 minutes watching the nest where I had studied earlier the antwrens' mode of incubation. The two five-day-old nestlings now bristled with long pinfeathers. The male brooded them for five periods, ranging from 11 to 31 minutes and totalling 104 minutes. The female likewise took five turns at brooding, but her sessions were shorter, ranging from 1 to 30 minutes and totalling 51 minutes. The nestlings were left uncovered for 50 minutes, or for slightly less than a quarter of the time that I watched them. With a single exception, each parent remained on the nest until the other came with food; and the female would undoubtedly have brooded longer if her mate had not persisted in returning so promptly. Each parent fed the nestlings 8 times, a total of 16 meals in nearly 3½ hours. As far as I could see, the food consisted of insects alone, frequently large ones. Droppings were carried off in the bill by both parents.

At another nest, which I watched briefly while the two occupants were in long pinfeathers, the male brought food four times, the female nine times, in only 67 minutes. The male brooded for periods of 1, 4, and 20 minutes; the female did not brood.

On one of my early visits to my first nest of the Slaty Antwren, the female sat until I looked at her with my eyes hardly a foot from hers. Her nest was unusually long, and she was deeply ensconced in it, with her tail tilted sharply upward. When finally she left, she pushed through the thin fabric of the side wall, making a small gap in it. This convenient but imprudent mode of exit was evidently continued in my absence, for on returning a few days later I found that the gap had been enlarged until the nest was almost completely torn from the supporting twig on that side. Only a few strands sustained the badly sagging structure, and the single nestling was in danger of falling out. To avoid this, I brought a needle and black thread and sewed the nest more securely to its supports. Antwrens' nests seem often to be inadequately attached, and before the young are fledged the nests may hang well below the forks in which they were built.

As in many other antbirds, the Slaty Antwrens give excellent distraction displays when frightened from their nests, both before and after their eggs hatch. However, there is great individual variation in these displays. At some nests, I have seen only the male perform; at some, only the female; at some, both parents; and at yet others, neither parent displayed, but both were so elusive that I rarely saw them. At my first nest, the female, after staying on her nest until I could almost touch her, would slip through her peculiar side entrance and fall to the ground, where she acted like a crippled butterfly. Her performance over, she vanished in the dense surrounding undergrowth. The alert male always stole from the nest before I could see him and never simulated injury, but instead of disappearing he flew to the branches above and complained in fine, low, nasal notes.

At my third nest, the female always fled while I was still a long distance away. Her mate, on the contrary, sat firm until I advanced within reach of him; then he simulated injury. These displays, convincing enough while the nest contained eggs, were intensified after the eggs hatched. Then, dropping almost straight down from his four-foot-high nest, the male clung to a thin stem a few inches above the ground and slowly beat his widely spread wings, revealing a small white patch, ordinarily invisible, at the junction of each wing with the body. These epaulets contrasted sharply with his slaty upper plumage. After continuing this striking display for a considerable period, he flitted to a similar upright perch a few feet farther from me and beat his extended wings as before, but now more briefly. I followed; and he fluttered from sapling to sapling ahead of me, trying earnestly to lure me on, sometimes waiting until I was only a pace or two away before he retreated to another perch. Almost always he clung to upright stems. His wing displays became briefer and briefer as he drew me farther on, and finally they ceased altogether. When he had led me a good distance from his nestlings, he vanished in the undergrowth and called his mate. He never failed to give this display when I found him brooding, although on some days it was more prolonged than on others.

At my fifth nest, the parents' behavior underwent an interesting change as incubation proceeded. I usually approached this nest from the east, and I first came in sight of it when I emerged from a patch of rather dense undergrowth about 60 feet distant from it. From this point, I advanced through rather open forest, enjoying a fairly unobstructed view of the nest, and of course I was clearly visible to the sitting antwrens. When the eggs were newly laid, the birds would flee the moment they caught sight of me, although I was still 60 feet from the nest. At this stage of incubation I rarely saw the shy parents. Then, at about the middle of the incubation period, their conduct suddenly changed: the male sat while I walked across most of the open space in full view of him, and when I was fairly close, he dropped from the nest and "feigned injury." Two days later, the female also displayed after permitting a close approach. But three days after this, when the eggs were nearly ready to hatch, the parent retreated the moment I came in sight, and I could not distinguish its sex.

The interesting point is that these antwrens either fled from their nest at the first glimpse of me and vanished in the forest, or they permitted me to come close, and then gave a distraction display. They never left the nest when I was only a quarter, or a half, or three quarters of the way across the clear area where they had me in view. Such behavior would have been extremely imprudent and would have exposed their nest needlessly to the danger of detection. A small, obscure nest is not likely to be noticed unless the attendants call attention to it by their movements. If a bird does not slip unobtrusively from its nest while an approaching enemy is still distant, the only effective course is to sit motionless until it is sure that it has been noticed, or until the predator, if flightless, is almost close enough to spring upon it. Then it may still save its nest by luring the intruder away with a distraction display.

As the day of hatching approached, and also while they brooded nestlings, both parents of this nest repeatedly performed fine distraction displays. Their method was the same as that of the male at the third nest. Instead of performing on the ground, they clung to upright stems close to the ground while they beat their widely spread wings, and then they retreated to a more distant perch to resume the

performance. They repeated this procedure until they had led me a good distance from the nest. Despite their devotion, this nest was attacked by some predator, probably in the night, for, when the nestlings were a week old, I found one of them hanging downward from the outside of the nest, dead. The other had vanished.

The newly hatched nestlings have no down. When they are six days old they bristle with long, unopened, blackish pinfeathers. The escape of the feathers from their sheaths is amazingly rapid. One day I found the nestlings with scarcely any expanded plumage; 24 hours later they were well feathered. At this time the nestlings are brownish olive above and buffy brown below. A day after their plumage expands, they leave the nest. Since my only successful nest was found when the young were already several days old, I could not learn the exact length of the nestling period, but it is probably about nine days. The nestlings are at times infested with a few of the dipterous larvae called *tórsalos*, which live beneath their skin and cause prominent swellings; these larvae do not seem to retard the development of the nestlings. As the young antbirds grow older, the interior of the mouth, which at first is yellow, deepens to orange.

As already stated, the male Slaty Antwren acquires the adult plumage slowly and may breed in transitional plumage. The one male in transitional plumage that I found attending a nest had olive dorsal plumage. His middle (?) wing-coverts were blackish, tipped with white, forming a broad dark band bordered distally by a narrow white one. The greater coverts and remiges, as far as seen, were deep brown, as was the tail. The cheeks and sides of the neck were gray. A slate-colored shield, straight at its posterior margin, covered the throat and most of the breast. The extreme sides of the breast, the sides, the abdomen, the flanks, and the under tail-coverts were buff.

SUMMARY

In Costa Rica, the Slaty Antwren inhabits the higher elevations of the Tropical Zone, where it wanders through the heavy forests in company with other small birds. There is usually one pair of these antwrens in each mixed flock. The Slaty Antwren forages in the foliage of the underwood much in the manner of a wood warbler. Its calls are low and whining, and at times it delivers a simple but attractive song.

In El General, breeding begins in April and is at its height in May. The nest, a frail cup or pouch of black fibrous materials, unadorned by green moss, is suspended between the arms of a horizontal fork of a sapling. It is placed from 3 to 6 feet up in the undergrowth of the forest. The two eggs are white or cream, with purplish brown blotches.

The female incubates by night and alternates with her mate during the day. The male incubates the larger share of the diurnal hours. Sessions may exceed two hours in length. At one nest, the incubation period was about 15 days.

The newly hatched nestlings have no down; the inside of their mouths is yellow. They are brooded and fed by both parents, who give them chiefly insects.

Distraction displays by the parent birds are frequent, but there are great individual differences in this respect. At some nests, no parent displays; at some, both parents display; whereas at others, it is the male or female only who performs. At one nest, the parents either slipped away unobtrusively while the observer was far off, or else they waited until he came near and simulated injury, thus avoiding intermediate modes of behavior, which would be more likely to betray the nest to predators.

WHITE-FLANKED ANTWREN¹

Myrmotherula axillaris

The White-flanked or Black Antwren is a very small bird, slightly over three and a half inches in length. The male is almost wholly black, with white spots on the wing-coverts and on the tips of the outer tail feathers. When he lifts his wings, he reveals a conspicuous area of long, soft, white feathers on each flank. He has also, in common with some other members of the genus, a narrow white band on each shoulder, which is rarely displayed. The dorsal plumage of the female is olive, becoming gray on the head; her under parts are buff. She is a very plainly colored little bird, easily confused with other species in the areas where she dwells. This antwren inhabits lowland rain forest from southern Honduras to Bolivia and eastern Brazil. In Central America, north of the Isthmus of Panamá, it seems to be confined to the wetter Caribbean side at low altitudes, chiefly below 1500 feet.

The White-flanked Antwren is one of the higher-ranging of the forest antbirds, seldom foraging on the ground or through the lowest stratum of the vegetation, yet at the same time avoiding the lofty upper stories. It probably spends most of the day between 6 and 40 feet above the ground, in the tops of the shrubs and among the lower branches of the taller trees. Here it hunts through the foliage much in the manner of a wood warbler, flitting from branch to branch and hopping along the finer twigs, inspecting leaves and bark for small insects and spiders, sometimes darting out to catch a tiny flying creature in the air. Like other members of the family, the White-flanked Antwren is largely, if not wholly, insectivorous. As he flits from branch to branch, the male alternately exposes and conceals the white patches on his flanks as he spreads and folds his wings.

In the lowland forests of Central America where the White-flanked Antwren dwells, there are no resident, arboreal warblers. The role which these warblers play in the economy of the woodlands of the temperate portions of North America and the more elevated regions of tropical America is here largely taken by the smaller and more arboreal of the antbirds. In the forests of central Panamá, the three antbirds which most resemble the wood warblers in their manner of foraging are the White-flanked Antwren, the Fulvous-bellied Antwren, and the Velvety Antwren. These three species often flock together, roaming through the forests in company with other birds even in March and April, when at least some of each kind are nesting. In the spring, when warblers are passing northward through these forests, they may temporarily join the mixed flocks in which the White-flanked Antwren forages.

The notes of the White-flanked Antwrens are weak and of an indescribable tonal quality. Little chirps, twitters, and low churrs are the only utterances that I have heard from them, but these are frequently voiced.

At about 4:00 p.m. on February 10, 1935, in the undergrowth of the forest on Barro Colorado Island, I came upon a party of White-flanked Antwrens. The group consisted of one male and two females, who behaved most oddly and seemed to be engaged in a courtship ceremony. Perching on low twigs, usually between two and ten feet above the ground, they continually uttered a weak little call, or possibly it

¹ This life history is an abridgement of an account in Skutch, 1946a.



Fig. 14. Humid forest of the Caribbean lowlands in the Almirante Bay region of western Panamá, habitat of the Chestnut-backed Antbird, Slaty Antshrike, White-flanked Antwren, Fulvous-bellied Antwren, Velvety Antwren, and Bicolored Antbird.

should be considered a song, consisting of two syllables. While calling they flitted their wings, raising them one at a time with a very rapid motion, and closing them just as quickly. The movement was so rapid that it was difficult for the human eye to follow. As the antwrens lifted their wings, they turned quickly from side to side, or about-faced on the perch and frequently moved from one twig to another.

The male and the females behaved in a similar manner, but the females were more active both in calling and in exercising their wings. In the male, the lifting of the wing revealed momentarily the long, white feathers of the flanks, which are practically concealed when the wings are folded; but the females, although they constantly moved their wings, had no similarly conspicuous plumage. The birds continued these antics for about half an hour, moving about through a small area of undergrowth. They never came very close together nor performed in any definite spatial relation to each other. One of the females voiced a low, rapid, churring call. The lifting of the wings by the male White-flanked Antwren to expose the feathers on his flanks may be compared with the Velvety Antwren's habit of spreading the black feathers on his back to reveal the snowy area in their midst as he courts the female.

That the female White-flanked Antwren may take the more active part in courtship was likewise suggested by another observation that I made two months later, also in the forest on Barro Colorado Island. On the morning of April 5, while I sat in my blind watching a Brown Flycatcher build her nest, a flock of small antbirds wandered through the forest above my head. Among them was a pair of White-flanked Antwrens. When they were directly above me, I saw the female give the male an insect she had caught. The male was in adult plumage. Although the feeding of the male by the female is unusual among birds as a whole, other instances of this reversal of the normal relationship between the members of a pair have come to my notice. Some years later, I watched a female Tawny-bellied Euphonia surrender a caterpillar that she had just found to a male in fully adult plumage.

NESTING

On Barro Colorado Island, I found a nearly completed nest on March 29, 1935, one with newly hatched nestlings on April 16, and one in which eggs were laid on May 5 and 7. Aside from these, no records of the nesting of this species in Central America have come to my attention. All of my nests were in heavy forest, at heights of 22 inches, 28 inches, and 4 feet above the ground. The highest nest was in a forked twig of a slender bush, shaded by a palm leaf. The next highest was suspended between the petioles of two diverging leaves of a climbing aroid, well concealed by the foliage. The lowest was in a small sapling beside a nearly dry stream bed. Each of these nests was a deep, well-made cup, attached by its rim to the arms of a slender, horizontal, forking branch or in some similar situation. A typical structure was composed chiefly of pieces of dead leaves, some of which had been reduced by decay to lacy skeletons. It was bound together and attached to its supports by long, black fungal filaments, which also formed a thin lining in the bottom. A nest found by Cherrie (1916:282) at Maipures, Colombia, on the Orinoco River in January was apparently quite similar in construction, but the component leaves were chiefly those of bamboo, and it was higher, seven feet up in a thick tangle of overhanging bamboo branches in the undergrowth of high, dense forest beside the river.

Two of my nests contained sets of two eggs and the third held two nestlings. The eggs were white, speckled with reddish brown or chestnut, with most or all of the spots gathered in a wreath around the large end. The four eggs measured 16.7 by 12.3, 17.1 by 12.3, 17.5 by 12.7, and 17.5 by 12.7 mm. At one nest, an interval of two days separated the laying of the first and second eggs.

Incubation is performed by both sexes, but these antbirds sit far less constantly

than other antbirds that I have studied. At 11:50 a.m. on April 11, I entered the blind near my first nest, in which the last egg had been laid eight days earlier. I watched until 6:45 p.m., when the nest had become invisible in the dusk. Returning at 6:00 next morning, while the light was still dim in the forest, I continued to watch until 12:21 p.m. The female entered the nest at 6:08 p.m. on April 11 and evidently remained there until 6:10 next morning, when I saw her dart away in the dim light. Accordingly, the diurnal period may be considered to extend from 6:10 a.m. to 6:08 p.m. Between these hours, the male took four sessions on the nest of 3, 20, 136, and more than 174 minutes. His average session was 83+ minutes. The female took two sessions, of 98 and 140 minutes. She averaged 119 minutes on the nest. In the daytime, the male covered the eggs for 333 minutes and the female covered them for 238 minutes. The nest was left unattended for five periods, ranging from 11 to 94 minutes and totalling 178 minutes. The eggs were covered for only 76 per cent of the day.

The long periods of neglect of the eggs were so surprising that I made additional watches at this and another nest, which showed that these antwrens had not been behaving abnormally. In a morning at the second nest, the male took one long session of 134 minutes and the female a session which had lasted 33 minutes when I left at 11:30 a.m. The eggs were neglected for two periods, lasting 75 and 90 minutes. This nest was attended only 50 per cent of the 5¾ hours that I watched it.

On three mornings, I saw the antwren that had slept in the nest, evidently the female, fly away while the light was still too dim to see her clearly. Then the eggs were left unattended for periods ranging from an hour and a half to nearly two hours, after which an antwren came to warm them again. In two instances at the first nest, the female now returned; in one instance at the second nest, the male came to take charge. At the first nest, the male first arrived on one morning at 8:26, 21 minutes after his mate's return, but on another morning he did not appear until 9:22, 98 minutes after the female had resumed incubation. Later in the day, the intervals of neglect were shorter than that which started off the morning. Although these little antwrens were capable of sitting for two or three hours continuously, their strong sociability often drew one of them from the nest to forage with its mate after it had been incubating for a far shorter period. This desire for companionship was well illustrated at 9:25 a.m. on April 12, when the male left the nest on hearing his mate's voice, only 3 minutes after he had replaced her there. Following her, he remained absent for 11 minutes, then returned to the eggs. In several other instances, the calls of the foraging partner seemed to draw the incubating partner from the eggs before the former was ready to take over. Other species of antbirds forage alone during the period of incubation.

Sometimes, as he alighted beside the nest to cover the eggs, the male antwren briefly displayed his usually concealed white shoulder bands. He sat far more steadfastly than the female, at times permitting me to bend over his low nest, or to advance my hand to within a foot of him, before he jumped off and flew slantingly downward until he almost touched the ground. Despite her concealing coloration, the female was more wary; she nearly always left her eggs and flew rapidly out of sight while I was still several yards from the nest.

At one nest, the incubation period was 16 days. The newly hatched antwrens were pink with blackish heads and they had no trace of down. Their eyes were tightly closed, and the interior of the mouth was yellow. They developed rapidly, and

three days after they hatched, their eyes were opening and their pinfeathers were lengthening. When they were six days old, their feathers began to escape from the ends of the horny sheaths. The following day their nest was empty.

When the two nestlings of the first nest were four days old and bristled with long pinfeathers, they were fed 13 times in the first four hours of the morning, 7 times by the male, 6 times by the female. As far as I could see, the nestlings' food consisted wholly of small insects. The female brooded three times, for 3, 26, and 35 minutes, or a total of 64 minutes. The male brooded once for 7 minutes and another time he stood on the nest's rim, guarding, for 6 minutes, then settled down to brood just as my watch ended. He continued to sit, looking up at me, as I bent over him until my face was only a foot from his. But before my advancing hand could touch him, he jumped from the nest and skimmed rapidly over the ground for a distance of about 20 feet. Then he rose into the bushes and called for a long while, uttering a sort of chitter in his indescribably queer tones. His mate answered from a greater distance.

The female of another nest gave far better distraction displays. When I found her brooding nestlings a few days old, she remained sitting until I came within a yard or two of her. Then she dropped suddenly to the ground and dragged herself over it for many yards, as though unable to fly. I have seen few birds convey more convincingly the impression that they were severely injured and trying frantically to escape. When she had lured me a good distance from the nest, she flew up into the bushes to join her mate in uttering the queer calls characteristic of these antwrens.

From one nest the nestlings vanished when seven days old, and from another they disappeared at the age of eight days. Probably they left the nest spontaneously, although this would make their nestling period a day or two shorter than that of any antbird for which this period was definitely established.

FULVOUS-BELLIED ANTWREN

Myrmotherula fulviventris

The Fulvous-bellied Antwren is a very small, plainly attired bird, slightly under four inches in length. The male is plain olive on the upper parts, somewhat brown on the upper tail-coverts and tail. Most of the wing-coverts are black with prominent spots of buff. The sides of his head are dull grayish white with indistinct dark streaks. The chin is white, and the throat is black, with a large white spot at the tip of each feather. The rest of the under parts are buffy olive, which becomes clearer buff on the abdomen. The female resembles the male, but she has a plain buffy throat and dusky instead of blackish wing-coverts.

This diminutive antwren ranges through the rain forests from northeastern Honduras to northwestern Ecuador. North of the Isthmus of Panamá, it is confined to the Caribbean lowlands and foothills, extending no higher, according to Carriker (1910:607), than 1500 feet above sea level. In pairs or small flocks, it moves restlessly through the lower strata of the forest, scrutinizing the low herbage and examining the fronds of ferns down to their roots. It carefully investigates curled dead leaves that have lodged in the vegetation near the ground, and sometimes it bites along the fold of a withered leaf, to force out any small creature that might be hiding in it. It does not, however, actually hunt over the ground, and at times it ascends into the boughs of the smaller trees, up to possibly 30 feet, where it forages amid the foliage, sometimes in company with White-flanked Antwrens and other small birds. Like other small antbirds, it appears to subsist wholly on insects, spiders, and other invertebrates.

While searching tirelessly for food, Fulvous-bellied Antwrens repeat low, pleasant cheeps and chirps. Their song is a rapid series of soft, peeping notes in varying keys. Eisenmann (1952:35) paraphrased one version of the song as *pü-peh-pey-pih-piy-pee-pyee*—a series of high whistles ascending in pitch.

In the forest on Barro Colorado Island, where these antwrens are abundant, I found them exceptionally active and noisy in late November of 1939, when they appeared to be courting. Two males, facing each other on twigs about a foot apart in the undergrowth of the forest, lowered their heads, fluffed out the plumage of their backs, and turned from side to side as they rapidly and incessantly repeated sharp, squeaky notes. They continued this performance for many minutes, without changing their perches. At last one of the contestants flew away, leaving the other to continue his calling alone. The latter soon followed, and they came together again. They faced each other as before, resumed their rapid, squeaky chirping, but now they continued it for a shorter interval. Then they moved to a third position and performed briefly in the same manner. While the males displayed to each other, several females flitted around them, taking no part in the dispute. At last all the antwrens filtered away through the undergrowth. I never saw any fighting in this species.

On Barro Colorado in July, Harrower (MS) watched a similar performance between two male Fulvous-bellied Antwrens. It lasted about half an hour, while a female looked on and chirped. These displays between males, witnessed by non-participating females, resembled similar encounters among Blue Honeycreepers.

NESTING

On Barro Colorado Island, the Fulvous-bellied Antwrens appear to breed through much of the year. I found occupied nests in January, 1931 and February, 1935, and Eisenmann (1952:35) mentioned a nest with eggs found there by Dr. A. A. Allen on October 20, 1944.

Each of my nests was a pouch-like structure, attached to a fork at the end of a slender, drooping branch in the undergrowth of the forest, 6 feet above the ground. When discovered on February 9, 1935, one nest was still in an early stage of construction. The deep purse of fibrous materials hung from the arms of the fork, between which was the entrance. When I found that the nest was progressing slowly, I set up my blind to watch the birds, of whose identity I was not yet certain. I entered the blind at seven o'clock in the morning, and soon afterward two very small and obscurely colored birds flew up from the forest and perched side by side on the top of the nest. They were evidently antbirds, but only after the sun rose higher could I see their markings well enough to be sure that they were Fulvous-bellied Antwrens.

After their visit of inspection, both set to work, bringing short, broad pieces of brown, dry palm fronds, or similar leafy material, for the middle layer of the pouch. The strips of leaf were large in relation to the tiny, short-tailed birds, and of much the same color. Each antwren arranged its own contributions, pressing itself down until nearly hidden in the pouch as it molded the piece to the nest's contour. Even if one antwren alighted on the rim with material in its bill while its mate was inside, it did not pass the piece to its partner but waited until the other flew out; then it entered and worked its own contribution into place. While resting on a low twig near the nest, or while sitting in the nest, the antwrens often sang, giving a soft *cheep* rapidly repeated. Each sang chiefly while its mate was away searching for more material. Both members of the pair built actively from 7:00 to about 8:15 a.m. After that I did not see them, although I waited in the blind until 9:00. Leaving then, I made careful mental note of the condition of the nest, and when I returned at 2:00 p.m. it had not changed. The antwrens had ended their day's work early.

Two days later, an inner lining of fine, fibrous material was being applied, and after two additional days the nest appeared to be finished, eight days after I had found it when already well begun. Since I have a fuller description of my first nest of this species, I shall present it here. This nest was purse-shaped, with an oblique opening at the top. The outer layer was composed of fine black fibers, rootlets, partly decayed leaves, and bits of herbaceous stems. Within this was a layer of dead leaves, and there were fine fibers on the bottom. I found no cobweb in this nest. Its total length was 6 inches, and it was $3\frac{1}{2}$ by 3 inches in external diameter. The cavity was $1\frac{3}{4}$ inches in diameter, and the opening between the arms of the supporting fork was $2\frac{1}{4}$ by $1\frac{3}{8}$ inches. The nest of this species differs greatly from that of the Slaty Antwren, which is much shallower, a cup rather than a pouch, and is composed wholly of dark fibrous materials, without leaves. But the nest of a third member of this genus, the White-flanked Antwren, is transitional between these extreme forms. In shape, it is closer to the deep cup of the Slaty Antwren than to the pouch or purse of the Fulvous-bellied Antwren, but it resembles the nest of the latter in containing pieces of leaves, which are often its chief constituent.

In the nest which I watched the birds build, the first egg was found at noon on February 22, five days after the structure seemed to be finished. The second egg

was laid two days after the first, and incubation began promptly. The eggs were white, with fine spots of reddish brown crowded on the thick end. Two eggs found on January 14, 1931, were white, very finely spotted and scratched with pale lilac, especially in a wreath around the thick end. They measured 18.3 by 13.5 and 17.5 by 13.5 mm.

At 12:30 p.m. on March 2, 1935, I entered my blind to watch the later of these nests. The eggs were unattended when I came in sight of the nest. Soon the male and the female returned together. With much low, rapid chirping, they foraged all around the brown tent that concealed me, showing no mistrust of it, and coming within my reach. Finally, at 12:55, the female settled on the eggs, while her partner continued to forage among the low palm fronds and bushes in front of the blind, voicing low *chip*'s. His hunger at last satisfied, he alighted on the nest's rim at 1:14, above his mate, who thereupon flew away without a sound. He immediately entered the pouch, where he sat until 1:53, when he went off for no apparent reason. The eggs were left unattended until 2:12, when the female silently arrived to take charge of them. She sat for nearly 2 hours, until 4:05, when the male came silently to relieve her. At 4:20 I left him in the nest. Both he and his mate always sat facing out from the fork that held the structure, with their heads toward the lowest part of the rim. Each was so deeply ensconced in the nest that, from my post above them on the slope, I could see only the top of the head and bill, with sometimes part of the throat.

A few days later, I replaced my blind to make a longer study of incubation at this nest; when I returned to begin my watch, the eggs had vanished. I have not seen nestlings of this antwren.

SUMMARY

The Fulvous-bellied Antwren inhabits lowland forest, where it searches for insects among living foliage and curled dead leaves. It forages from the ground up to the lower boughs of the trees, about 30 feet above the ground.

Its song is a rapid series of soft peeping notes, and while foraging it continually utters low chirps.

Rival males display to each other by posturing with outfluffed plumage while they voice sharp, squeaky notes, but apparently they do not attack each other. Females watch the displaying males without participating in their dispute.

On the Isthmus of Panamá, breeding has been observed in October, January, and February. The pouch-like nest is suspended from a fork at the end of a slender, drooping branch in the undergrowth of the forest, at a height of about 6 feet. The oblique opening to the nest is at the top, between the arms of the fork. The structure is composed of fibrous materials and partly decayed leaves, with an inner layer of dead leaves and a lining of fine fibers in the bottom. Male and female share the work of construction.

Each of two sets I found consisted of two eggs, which were white, finely speckled with pale lilac or reddish brown. At one nest, the second egg was laid two days after the first.

Both sexes incubate, sitting very deeply in their hanging pouch. The incubating bird sometimes remains on the nest for nearly 2 hours.

VELVETY ANTWREN

Microhopias quixensis

The Velvety Antwren, also called the Dot-winged Antwren, is an attractive bird, slightly over four inches in length. The male is almost everywhere deep, velvety black. On each wing he has a conspicuous white bar, formed by the tips of the greater coverts, and white spots on the lesser and middle coverts. All except the central tail feathers have white tips, which become progressively broader outward. His eyes are brown, his bill is black, and his legs and feet are blackish. The upper plumage of the female is blackish-slate, marked with white on wings and tail as in the male, but the lower plumage is everywhere chestnut or rufous-tawny, the color varying geographically. Her eyes, bill, and feet are colored as in the male.

The species ranges from southern México to Bolivia. In Panamá and southern Costa Rica, the Velvety Antwren occurs on both sides of the continent, but north of the Gulf of Nicoya, where the Pacific coast is drier, it is restricted to the Caribbean side. A heat-loving bird, this antwren is confined to the lower parts of the Tropical Zone. In Costa Rica it ranges only to about 2500 feet above sea level, far lower than many other lowland birds. It wanders through the primeval forest and older second-growth woodland in company with antwrens of different species and with other small birds. Although various observers have reported flocks of Velvety Antwrens containing up to 15 individuals, I have never seen more than six together.

These antwrens search for insects in warbler fashion among the lower boughs of the great trees and in the crowns of the small ones. Generally in the forest the Velvety Antwren remains well above a man's head, but when it forages at the edge of a clearing it may descend almost to the ground in the dense shrubbery and rank herbage at the forest's margin. The Velvety Antwren has rictal bristles which facilitate the capture of insects.

In the breeding season, it is rare to see more than one male and one female together, but in the remainder of the year, several males may be found with a female. In the vicinity of the Golfo Dulce in the Pacific lowlands of Costa Rica, this species is very abundant. While I lived in the heavy forest of this region, I often saw a flock of five at the edge of the narrow clearing where my house stood. This party consisted of four males and one female, which kept close company from late October until at least mid-December. They seemed always to be in perfect harmony. On my farm in El General, I found two males and a female foraging together at the edge of tall second-growth woods in early October, and more than a month later I met what appeared to be the same trio in the same spot. From October to January I have seen, in addition to single pairs, parties consisting of two females and a male and of two males and a female. In the Golfo Dulce region, where the Velvety Antwren was so abundant, I received the impression in November and December that males were twice as numerous as females; this probably accounts for the association of several of the former with one of the latter.

The male Velvety Antwren frequently feeds his mate, as I have seen in widely separated parts of its range and at all seasons: on Barro Colorado Island in the Canal Zone in March; in El General in September; and in the Golfo Dulce region at the end of November, when it is doubtful that these birds were nesting or preparing

to breed. Near Pasaje, in the Province of El Oro in southwestern Ecuador, on November 16, 1940, I watched a male Velvety Antwren foraging in a clump of bamboos beside a shallow lagoon at the edge of a cacao plantation. Soon he found a big insect, whereupon his mate flew up beside him, begged with relaxed and quivering wings, and was promptly given the food. Then he stood upon her back.

One drizzly afternoon in October, I watched a female bathe in the water which had collected at the base of one of the broad leaves of a tank bromeliad that grew on a small tree at the edge of second-growth woods. After splashing in the aerial pool she left, and then one of the two males who accompanied her took his bath in exactly the same place. Soon all three flew back into the woodland.

VOICE

I had known the Velvety Antwren for many years before I became familiar with its song late in April of 1954. A male was performing in the early morning, in old second-growth woods adjoining heavy forest, and I searched for a long time before I saw him. The song began with six weak notes, each higher in pitch than the preceding note, and ended with a little falling rattle, typically antbird-like. *Chee chee chee chee chee chr'r'r'r'r* is the best transcription that I could make. On two mornings I heard this song in the same place. It is probably significant that this male antwren had no visible partner, although one nearly always finds these birds in pairs or small groups.

Other notes that I have heard from the antwrens are soft twitters and chirps, and a sharp, clear *peep* when the birds are excited. The note of alarm or complaint is a plaintive *tweo*, often repeated.

COURTSHIP AND OTHER DISPLAYS

Courtship and hostile displays may well be considered together, because in both types the usually concealed white bases of the feathers of the upper back are exposed. Both sexes can, by spreading these feathers, produce an area of immaculate white between the shoulders, but the male's is more extensive. On April 12, 1939, I saw a male display before his mate. With a patch of snowy white gleaming in the midst of his black dorsal plumage, he repeated sharp, clear notes, so rapidly that they almost formed a trill. Before I could see as much as I wished of this behavior, the chestnut-breasted female flew away. Covering the white patch, the male followed her.

In June of the following year, I was walking through the forest when shrill, cheeping calls drew my attention to two females and two males, probably their mates. The females were evidently hostile for they were perched upright, with heads raised and bills pointing skyward. The feathers of their backs and rumps were raised and spread, converting the whole upper surface into a fluffy puff, white on its forward face. Their slaty wings were relaxed, displaying the conspicuous white areas on the coverts. The tails of both were depressed and fanned out, revealing the prominent white ends of the feathers. When not flitting nervously from twig to twig, they perched face to face, repeating rapidly and almost incessantly loud, sharp *peep*'s, interspersed with grating nasal rattles. They maneuvered back and forth, and often one flew at the other; yet they never came to grips in my presence. This displaying and calling continued for about ten minutes. The birds were chiefly in the tops of the taller saplings, from 10 to 20 feet above the ground.

The two males from time to time displayed in the same manner as the females, but they were primarily spectators rather than active participants in the quarrel. The males' display was similar to that given by the male I saw courting. Finally, the four antwrens drifted out of sight in the foliage, apparently without having settled the argument. As usually happens, this noisy dispute had attracted as onlookers a number of small birds of other kinds, among them a male Black-hooded Antshrike, which rattled loudly.

In April, some years later, I watched a dispute in which at least five antwrens, three males and two females, took active parts. The males, perching close together, displayed to each other by spreading the feathers of their backs to reveal the central area of white, drooping their wings, fanning out their white-tipped tails, and voicing sharp notes in two keys. The females displayed to each other in similar fashion. As I have always seen in these antwrens, as in numerous other birds, males contended exclusively with males, females with females, and there was no actual fighting.

NEST BUILDING

The Velvety Antwren's breeding season is long. On our farm in El General, near the upper limit of this species' altitudinal range, I found a pair building at the end of January, 1944, and, almost in the same spot, I watched a pair feeding a full-grown fledgling on September 14 of the same year. In this locality, two other pairs were found building in early May. On Barro Colorado Island, I watched a pair building in late February; some years later, Johnson (1953:496) was shown a nest in which the eggs hatched on February 6. This antwren breeds in both the dry and the rainy seasons.

Of all the antbirds' nests that I have seen, except those of the Russet Antshrike, those of the Velvety Antwren were highest. However, they were not as high as certain exceptional nests of the Black-crested and the Barred antshrikes found in Trinidad by Belcher and Smooker (1936:804-805). Three of my Velvety Antwren's nests were built about 14, 20, and 25 feet above the ground, in small or middle-sized trees in tall secondary woods or primary forest. The fourth nest was about 20 feet up at the edge of a tangle of climbing bamboo (*Lasiacis*); it was attached to a very slender twig which projected out into an open space. At times, however, the Velvety Antwren chooses a low site, as shown by Johnson's (1953) discovery of a nest only 42 inches above the ground. Whatever its height, the nest is attached to the arms of a slender forked branch; it is usually well out from the trunk and amid clustering foliage which screens it from view.

On February 22, 1935, while walking through low, rather entangled, second-growth woods on Barro Colorado Island, I saw a male antwren carry a large dead leaf to a horizontal fork of a slender branch, 14 feet up. In this fork a nest had been newly begun, as revealed by the few fragments of dead leaves fastened there with cobweb. During the three days which elapsed before I could watch it, the nest progressed considerably; yet it was still well short of completion when I set my blind before it early on February 25. Ten minutes after I had settled down to watch, the male and female antwrens flew up together, both with empty bills, uttering soft twitters. The male went first to the nest, perched on its rim, and called his mate by peeping and twittering. She followed and, as soon as he made way for her, she entered the nest to shape it. The cup was so deep that only her bill and the tip of her tail were visible while she sat in it. After she left, the male returned to sit in the nest

as the female had done. Then they flew off and searched among the surrounding trees and vines until each found a small dead leaf, which it took to the nest. Before departing, each brought four more leaves or pieces of leaf to the structure. They worked in exactly the same manner, each placing its own contribution in the nest rather than passing it to the other to be worked into place.



Fig. 15. Nest of Velvety Antwren. Barro Colorado Island, Canal Zone, March 1935.

After an interval when they were out of sight and hearing, the pair returned at 8:54 a.m., again with empty bills; again the male went first to the nest and called his mate. After bringing one leaf each, they left the vicinity. Twice more during the morning they returned, and always the male preceded his partner to the nest. They worked at a leisurely pace, and from 7:45 to 10:15 the male brought material only nine times, the female, eight times.

At three nests in El General, the male and female shared the work of construction, as they did at the nest in Panamá. Here I have seen them gather small leaves of the climbing bamboo, chirping as they worked. A pair which I watched on our farm built much more rapidly than the Panamanian pair. In half an hour, the male carried six billfuls of material to the nest; his mate brought four billfuls.

When completed, the first nest I watched being built was a deep open cup, loosely

suspended beneath a horizontal fork of a slender twig by a few black fibers passing over the fork's arms. The thick walls were composed of many pieces of partly decayed leaves, intermixed with, and held together by, long black fibers, probably fungal hyphae. The interior was sparsely lined with the same dark fibers. The overall measurements were $3\frac{1}{4}$ inches high by $2\frac{1}{2}$ inches in diameter. The cavity was 2 inches deep by $1\frac{1}{2}$ inches in diameter. In the Costa Rican nests, which were inaccessible, whole small bamboo leaves appear to have been used in considerable numbers, instead of pieces of dicotyledonous leaves.

THE EGGS AND NESTLINGS

In the nest which I found when it was barely begun on February 22, I saw the first egg on March 5, although possibly it had been laid on the preceding day. On March 6, the second and last egg was laid. Because of their premature disappearance, I have no description of these eggs. Fortunately, Johnson (1953:496) has provided a description of a set of two found on Barro Colorado Island at the beginning of February. They were "white with small brown spots over the entire surface and with heavier blotches around the large end."

On early visits to the nest on Barro Colorado, I found sometimes the male, sometimes the female, covering the eggs. They sat so deeply in the pensile cup, well screened by foliage, that I could at most see a bill projecting above the rim, and often they were wholly invisible from the ground. They seemed oblivious of my presence, or indifferent to it, until my mirror, which I raised on a stick to look into the nest, touched the surrounding foliage. Then the sitting bird would jump out and perch close by, repeating the *tweo* note as long as I remained near the nest.

After three preliminary visits, I came at noon with my blind and set it up, but after three hours no changeover had occurred. At last I began to doubt whether there was a bird on the eggs; when I held my mirror above the nest, no eggs were reflected to my view. Some marauder had taken them. These were the only eggs of the Velvety Antwren that I ever saw; all my later nests were too high, and too far from a stout trunk, for their contents to be seen, even with a mirror.

According to Johnson (1953), the newly hatched antwrens have light, flesh-colored skin, devoid of down, and their eyes are closed. The interior of the mouth is yellow. In 585 minutes of observation spread over the first five days after hatching, the two nestlings were fed 9 times by the male and 13 times by the female. Brooding, by both parents, was observed only on the day of hatching and on the following day. On the sixth day, the nest was found destroyed.

SUMMARY

The Velvety Antwren lives in primary and older secondary forests from sea level up to about 2500 feet in Costa Rica. It roams the woodland in company with other small birds, foraging, warblerlike, among the foliage of the lower boughs of the great trees and in the crowns of the small ones. In some regions, there appear to be twice as many males as females; in the nonbreeding season, up to four males have been found keeping close and amicable company with a single female. In widely separated regions, and at all seasons, males were seen to feed their mates.

These antwrens bathe in water which collects in tank bromeliads.

The rather elaborate song, consisting of six weak notes, rising in pitch and followed by a slight falling rattle, was rarely heard. Other notes are twitters, chirps,

a sharp *peep*, given at times of excitement, and a complaining *tweo* uttered when the nest is disturbed.

In courtship display, the feathers of the back are spread to reveal a large white area, usually concealed, between the shoulders; at the same time wings and tail are expanded, showing their white markings to best advantage. The antagonistic display is similar. In this, males display to males, females to females; no physical contact was observed.

In El General, the breeding season extends from January to September. The Velvety Antwren places its nests higher than most members of the family. Not infrequently nests are from 15 to 25 feet up, although occasionally they are found as low as 3½ feet above the ground. The deep cup or pouch is attached by its rim to the arms of a horizontal fork, amid clustering foliage. It is composed of many dead leaves bound together by long, dark fibers. Both sexes build, but the male seems to take the initiative and to perform the larger share.

Each of two nests contained two eggs, which are white, spotted and blotched with brown.

Incubation is performed by both parents, but its duration is unknown.

The nestlings are hatched without down and the interior of their mouths is yellow. They are fed and brooded by both parents. The nestling period is not known.

TYRANNINE ANTBIRD

Cercomacra tyrannina

This is a slender antbird of medium size, about five and a quarter inches in length. The sexes differ greatly in coloration. The male is blackish slate-color above and below, with concealed white at the bases of the feathers in the center of the back, conspicuous white tips or margins on the wing-coverts, and all of the tail feathers except the central pair usually narrowly tipped with white. He has a blackish bill, brown eyes, and dark legs and feet. The upper plumage of the female is brownish olive or grayish olive, with olive-buff tips on the wing-coverts. Beneath she is orange-tawny, strongly tinged with olive on the flanks.

The Tyrannine Antbird ranges from southern México to western Ecuador, the Guianas, and Brazil. In northern Central America it is confined to the Caribbean watershed, but in Costa Rica it is abundant on both coasts. A lowland species, it extends upward to nearly 4000 feet on the Pacific slope of extreme southern Costa Rica and to 3000 feet in British Guiana (Ridgway, 1911:94).

The favorite habitat of the Tyrannine Antbird is the margin of the rain forest in the humid lowlands. Where it adjoins a clearing of any sort, a waterway, or a wide roadway traversing its depths, the forest's edge becomes a wall-like mass of verdure, composed of bushes of varying heights, the outermost boughs of the trees, and the creepers which clamber over everything else, binding trees and shrubs together with rope-like tangles and spreading their foliage over the upright woody plants. Through this entangled vegetation, behind the heavy marginal tapestry of foliage, at no great height about the ground, the Tyrannine Antbirds hunt, keeping themselves well screened, but often announcing their presence by their trills. If the forest is tall and unbroken, they seldom penetrate its depths for more than a few yards to forage or to nest. But where the forest has been thinned by lumbering or where gaps have been left in its canopy by the falling of great trees before the wind, allowing bushes and vines to spring up in greater profusion and creating conditions which simulate those at the forest's edge, the Tyrannine Antbirds are more generally distributed through it. They also live in the taller and heavier second-growth woodlands and thickets, but here, too, they are most often found at the edge. They are found in pairs throughout the year.

FOOD

In size and form of bill and body the Tyrannine Antbird resembles a middle-sized wren, and its manner of hunting through the densely entangled vegetation is decidedly wren-like. It creeps among the twisted vines and the clusters of leaves, living and dead, searching assiduously for spiders, caterpillars, moths, and insects of many sorts. I have not seen it eat fruit of any kind.

One morning in October, at the edge of the forest behind my house, I watched a female Tyrannine Antbird try to catch a big, brown, hairy spider that clung to a leaf. The bird was afraid of her intended prey, and from a respectful distance she stretched forth her neck to seize it with the tip of her bill. The spider kept its two pairs of forelegs elevated, with the two raised legs on each side in contact except at their slightly separated tips, so that they bore considerable resemblance to the

pincers of a scorpion. Whenever the bird came near, the spider waved these lifted legs, causing her to draw back. At last she flew away, leaving the spider uneaten. When left alone, the spider crept into its retreat between two leaves that it had fastened together. It measured possibly 2 inches across its spread legs and was a big creature for so small a bird to tackle.

VOICE

The song of the male Tyrannine Antbird is a clear, mellow whistle rapidly repeated with ascending pitch, forming what Chapman (1929:43) characterized as a "quaint, cosy little trill." The answering trill of the female is distinctly softer and higher in pitch than that of the male. These two trills, one high in pitch and one low, are often heard sounding back and forth as a mated pair of antbirds forage unseen in the dense vegetation at the woodland's edge. The song is delivered through much of the year. On Barro Colorado Island, where the Tyrannine Antbirds were abundant in the bushes and vine tangles surrounding the narrow clearing in which the buildings stood, their trills were an important component of the dawn chorus. Quite in contrast to this appealing song is this antbird's harsh, rattling note of suspicion or alarm.

NEST BUILDING

On Barro Colorado Island in the Canal Zone, I found a pair of Tyrannine Antbirds building in mid-February, but their work was abandoned before the nest was completed. Eggs, apparently newly laid, were discovered here on April 29 and June 2. In the valley of El General in Costa Rica, a nest with newly hatched nestlings was found on May 20, and nests with eggs were found on May 27 and June 17. On October 10, I watched a female feeding a stubby-tailed fledgling. Although the records of nesting are few, they indicate a long breeding season.

The nest may be placed at the edge of woodland, where it is more or less visible from the adjacent clearing, or it may be placed a few yards inside the edge of the forest, or in openings still farther within the forest. Of the six nests that I have seen, two were in each of these situations. For the support of their deep, swinging pouch, the birds select a fork near the free end of a slender, drooping vine, bough, or the like, rarely far above the ground. One of my nests was 22 inches up; four were between 3 and 4 feet up; and one was 9 feet above the ground. Within these limits, the sites and attachments of the six nests were so various that it will be illuminating to give them in detail:

Nest 1 was 3 feet, 8 inches up in the fork of a slender, hanging dead twig in bushy growth at the edge of the woods, beside a banana plantation. It was found under construction on Barro Colorado Island on February 15, 1935, and abandoned, unfinished, possibly because its support was unstable.

Nest 2 was 3 feet up in a fork of a slender hanging branch in a bamboo thicket in a little opening in the woods. It was found on Barro Colorado Island with one egg on April 29, 1935, and on the following day it was empty.

Nest 3 was 4 feet up, near the end of a slender hanging branch of a bush, in the angle between a petiole and the branch. This nest was just inside the edge of the forest. It was found on Barro Colorado Island with one newly laid egg on June 2, 1935, the day of my departure from the island.

Nest 4 was 9 feet up, suspended in a pendent skein of brown, dry *navajuela* (a

scandent sedge, *Scleria*, with long, knife-like leaves). The sedge was growing beside a rivulet at the edge of a narrow strip of forest. This nest was found in El General, 2200 feet above sea level, with two eggs on June 17, 1939.

Nest 5 was 3 feet, 10 inches above the ground and about 75 feet inside of the forest. The nest was in a fork at the end of a long, slender, descending branch of a stump sprout of a "coral" tree, that was beside an obscure, little-used path through low bushes in an open part of the forest. It was found in El General, 2500 feet above sea level, with two newly hatched nestlings on May 20, 1942.

The rim of nest 6 was attached to a hanging frond of a climbing fern (*Salpichlaena volubilis*), with the opening of the pouch between two primary pinnae. This nest, about 22 inches above the ground, hung close beside a small spiny palm and was screened on one side by a drooping dead palm frond. It was a few yards from the edge of the forest where there was a low thicket. The nest was found when nearly completed in El General, at an altitude of 2500 feet, on May 24, 1947.

I watched the pair of antbirds as they built nest 1, at the edge of the woods on Barro Colorado Island. When found on February 15, the recently begun structure was a loose and open fabric of fibrous materials intermixed with a few thin dead leaves. The pouch-like form was already indicated by the outline of the flimsy weft. Even as I watched, standing a few feet away and in plain sight, the male and female flew up and each added a billful of material to the structure. That same afternoon I set a blind at the edge of the clearing by the nest.

At 7:50 next morning, I took my place within the blind. The male antbird was the first of the pair to appear. At 8:12 he emerged from the bushes, perched above the nest on one of the arms of the supporting fork, and uttered a low twitter. A moment later his brownish mate arrived, stood on the other arm of the fork facing her slate-colored partner, and joined him in twittering. Then both flew back into the bushes at the woodland's edge, to return after a few seconds and repeat this behavior. The male was the first to get down to the business of the morning, and after coming three or four times to perch on the nest with empty bill, he brought a dead tendril out of the vine tangles and deposited it in the bottom of the pouch. After he flew off, the female came again with empty bill and arranged the tendril with greater care.

The male was the more active in carrying materials to the nest. In the two hours of my watch, he came 29 times with something in his bill, whereas the female brought material only 17 times. Frequently she arrived with empty bill and perched on one of the twigs that supported the nest while she tucked in loose ends of fibers and generally tidied up the structure, or else she sat snugly in the cavity of the growing pouch and shaped it with her body and feet. The male antbird also attended to these necessary details in no small measure, and he always put into place the materials that he brought. But it seemed to be the female's special province continually to inspect the work as it progressed and to give the structure its proper shape. Still, I believe that the male was the leader in the undertaking, for after an intermission in building, when the pair sought food beyond my view, it was usually the male who returned first to the nest. Then he called his mate with fine twitters or, if she delayed long, with a louder trill; and as soon as she joined him, building was resumed.

The materials taken to the nest included fine and coarse fibers, broad, thin, dead blades of grasses, and strips of palm fronds. These were brought in no definite order, with the result that the growing fabric was a rather random mixture of all these

components. Although the birds sat in the nest to give it shape, the bottom was still frail, and occasionally, as they worked their toes to entangle the fibers, a foot broke through. Twice, while sitting in the nest, the male sang his little trill.

The completed nest of the Tyrannine Antbird is a pensile pouch attached by its rim to the arms of the supporting crotch. The nest is much higher at the back than at the front, and the opening is strongly oblique, facing upward and outward. The deep pocket is widest near the bottom and narrows toward the orifice. The thick walls and bottom consist largely of dry leaves. In one nest there were bamboo leaves and fragments of the leaves of dicotyledonous plants; in another nest there were grass blades and other leaves; in a third nest there were papery strips of dead monocotyledonous leaves; while in still another nest there were pinnae of fern fronds and narrow strips from dead palm fronds. This leafy material is loosely held together and attached to the supporting fork by black fungal strands, brown fibers, and the like. Some nests have more or less green moss about the rim and on the outer surface. The lining is usually scanty, consisting of a few fungal filaments or other fibers coiled down in the bottom to form a flattish mat. The overall measurements of three nests varied from 5 to $7\frac{1}{4}$ inches in height and from 3 to 4 inches in diameter; the interior was from $1\frac{3}{4}$ to $2\frac{3}{4}$ inches in depth measured at the front, and from $2\frac{1}{8}$ to $2\frac{3}{8}$ inches in diameter. In one nest the depth from the rim to the bottom of the cavity was $2\frac{1}{8}$ inches at the front, but at the back, where it was attached to the hanging stipe of a climbing fern, the depth was 5 inches.

THE EGGS

Of the three nests found on Barro Colorado Island, one was never finished and the other two contained single eggs, which apparently did not represent complete sets. Each of the three nests that I found in Costa Rica held two eggs or nestlings. In one of these nests, an interval of two days separated the laying of the first and second eggs; the first egg was laid before 8:30 a.m. on May 25, and the second egg was laid before 7:25 a.m. on May 27. These eggs were dull white, spotted with reddish brown over the whole surface, but most heavily on the thicker end. They measured 20.6 by 14.3 and 21.4 by 15.1 mm. A single egg on Barro Colorado Island was white, thinly spotted with reddish brown on the larger end, and it measured 19.4 by 14.3 mm.

INCUBATION

Incubation is performed by the female at night and by both sexes alternately through the day. At nest 6, I found the male covering the single egg at 7:05 a.m. on May 26, the day after it was laid, but on two other visits later in the same day I found the egg unattended. The next morning at 7:25 the male was covering two eggs. When I came to set my blind in front of this nest at 8:50 a.m. on June 2, the female was sitting and she stayed in the nest, watching me work only 15 feet away. Even when I cut some bushes which obstructed my view, she did not take flight.

I watched this nest from 5:30 to 11:30 a.m. on June 3, and on June 4 I watched from 5:30 to 9:41 a.m. and from 12:05 to 5:00 p.m. Showers fell on both mornings, and much of my afternoon vigil on June 4 was made in a long, drenching rain, which approached the forest with a roar and made the light so dim beneath the trees that I could scarcely distinguish the antbird in the nest. In 15 hours of watching, I timed seven sessions by the male, ranging from 11 to 153 minutes and averaging

57.3 minutes. Three completed sessions by the female ranged from 79 to 124 minutes and averaged 97 minutes. Seven periods when the nest was unattended ranged from 1 to more than 59 minutes and averaged 22+ minutes. Counting only the parts of my watches which fell after the female antbird ended her nocturnal session, the male was in the nest a total of 401 minutes, the female, 291 minutes, and the nest was neglected 154 minutes. The male and female together kept the eggs covered for 81.8 per cent of the 14.1 hours of my record that fell within the period of the female's diurnal activity.

The behavior of the antbirds, especially that of the male, was very different on the two consecutive mornings that I watched their nest. On June 3, the female ended her night session at 6:00 a.m., 10 minutes after the light beneath the tall trees had become strong enough to reveal her in the nest. At 6:17, the male came trilling and settled on the eggs. At 6:28, after only 11 minutes of sitting, he suddenly left, then he sang at the forest's edge. At 6:40 he returned and at 6:51 he again went off. At 7:19 he returned in silence and sat until 7:31, when the female approached through the undergrowth, coming from the edge of the forest. As she flitted close by the blind she uttered a harsh, rattling note. Although she may have seen a portion of my face through the side window, she did not appear to notice it. On reaching the nest, she alighted on the side of the rim above her mate, who after a few seconds flew away. She ate something, possibly a feather, that she picked out of the nest, loudly clacking her mandibles as she finished swallowing it. Then she lowered herself slowly into the nest. When an airplane passed over, flying low, she merely raised her head. At 8:15, a drizzle began.

At 8:59 a.m., the male came silently in the slow rain and replaced the female. At 9:15 the rain became harder. At 10:07, after sitting for 68 minutes, the male went off in the rain. The eggs were exposed to the rain until the male returned in silence at 10:40. He sat steadily until the female came with fibers in her bill at 11:24, uttering a single low note. She alighted on the rim above the male, and after he went off she laid her material in the bottom of the nest, then settled down to incubate. The rain now stopped, and at 11:30 I ended my six-hour watch. I believe that the male antbird's impatient sitting on this morning was caused by the invasion of his territory by a trespasser of his own kind. Although I did not see the intruder, sounds that came from the forest's edge suggested some disturbance of this sort.

On June 4, after a rainy night, I resumed my watch at 5:30 a.m. At 5:45 I first heard the male antbird's song. At 5:50 the female left the nest, while the light was still very dim, and a minute later the male came to take his turn on the eggs. He sat steadily for 102 minutes, during which a shower fell for half an hour. At 7:33 the female approached, repeating her harsh, rattling note, and replaced him. After leaving the nest, he trilled. An hour later, while the female was in the midst of her long session, the male sang at the edge of the woods and she repeatedly trilled from the nest in answer, in tones weaker than his. She left at 9:37, after sitting for two hours and four minutes. At 9:41 the male entered the nest, and I ended my vigil.

Returning at 12:05 p.m. that same day, I found the nest unattended, and it remained so until, at 1:04, the female approached, repeating her harsh note many times, and entered the pouch. During the last half hour of her long session she drowsed, keeping her eyes closed most of the time, but opening them every now and then. At 2:23, after she had sat for 79 minutes, the male silently replaced her. For

the next 2½ hours he sat quietly, while most of the time rain fell in a deluge. At 4:56 the female came in the hard rain and relieved him. At 5:00 I went home, thoroughly drenched.

Whenever one member of the pair sat until the other arrived, the changeover was made in the same manner. The new arrival alighted on the slanting rim of the nest on the side toward the neighboring clearing, whence it had come, and stood for a few moments above its sitting mate. The latter would then fly away, and the newcomer would lower itself slowly and deliberately into the deep pouch, as though it were a tight fit. The movement reminded me of fitting a slightly oversized cork into the mouth of a bottle. The antbirds of both sexes invariably sat with their heads at the front of the nest, where the rim was lowest, and their tails were held erect against the high wall at the rear. When the incubating bird was perfectly at ease, its head was just visible above the rim at the front of the nest.

On visits toward the end of the night to this and another nest, I found the female sleeping on her eggs or nestlings. Her head was invisible, and the long feathers of her back were spread in all directions, completely destroying her outline. She resembled a bunch of loose feathers stuck into the pouch rather than a living bird. Once when she awoke and extracted her head from beneath her relaxed plumage, a forward-turned tuft of long feathers formed, temporarily, a curving hood above it. The Slaty Antshrike, the Bicolored Antbird, and doubtless other members of the family, have the same peculiar habit of turning out the feathers of the back in all directions, and so ceasing to resemble a bird, while sleeping in the nest at night. I have long wondered whether they do the same when they roost among the bushes, but I have never found a roosting antbird to provide an answer to my question.

At my highest nest, hung 9 feet up in *navajuela* sedge beside a rivulet at the forest's edge, I found sometimes the male, sometimes the female, in charge. The pouch was so deep that the sitting bird could not be seen from the ground. If alarmed, the bird would rise until it could look over the lowest part of the rim, thereby exposing its eyes, bill, and the top of its head, but otherwise remaining invisible. These birds felt secure in their high nest and allowed me to approach them closely. Often they would not desert their eggs until I shook the nest. Twice I saw the male, when thus driven from the eggs, expose the white bases of the feathers in the center of his back by turning these feathers outward. Once he did this while standing on a fallen log below the nest. For a few seconds, a broad area of pure white gleamed out in the middle of his slate-colored back, to disappear when he returned his feathers to their normal position. He did not simulate injury.

Because of the premature loss of the eggs from the nests found before the set was complete, I have been unable to learn the period of incubation.

THE NESTLINGS

When found on May 20, 1942, nest 5 contained two tiny nestlings, at most a day or two old. Their black skin was perfectly naked and devoid of down, but the buds of the remiges were already visible through it. Their eyes were tightly closed, and the interior of the mouth was yellow.

On May 23, 24, and 25, I devoted 12½ hours to watching this nest from a blind. The two nestlings were fed a total of 56 times, or at the rate of 2.2 meals per nestling per hour. The female brought food 37 times, the male only 19 times. She brooded once for 20 minutes in the morning and for 76 minutes continuously while rain fell

in the early afternoon, for a total of 96 minutes. The male also brooded twice, for periods of 12 and 27 minutes, a total of 39 minutes.

Such great disparity in attention to the nestlings by the two parents is not usual in antbirds. When a difference in the rate of feeding or the amount of diurnal brooding does occur, it is likely to be the male which does the greater share. But this male remained away from the nest for long periods, from 8:56 to 11:02 a.m. on May 23, and from 12:40 p.m. until after I ended my watch at 3:35 on May 25. During these periods of neglect by the male, the female usually attended the nestlings, thus accounting for her better record in feeding and brooding. But through much of the male's long absence on the morning of May 23, the female also stayed away from the nest, and the nestlings were unattended for one hour and 41 minutes.

This long period of neglect had a peculiar effect on the subsequent rate of bringing of food by the parents. The nestlings had been fed five times in the 1½ hours from 6:15 to 7:45 a.m. and three times from 7:45 to 8:56. Now followed the period when both parents were inexplicably away from the nest, and I neither saw nor heard them. By 10:00 the nestlings were becoming increasingly restless; they shook their swinging cradle and called in weak voices that sounded far away. At 10:37 the female at last arrived with food, and after delivering it she cleaned the nest. She then brought five meals in the next 24 minutes. Then, at 11:02, the male came with an insect and began to help appease the nestlings' hunger, which had become acute during the long period of neglect. From 10:37 to 11:46, the nestlings were fed 17 times by the female and six times by the male, making a total of 23 meals in 69 minutes, or at the rate of 20 times per hour. This was more than four times the average rate of feeding. The period of most active feeding was the quarter-hour from 11:00 to 11:15 a.m., when food was brought nine times. By 11:46 the nestlings appeared to be satiated, and the parents stayed away for the next half-hour.

During the whole interval of frequent feedings, from 10:37 to 11:46 a.m., the insects brought to the nest averaged far smaller in size than those which were delivered when the parents' visits were more widely spaced. Apparently during the period of frequent feedings, they brought the first edible morsel that they found, whereas at other times they sought more substantial objects for the nestlings, probably swallowing the smaller insects which they discovered while they hunted. I did not again witness a similar period of concentrated feeding at this nest. Such well-marked intervals of "attention" and "inattention" are, in my experience, rare while parent birds attend their nestlings, unless they have been kept from the nest for many minutes. As a rule, feedings are more evenly spaced.

The nestlings were given a considerable variety of insects, insect larvae, and a few spiders. To deliver the food, the parents did not rest on the front rim of the nest, where it was lowest, but on the much higher slanting sides. To reach the nestlings from this stance, each parent had to bend so far forward that its tail stood up above its head. To brood, the parent birds always backed down into the pouch with the tail toward the support. They sat with the head at the front of the nest, where the rim was lowest, and the tail held upright against the high wall at the rear, exactly as the members of another pair sat while they incubated. I never saw them reverse this orientation. Apparently they delivered food from the side of the nest, where it was more difficult to reach the nestlings, because they had formed the habit of alighting here when replacing each other on the eggs, and because from this point it was more convenient to enter the nest to brood in their customary position.

By May 23, when these nestlings were about four days old, the sheaths of their remiges were becoming very long and those of the contour feathers were sprouting. Two days later, the feathers on body and wings were beginning to escape from the ends of the long sheaths. When about eight days old, the nestlings were nearly clothed with plumage, at least on their upper parts, although their heads were still bristly with unopened pinfeathers. By May 30, when probably not over 11 days old, the young antbirds had left their nest.

SUMMARY

The Tyrannine Antbird is found chiefly along the forest's edge and in the more open parts of its interior. It is likewise found in the taller second-growth, especially near its margins. It ranges from sea level up to nearly 4000 feet on the Pacific slope of southern Costa Rica. It is paired at all seasons.

Its food appears to consist wholly of insects, spiders, and other invertebrates, which it hunts in densely entangled vegetation.

At all seasons, the male and female sing responsively with a clear trill. The trill of the male is somewhat stronger and deeper. The alarm note is a harsh rattle.

In southern Central America, the breeding season extends from February to October. The nest, which is from two to nine feet above the ground, is a deep, pensile pouch with a strongly oblique opening at the top. It is composed of leaves and fibers and is slung below the fork of a drooping slender branch or vine, 2 to 9 feet above ground, often at the woodland's edge or beside an opening in the forest. Both sexes build, but the male of one pair took the initiative and did the greater share of the work.

The set consists of two eggs, which are dull white, spotted over the whole surface with reddish brown which is heaviest on the thick end. The second egg is laid two days after the first.

The female incubates at night, with her feathers so relaxed that she hardly resembles a living bird. By day the two sexes alternate in the nest, taking sessions which usually last more than an hour and sometimes exceed two hours. One pair kept their eggs covered for 82 per cent of 14 hours in the daytime. When driven from his nest, a male dropped beneath it and spread the feathers of his back to reveal a usually concealed patch of white in its center. He did not simulate injury. The incubation period is not known.

Newly hatched nestlings have dark, naked skin, and the interior of the mouth is yellow. They are brooded by both parents, who feed them insects and spiders. In 12½ hours of watching, two nestlings a few days old were fed at the rate of 2.2 times per nestling per hour. At this nest, long periods of neglect of the nestlings were followed by spells of very rapid feeding. Insects brought at that time averaged smaller in size. The nestling period is about 11 days.

CHESTNUT-BACKED ANTBIRD

Myrmeciza exsul

Two well-marked forms of the Chestnut-backed Antbird occur in Central America, north of the Panamá Canal. *Myrmeciza exsul exsul* is found in the Caribbean lowlands and foothills from central Panamá to Nicaragua. *M. exsul occidentalis* is restricted to the Pacific side from the Gulf of Nicoya in Costa Rica to western Panamá. The latter, to which this account is chiefly devoted, is brighter than the eastern form and was formerly classified as a distinct species. In the male of this western form, the head and neck, including the throat, are black or slate-black. The remaining dorsal plumage is chestnut, somewhat darker on the tail. The breast, sides, and abdomen are blackish slate; the flanks and under tail-coverts are chestnut-brown. The female differs from the male in the slightly paler color of her head and upper plumage, and in having the under parts, posterior to her slaty throat, bright tawny-chestnut and brown instead of blackish. Both sexes are about five and a quarter inches in length. In both, the bill is black, sometimes with a light tip, and the large eyes are brown with bright blue lids encircled by naked skin of the same color. The legs and feet of some individuals that I examined at close range at their nests were black, but on others they appeared to be blue-gray.

The eyes of these antbirds are very mobile, constantly turning from side to side and up and down. As they turn in a certain direction, the area of bare skin on that side of the orbit contracts, while that on the opposite side expands. Perhaps the absence of feathers in the circumorbital region of this and a number of other antbirds could be an adaptation to facilitate the mobility of their eyes. Bare skin should yield more readily, and oppose less obstruction to the oblique glance, than feathered skin.

The Chestnut-backed Antbird dwells in the dark undergrowth of the rain forest, where it remains on or near the ground. On the Pacific side of southern Costa Rica, it occurs from sea level upward to about 2500 feet in the valley of El General. At the upper limit of its range, where the following studies were made, it prefers wooded dells to the drier ridges, and it never ventures even a short distance beyond the heavy forest. But in the Almirante Bay region of Panamá, years ago, I sometimes met the eastern race of this species in dense canebrakes and tall, rank secondary growth near sea level.

While I lived in a narrow clearing in the heavy forest near the Golfo Dulce in southwestern Costa Rica, a female Chestnut-backed Antbird entered a dark storeroom at ground level, evidently in search of food. Having gone in through the open door, she tried to escape through the screened window until she was caught and released.

These antbirds live in pairs throughout the year. One afternoon in early May, while I stood in the roadway that passes through the forest on our farm, I heard the harsh *waaa* of a Chestnut-backed Antbird. It was promptly answered by another antbird on the opposite side of the roadway, and the grating notes sounded back and forth several times. Presently one member of the pair flew across the road to its mate. Then one of them perched on a slender branch of a low shrub, its head stretched up with all the feathers sticking out, leaving the skin of the neck largely exposed and giving the little bird a vulturine aspect. Meanwhile the mate stood on

another twig close by and nibbled at the erected head feathers of the first. In the dim light, I could not tell which sex gave, and which received, this attention.

FOOD

Chestnut-backed Antbirds forage on and near the ground in heavy or dense woods. They move over the more open spaces of the forest floor by hopping rapidly—never walking—and from time to time they pick up a small edible object. Occasionally they flick a leaf aside with the bill, but apparently they do so only when they have seen a small creature take refuge beneath it, as this is not their usual manner of hunting. Where the low ground cover is dense, they advance by flitting from stem to stem close above the ground. Much of their food is found amid tangles of vines, on trunks wreathed in creepers or covered with moss and epiphytes, among dead leaves which lodge among the vines, and between old fronds which drape the stems of small palms. Sometimes they work up through tangled creepers to a height of about 10 feet, but usually they stay lower. Occasionally they forage with the army ants, in company with a variety of other small and middle-sized birds. Carriker (1910:616) and Howell (1957:92) record this manner of hunting in the eastern form, and I have seen the western race foraging so, both in El General and, with relatively greater frequency, in the coastal region. But the Chestnut-backed Antbird is not, like the Bicolored Antbird and a number of other species, a persistent follower of ants, and it probably accompanies them only when they invade its usual feeding area. I have seen it pass through a party of mixed birds foraging with ants, without delaying long.

The food of this antbird apparently consists wholly of insects and other small invertebrates, varied by an occasional small lizard and doubtless also tiny frogs.

VOICE

The song of the Chestnut-backed Antbird is a full, mellow whistle, so similar to that of the Black-faced Antthrush that the two are readily confused. But the Chestnut-backed Antbird's whistle is less bright and resonant, slightly more plaintive, than that of the antthrush. Moreover, two, or rarely three, of these whistles are given together, and in my experience never more, whereas the antthrush usually delivers three or more notes in a series. Sometimes the Chestnut-backed Antbird introduces its song with several lower, half-whistled notes, which are audible only when the bird is close at hand. Male and female have similar whistles, which they utter from a perch not over two yards above the ground. In El General, these mellow, plaintive notes are heard through most of the wet season, from April until November, but they are rarely heard in the dry months which start off the year. Chapman (1929:184) paraphrased the song of the eastern race as *come here*, or *come-right-hère*. He succeeded in drawing the bird to him by imitating these whistles and noted that when the male has a mate "she dutifully repeats his notes, but is always a little off his key. . . ."

The call note, used by the mated pair in answering each other, is a harsh, grating, nasal *waaa* or *aaaa*, as I have written it at various times. While nesting, the male and female communicate chiefly by means of this note which is so unpleasant to human ears. The alarm note or scold, uttered when a nest is disturbed, is a rapid rattle delivered in several keys and with varying inflections: *wittit wittit wittit wittit*.

CONFLICTS

At the end of April of 1957, I often heard the Chestnut-backed Antbirds while I sat in the forest watching an euphonia's nest. Once, I noticed two male antbirds posturing to each other. Perching not far apart near the ground, they stretched up their necks and displayed prominent white patches at the forward edges of their wings, where usually no white is evident. These white patches contrasted sharply with the black of their under plumage. At the same time, they uttered their mellow double whistles and also an attractive note, between liquid and whining. They drifted away through the undergrowth before I could see much of this display, which was unique in my experience.

In October of an earlier year, I watched a pair of Chestnut-backed Antbirds foraging in the herbage beside a path that ran through a narrow clearing in the heavy forest of the Pacific lowlands near the Golfo Dulce. They often uttered their plaintive double whistles. When a second female approached the pair, both of the females puffed out the feathers of their backs, giving themselves a hunch-backed aspect, and voiced high, soft notes, very different from their ordinary call. As far as the rank herbage permitted me to see, they did not come to grips; and soon one of the females vanished, leaving the other with her mate.

NEST AND EGGS

The Chestnut-backed Antbird breeds late, after repeated rains have soaked the fallen leaves and activated the small invertebrates which they harbor. In 1958, when showers were frequent in March and early April, I discovered a nest with eggs in mid-April, but in the other three nests found on my farm eggs were laid in July. All four nests were located, over a period of 11 years, in the same wooded dell, within a span of about 100 yards. It was in this same area that I saw the antbird attend to its mate's feathers and the two males displaying.

These four nests were placed from 10 to 16 inches above the ground in the dim undergrowth of the forest. Two were in or beside clumps of low, spiny palms entwined by the climbing fern *Salpichlaena volubilis*. One was 13 inches up in low herbage. The lowest was supported by the nearly horizontal stem of a slender bush and by a small plant (*Piper* sp.).

All of these nests were open cups, but they differed in size and compactness. The first, relatively well-made and neat, had a loose, open foundation composed of long pieces of dead stipes of the climbing fern. The middle layer consisted of rather large dead leaves, and the lining was of dark, fibrous rootlets, which failed to conceal the underlying leaves. The outer wall contained some green moss. This nest measured 4 inches in diameter by 2¾ inches in height. The cavity was 2¾ inches in diameter by 1¾ inches deep. In contrast to this, the last of the nests, a very bulky, untidy structure, which resembled an accidental accumulation of dead vegetation rather than a bird's nest, measured about 4½ inches in both diameter and height, not including the projecting ends of the materials. Its cavity was 2½ inches wide and 2 inches deep. The loose foundation and outer framework of this nest consisted of coarse fern rhizomes, rootlets, lengths of decayed vines, a few sticks and branched inflorescences, and similar coarse materials, including a length of the creeping fern *Rhipidopteris peltata* with finely divided living fronds and a small orchid plant with green leaves. The thick middle layer contained assorted leaves and fragments of palm fronds. The largest dicotyledonous leaf was 8½ inches long by 3 inches wide,

and it stood up 5 inches above the nest's rim. A brown pinna of a palm frond hung 8 inches below the bottom. The lining consisted of long, coarse, blackish fungal hyphae or "vegetable horsehair" and fibrous rootlets which, although liberally applied, failed to conceal the leaves on which they rested. Another nest, intermediate between these two in bulk, was even deeper than the one just described, its internal depth being $2\frac{3}{8}$ inches.

When found on August 13, 1947, the first nest contained a single egg already on the point of hatching. Not far from the site of this nest, I found on July 21 of the following year a nest with a single egg that was pipped the next day. These nests probably belonged to the same pair of antbirds, and apparently a single egg was laid in each. The third nest contained two naked nestlings on July 25, 1953, and the fourth, two eggs on April 15, 1958. The Chestnut-backed Antbird's eggs are unusually beautiful. On a dull white ground, they are heavily blotched, speckled, and streaked with deep, rich purplish or rufous brown. The markings are heaviest on the thick end, where they almost obscure the ground color; they are elongated in the direction of the long axis of the egg on its sides, and they thin out toward the sharper end. Two of the eggs had a strong suffusion of pale lilac between the heavier marks. The four eggs measured 24.6 by 15.1, 23.0 by 16.7, 23.8 by 17.1, and 23.8 by 16.7 mm.

Carriker (1910:616-617) found a nest of the western form of the Chestnut-backed Antbird at Pozo Azul de Pirris in the Pacific lowlands of Costa Rica on May 10, 1902. It contained two eggs. At Guápiles in the Caribbean lowlands, he discovered a nest of the eastern race with two fresh eggs on July 13, 1905. His accounts of the nests and eggs of these two forms show that they are quite similar and agree rather closely with those already described. On Barro Colorado Island, Dr. A. O. Gross found three nests with eggs of the eastern race between July 13 and August 5 (Eisenmann, 1952:35).

INCUBATION

To study the nest found with two eggs in April 1958, I set my blind on the opposite side of the thick, moldering log which upheld the slender, horizontal stem that supported the nest. Here I watched from 12:30 to 6:00 p.m. on April 21 and from 5:33 a.m. to 12:39 p.m. on the 22nd. The female settled on the nest for the night at 5:23 p.m. on April 21, and when I left at 6:00 it was too dark to see her. When I returned to the blind at 5:33 next morning, she was still invisible in the dusk. By 6:01 I could see her turn the eggs. Soon I heard the full double whistle of a Chestnut-backed Antbird in the distance. It was repeated over and over for many minutes. The female on the nest was becoming increasingly restless. At 6:21 a.m. she left, hopped along the supporting stem to the log, picked a small, light-colored leaf from its surface, and flew away with it. At 6:34 the male came, uttering loud double whistles, and settled on the eggs. He sat until 7:42, when he went off leaving the nest unattended. At 8:21 he returned, repeating his harsh *aaaa* as he approached through the undergrowth, and resumed incubation. At 9:06 he again left, and the eggs remained uncovered until the female, calling *aaaa* loudly, came at 9:40 to take charge of them. She stayed at her post until the male replaced her at 11:12. He then sat until after midday.

In the afternoon, during which a shower fell, each partner remained on the nest until it heard the other approaching, and the eggs were not left uncovered for more

than three minutes at a time. Throughout the day, the bird coming to take its turn at incubation usually repeated the harsh call over and over, and the sitting partner, especially the male, sometimes replied with a similar but more subdued note. As he went off, the male might continue these grating calls, but the female voiced low, soft notes, or else left in silence. Her favorite mode of approach was by hopping along the log, then out along the slender bush that supported the nest. The male came hopping over the ground and through the undergrowth. The nest was slightly tilted, and the parents preferred to sit with their heads at the lowest point of the rim.

In more than 12 hours of watching, I timed three completed sessions by the male, lasting 95, 68, and 45 minutes. The female's diurnal sessions lasted 136 and 92 minutes; her nocturnal session, extending from 5:23 p.m. to 6:21 a.m. next morning, occupied nearly 13 hours, or 778 minutes. In the afternoon, the eggs were left uncovered only twice, for 1 and 3 minutes, when the changeovers occurred. In the forenoon, the eggs were exposed for three periods lasting 13, 39, and 34 minutes. If we consider the antbirds' active day as extending from 5:45 a.m. to 5:45 p.m., an interval of 12 hours, then the eggs were incubated a total of 630 minutes and left exposed for 90 minutes. Both parents together kept the eggs covered for 87.5 per cent of the day. Including sessions interrupted by my arrival or departure, the male incubated for 344 minutes of the diurnal period and the female for 286 minutes.

These eggs vanished before they hatched, and I do not know the incubation period of the Chestnut-backed Antbird.

THE NESTLINGS

As I walked along a forest path at eight o'clock on the morning of August 13, 1947, the loud, continuous *wittit wittit wittit . . .* of a Chestnut-backed Antbird suggested the presence of a nest, and I almost immediately found it—my first. The single egg was on the point of hatching, and by noon the dark and completely downless nestling had emerged. The thick end of the shell was sticking to its head like an over-sized helmet; it was so firmly attached that I could lift the chick by this piece of shell, which was difficult to remove.

I promptly set my blind before the nest and watched all of the following morning, as well as on three later mornings. The results of 23 hours of observation are summarized in table 6, from which it is clear that the male was the chief attendant, performing by far the greater part of the feeding and of the diurnal brooding. On the day after the nestling hatched, it was brooded by the male for nine periods, ranging from 2 to 46 minutes and averaging 24.2 minutes. The female brooded for

Table 6
Care of a Nestling Chestnut-backed Antbird

Age of nestling	Brooding in approximately six hours of the forenoon (minutes) ¹				Meals offered		
	Male	Female	Total	Left uncovered	Male	Female	Total
1 day	218	62	280	70	14	2	16
3	119	148	267	67	5	4	9
6	98	0	98	254	11	1	12
8	0	0	0	348	20	2	26 ²
Totals	435	210	645	739	50	9	63 ²

¹ The observation period extended from 6:34 a.m. to 12:24 p.m. when the nestling was one day old; from 6:06 to 11:40 a.m. when it was three days old; from 5:53 to 11:45 a.m. when it was six days old; and from 5:57 to 11:45 a.m. when it was eight days old.

² This includes 4 feedings by a parent not positively identified.

only two periods, lasting 50 and 12 minutes. When the nestling was three days old, the male brooded it four times in the course of the morning, for 40, 14, 32, and 33 minutes, whereas the female brooded it only three times, for 45, 57, and 46 minutes. On this morning she sat more than her mate. But on August 19, when the nestling wore long pinfeathers that had not yet begun to open, the male alone brooded it, for four periods of 20, 30, 3, and 45 minutes.

On the morning after the nestling hatched, the male brought food 14 times, but three of these meals were swallowed by him when the nestling failed to accept them. The female fed only twice. I cannot account for the conspicuous drop in the rate of feeding when the nestling was three days old. In the four mornings, the male brought food at least 50 times, the female, at least nine times, and there were four feedings when I failed to identify the parent with certainty because of the poor light. As far as I saw, the nestling was given only insects, including moths and orthopterans, and other invertebrates. Its droppings were usually carried off in the parent's bill, although rarely they were swallowed.

The nest was situated in an area fairly free of undergrowth, and the parents usually approached it by hopping over the ground until they were almost beneath it. They left the nest by dropping to the ground and hopping away. More rarely they came flitting from bush to bush near the ground, but they never took long, direct flights. Sometimes they rested on the ground near the nest, and once the male continued to stand almost motionless below it for seven minutes. The parents sometimes exchanged their harsh notes of greeting as they came and left, but they were more silent than a pair which I later watched while they incubated.

When a Black-faced Antthrush walked close to the nest, tossing aside fallen leaves as it searched for food, the male, which was brooding, ignored the intruder, even when it was almost beneath him. But later when, returning with food, he found a Bicolored Antbird near the nest, he chased this smaller trespasser with loud clacking of his bill. But the parents' chief troubles were with agoutis (*Dasyprocta*), which often came to eat the large seeds that littered the ground beneath the towering palo de vaca (*Brosimum utile*) below which the nest was situated.

Early on the first morning that I watched, when the nestling was still less than a day old, an agouti passed almost beneath the nest without appearing to notice it. Less than a yard from the nest, the rodent sat on its haunches to eat a *Brosimum* seed, which it held in its forepaws. The male antbird approached quite close to the mammal and churred, then hopped over the ground nearby, flicked aside a fallen leaf with his bill, then brooded, while the agouti rested, and later ate more seeds, less than a yard away. The rodent was constantly twitching its ears, doubtless to keep off the mosquitoes which swarmed around it. Presently it moved all around the nest, scarcely a foot away, then raised its head to sniff the structure. At this point, the male antbird jumped from the nest and flew low over the ground. The agouti almost simultaneously bounded away in the same direction. Possibly it was startled by the bird's sudden movement. From the undergrowth beyond my view I heard the antbird's scolding *wittit wittit wittit*. Soon the rodent returned to its former position near the nest but paid no more attention to it, and after a few minutes the animal wandered away.

On subsequent mornings, the agouti foraged around the nest and sometimes came quite close without appearing to notice it, while the antbirds attended their nestling, ignoring the rodent. But toward midday on August 21, when the nestling was eight

days old and its feathers were beginning to escape their long, horny sheaths, two agoutis approached from one side while the male antbird was hopping away on the other side. The adult returned at once, dropped to the ground in front of an agouti, which had come very close to the nest, and fluttered away as though injured, causing the animal to start in his direction, whereupon the bird flew up out of reach. After following for only a foot or so, the agouti stopped and wrinkled its nose while it sniffed the air in the vicinity of the nest. The antbird continued incessantly to voice the alarm note, *wittit wittit wittit*, punctuated at intervals by the call *waaa*. Again and again he dropped down and "feigned injury" in front of the agouti, causing it to start in his direction, but without succeeding in leading it away from the nest.

These demonstrations by the male antbird seemed to excite the interest of the agouti, who previously, when the bird had largely ignored it, had paid little attention to the nest, although it occasionally sniffed the surrounding air. But now it sniffed and sniffed, wrinkling its broad pink nose and moving all around the little clump of vegetation which sheltered the nest. At last it touched the nest with the tip of its nose—when I violently shook the cloth which surrounded me and caused it to bolt with the usual sneeze-like bark of alarm.

The rodent had left the nest slightly tilted. Soon it returned and went toward the nest with a directness that left little doubt as to its intention. I burst forth from the blind and chased it off through the forest.

After the agouti's departure and my return to the blind, the male antbird came back, hopped over the ground below the nest, and clung low on upright stems until he found a small insect, which he took to the nestling. The female was not seen during the whole time the agouti was present. As I was leaving, I met the male antbird approaching the nest with another insect. He hopped rapidly down the pathway ahead of me, then circled through the bushes and scolded. Neither he nor his mate ever gave a distraction display for me, as he did for the agouti.

At break of the following day, I found the female antbird brooding her nestling in the nest, which I had propped up in its original position after the agouti had tilted it. I was obliged to be absent most of the day. I returned in the middle of the afternoon to find the nest torn from its supports and the nestling gone. I could not tell whether the agouti or some other animal had taken it.

In interpreting the antbird's failure to lure away the agouti by his distraction display, it should be borne in mind that this middle-sized rodent is largely vegetarian and appeared to have no interest in catching the bird. A predator like the tayra or the ocelot would probably have pursued the displaying antbird and been enticed farther away, as would have happened with a dog. But probably agoutis, like squirrels, are not averse to varying their vegetable diet with occasional eggs or nestlings. Possibly there are individual differences in the agoutis' dietary habits, and the agouti that finally showed so much interest in the nest may not have been the one that on past mornings seemed almost indifferent to it. Possibly, also, the parent antbird's excess of zeal finally suggested to the rodent that a meal was available.

The following year, the antbirds' nest was situated in a clump of spiny palms in a fork in the roadway. Both before and after the egg hatched, the female, after remaining on the nest until I came close, sometimes until I was within reach of her, fluttered down the path ahead of me with spread, beating wings, in an excellent distraction display. The male of this nest simulated injury less often and less convincingly. At the nest I found in 1958, both parents, when driven from the eggs

by my near approach, skimmed over the ground with wings expanded and nearly erect, in earnest distraction displays. After disappearing in the undergrowth, they raised a loud outcry of *wittit wittit wittit*. Thus, three nests varied as to the sexes which displayed and the parents' responses to intruders of different kinds.

The third of these antbirds' nests was found on July 25, 1953, by Robert M. Laughlin, who spent 8 hours and 22 minutes watching it while the two nestlings were in pinfeathers. The male brought food 15 times and the female eight times. The male brooded for a total of 144 minutes and the female for 73 minutes. His longest session on the nest was 48 minutes and hers 16 minutes. Thus at this nest, as at the nest that I had watched earlier, the male attended the nestlings more assiduously than the female, although the difference was less pronounced. Both members of this pair spent considerable periods, up to ten minutes, standing on the rim of their nest and pecking at small insects. In addition to orthopterons and caterpillars, Mr. Laughlin saw one of the parents bring a small green lizard to the young. On July 30, the nestlings' feathers were expanding, but by the following day the nest had been pulled apart, one young bird had vanished, and the other lay dead in the wreck of the nest.

Of the four nests with a total of six eggs, only the one found in 1948 was successful; this, too, would have failed without my intervention. At 3:00 p.m. on July 22, the single egg was pipped, but 24 hours later it was still unhatched. By 7:00 a.m. on July 24, the chick had pierced its shell, and small ants were entering through the perforation. I shook and blew them away. By noon the egg had hatched, and the empty shell had been removed.

The newly hatched nestling had dark skin with no trace of down, tightly closed eyes, and the inside of its mouth was yellow. A day after it hatched, the buds of the pinfeathers were visible beneath the skin on its head, body, and wings. Three days after hatching, its eyes were opening and the pinfeathers were pushing through the skin; those of the remiges were the longest. When the nestling was seven days old, the feather sheaths were very long but still unruptured. The young bird's skin, pinfeathers, bill, and feet were all so dark that it was everywhere nearly black, except the prominent yellow flanges at the corners of its mouth. A day later, the feathers were escaping from the ends of the long sheaths on both body and wings. When nine days old, the nestling was clothed, at least on the upper parts, with expanded feathers, which were dark brown. By the following morning, the nest was empty. The young bird apparently had left spontaneously, when slightly less than ten days old.

SUMMARY

The Chestnut-backed Antbird lives in the dark undergrowth of the rain forest or at times in rank secondary vegetation. It rarely rises as much as 10 feet above the ground. On the Pacific slope of southern Costa Rica, it is found from sea level up to about 2500 feet.

It is paired throughout the year, and mated birds preen each other's plumage.

When foraging, these antbirds hop over the ground, at times using their bills to toss aside fallen leaves. They work through tangles of vines, searching in the dead leaves caught up in them. Rarely they forage with army ants. They appear to subsist entirely on insects and other invertebrates, and an occasional small lizard or frog.

The song of both sexes is a series of two or, less often, three mellow, somewhat

plaintive whistles, and it is heard chiefly in the wetter part of the year. The call is a harsh, grating *waaa*. The scold or alarm note is a rattling *wittit wittit wittit*.

In antagonistic display, males spread their wings, revealing on their forward edges white patches that are usually concealed. In the same circumstances, females puff out the feathers of the back. No fighting was seen.

The Chestnut-backed Antbird nests in the wet season. In El General, eggs were found in mid-April after a rainy March, but three other nests held eggs in July. The nest, placed from 10 to 16 inches up in the undergrowth of the forest, is an open cup. The structure is at times fairly compact, but it may be very bulky and untidy, with large dead leaves sticking out in all directions. The complete set may apparently consist of either one or two eggs. These are beautifully marked with purplish brown on a whitish ground.

The female incubates through the night, and by day the two sexes alternate on the nest. The continuous diurnal sessions of one pair ranged from 45 to 136 minutes. Eggs were left uncovered as long as 39 minutes. The parents together kept the eggs covered for 87.5 per cent of the day. The incubation period is unknown.

At two nests, the male took the larger share in feeding the nestlings and in brooding them by day, and at one of these nests the difference in the attentiveness of the parents was very pronounced. At this nest, the parents sometimes ignored an agouti that on several days ate fallen seeds close by. When an agouti became interested in the nest, the male tried to entice it away with repeated distraction displays, but he was unsuccessful. The parent's distraction display seemed only to increase the rodent's interest in the nest. The nestling was finally taken by a predator, possibly the agouti.

The antbird which simulated injury before the agouti never did so before the human observer. But at other nests both parents gave excellent distraction displays to the observer, both before and after the eggs hatched.

The newly hatched nestling is sightless and bears no trace of down or feathers on its dark skin. The interior of its mouth is yellow. The pinfeathers sprout rapidly and grow long before the plumage begins to expand, when the nestling is about eight days old. A day later, the dorsal surface of the nestling is well covered with feathers. One nestling left the nest when ten days old.

SPOTTED ANTBIRD¹

Hylophylax naevioides

This small antbird, slightly over four inches in length, is easily recognized by the bold pattern of its plumage. The pure white breast of the male, crossed by a curving necklace of heavy black spots, immediately catches the eye and serves to distinguish him at a glance from any other inhabitant of the Central American forests. His upper plumage is rich chestnut-brown; the top of his head and hindneck are grayish. His black wing-coverts are boldly spotted with white and cinnamon-rufous. The female resembles the male but is easily distinguished by her buff-tinged rather than snowy white under plumage; her throat is whitish rather than black and the spots on her breast are olive or grayish rather than solid black. The species ranges through the humid lowland forests from eastern Nicaragua southward over the Caribbean side of Costa Rica to Panamá, Colombia, and western Ecuador.

The Spotted Antbird subsists largely on insects, spiders, and other small invertebrates, varied, no doubt, by an occasional small frog or lizard. In the tropical forests, such small creatures are often protectively colored and difficult to detect; they hide beneath the ground litter, in crevices in bark, under the sheathing bases of palm fronds, and in similar situations. But as a horde of army ants advances slowly and relentlessly over the ground and the lower parts of the plants, all of these little animals recklessly expose themselves as they rush out to escape the ants. In the lower levels of the tropical forest, such creatures are nowhere more easily caught than above and around the hunting ants. As a result, several kinds of birds have become so dependent up the army ants as purveyors of food that it is doubtful whether they would thrive where these ants are absent. Among the most constant attendants of the hunting swarms in the forests of southern Central America are the Spotted Antbird and the Bicolored Antbird. A fuller account of the mixed flocks which attend the army ants is to be found in the chapter devoted to the latter species (pp. 249-253).

One or several pairs of Spotted Antbirds may be present in a single mixed company of ant-followers. Of all the motley feathered crowd, they are among the smallest, the most active, and the most fearless of a human observer. Perching upon low branches, only a foot or two above the ground, or else clinging sideways to some slender upright stem, they intently watch the ground litter, which is turned a deeper brown by the legions of ants swarming over and through it. Suddenly one of the antbirds flies down, snatches up a cockroach, a beetle, or a spider as it abandons its hidden retreat in the face of the advancing army, quickly regains a low perch with its booty, then beats it against a twig and at last swallows it. Then the antbird continues to perch quietly, close above the ground, peering down with bright black eyes, until another tempting morsel evokes another quick descent among the ants. One rarely sees a Spotted Antbird as high as 6 feet above the ground. If a number of individuals of this species are present, one occasionally rushes at another, even when there appears to be food enough for all. The pursuer spreads the chestnut feathers of his back, revealing in their midst a conspicuous patch of white that is ordinarily invisible.

¹ This life history is a résumé of an account in Skutch, 1946a.

The call of the Spotted Antbird is a high, sharp *psip*, or at times a short, soft *peep*. It also utters a low *churr*, a note of anger or alarm. It sings a high-pitched trill and at least two other songs, both of which are delivered in a thin voice that sounds far away even when the bird is close at hand. One may be paraphrased *peede weede weede weede weede weede*, the successive notes uttered slowly and slightly descending in pitch. The second song sounds much like *peede peede peede peede sip sip sip sip*. I have heard the female reply with the *peede weede* song to the similar song of her mate. As in other antbirds, there is little or no difference in voice between the sexes. These songs, at best subdued utterances, are sometimes delivered in a whisper.

While I sat in a blind on Barro Colorado Island in late March, watching a Yellow-thighed Manakin's nest, a swarm of army ants approached through the forest with their usual avian attendants, including a pair of Spotted Antbirds, who appeared to be preparing to nest. The male was most attentive to his mate, and often, when he secured a fine morsel, called her to his side with low twitters and passed it to her. Their hunger satisfied for a while, they rested close, side by side on a fallen branch, and preened. When the buff-breasted female again became hungry, she pecked gently at her mate's black bill, whereupon the two returned together to forage with the ants. Strong conjugal attachment seems to be characteristic of the genus *Hylophylax*. Some years later, in the dripping forests of the eastern foothills of the equatorial Andes, I watched a mixed company of ant-followers which included a pair of Spotted-backed Antbirds. When not actively engaged in catching insects, the male and female perched side by side only a few inches above the ground on a fallen branch, much as the pair of Spotted Antbirds had done. The male preened the plumage of his mate's neck. The song of these Spotted-backed Antbirds reminded me greatly of that of their Central American relatives.

NESTING

On Barro Colorado Island, I found three occupied nests in April and May, and Eisenmann (1952:36) has since recorded nests in June and July. My nests were situated in small saplings, in fairly dense undergrowth of the forest, at heights of 12, 28, and 30 inches above the ground. One was in the fork of a horizontal branch, but the others were suspended between two diverging branchlets which adjoined the upright stem at different levels, with the result that one side of the nest was higher than the other.

On April 18, I watched a pair of Spotted Antbirds build a nest in a fork which contained the remains of an older nest that had become partly detached and hung by one side. The bottom of the new construction rested against the top of the older one. Both sexes shared the work of construction, but the male did a little more building than his mate. From 7:00 to 9:00 a.m., he made 19 visits to the nest, whereas she made only 13 visits. Although sometimes they flew up together with fibers in their bills, usually their visits alternated. Each bird placed and arranged its own contribution, but the male seemed more careful in shaping the nest than the female. If one member of the pair, flying up with material, found the other in the cup, it did not pass its burden to its mate but waited beside the nest until the latter departed, then placed and arranged its own material. Either bird, arriving alone at the nest, called the absent mate with short, soft *peeps*. Sometimes the male antbird,

sitting in the cup with his partner close by, sang in an undertone *peede peede peede peede, chip chip chip chip*. I did not hear him sing in her absence.

One nest was constructed largely of brown, dry, thread-like pistillate inflorescences of the small tree *Myriocarpa izabalensis*. In addition, there were fine fibers from other sources and an admixture of black fungal hyphae. Some fragments of dead leaves and twiglets were attached to the outside. This nest measured $2\frac{3}{4}$ inches in depth by $2\frac{1}{2}$ inches in internal diameter. Another nest was quite similar in form and construction, but it was black rather than brown in color because of the abundance of fungal strands used in its composition.

On Barro Colorado I found two completed sets of two eggs each. The eggs were very heavily and rather uniformly mottled all over with umber. This pigmentation covered half or more of the surface and was diffused into the whitish ground color. The eggs of one set measured 23.0 by 15.1 and 23.0 by 15.9 mm.

Incubation is shared by both sexes. At 12:10 p.m. on May 18, 1935, I entered a blind in front of a nest that held two eggs the incubation of which was well advanced when I found them a few days earlier. I watched until 6:50, when it was nearly dark, then returned as the night ended at 5:40 a.m. on May 19 and continued my vigil until 12:40 p.m. The late afternoon of May 18 was rainy, and a hard shower began just before noon of the following day. The diurnal sessions of incubation were long for birds so small; with a single change of occupancy by male and female, the eggs were covered nearly constantly in the morning and afternoon. The male took sessions lasting 77, 44, and 217 minutes. The female's diurnal sessions continued for 127, 36, and 164 minutes. In addition the female incubated through the night, from 6:30 p.m. until 6:05 a.m., an interval of 11 hours and 35 minutes. Counting only completed sessions of the diurnal period (1:06 to 6:30 p.m. on May 18, and 6:05 a.m. to 12:40 p.m. on May 19) the male covered the eggs a total of 338 minutes, the female covered them 327 minutes. The nest was unattended for only 54 minutes, of which 22 minutes were accounted for by one long intermission. The eggs were covered for 92 per cent of the day.

These antbirds approached their nest by flying from slender upright sapling to slender sapling, to each of which they clung briefly at a point about a foot above the ground. The male called *chip chip chip* as he advanced toward the nest, and both partners gave this call as they snuggled down on the eggs. Thereafter the antbirds incubated in silence. In contrast to their confidence in my presence while they foraged with the army ants, I found the Spotted Antbirds exceedingly wary at their nests. No matter how cautiously I approached, I seldom caught a glimpse of one on its eggs or nestlings, or even as it stole away. Their nesting activities could be watched only from concealment.

The newly hatched nestlings were sightless, black-skinned, and without a vestige of down. Fed and brooded by both parents, they developed very rapidly. When they were a week old, pinfeathers were becoming prominent on the body, and those of the remiges were already long. Soon the young antbirds bristled with long, dark-colored pinfeathers. After reaching full length, these sheaths were rapidly shed, leaving the nestlings well feathered when they were ten days old. On the following day their nest was empty. It appeared that the young had left spontaneously at the age of 11 days.

BICOLORED ANTBIRD

Gymnopithys leucaspis

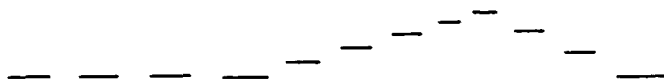
Clad in rich brown and white, the Bicolored Antbird (frontispiece) is a more colorful bird than one expects to find in the shadows of the tropical forest. It is also exceptional among the less plainly attired antbirds in having the sexes alike. This antbird is about five and a half inches in length. In the form with which this account chiefly deals, *Gymnopithys leucaspis olivascens*, all the dorsal plumage, including the wings and tail, is chestnut-brown. Below and behind the bare skin that surrounds each eye is a black patch which covers the lower cheeks and the auricular region. The sides of the neck and body are plain brown, which abuts irregularly on the broad band of pure white that covers the central under parts from the chin to the abdomen. The under tail-coverts are brown with whitish or buffy tips. The large brown eyes are surrounded by bright blue, featherless skin. The bill is largely black. The legs and feet are light bluish lead-color.

The Bicolored Antbird inhabits the rain forests from Honduras to Ecuador. In the northernmost parts of its range it appears to be confined to the Caribbean drainage, but south of the Gulf of Nicoya it occurs on both sides of the continent. On the Pacific side of southern Costa Rica it extends from sea level up to at least 5000 feet, and in neighboring parts of Panamá it has been found from 4000 to 6000 feet (Ridgway, 1911:134). It passes its life in the undergrowth of the forest, rarely rising as high as a man's head, but descending to the ground only briefly to pick up prey that it has sighted, or to give a distraction display at its nest. Sometimes, however, it extends its forays into tall second growth adjoining primary forest, into abandoned banana plantations and even into those plantations which are kept fairly clear of weeds, and, especially in long-continued wet weather, it may even visit the denser shrubbery about houses near the forest. Once I watched one of these antbirds making its way across a pasture by flying from one to another of the scattered trees and bushes. It was already at least 200 feet from the woodland and it was moving farther away.

The Bicolored Antbird is often found in pairs, even from November to February when it is least likely to be breeding, and it seems to remain mated throughout the year. These antbirds are most often seen with the army ants, and from four to six individuals, more rarely ten or twelve, may forage together. Their behavior then usually fails to reveal association in pairs.

VOICE

At its best, the Bicolored Antbird's voice is pleasant rather than musical. Its song is an extended series of clear, thin notes, which are at first fairly long and distinct. As the song proceeds with accelerated tempo, the notes become shorter and rise in pitch, until at times they almost merge into a trill. Finally, there are a few longer notes which fall rapidly in pitch. The song may be represented thus:



This song has many modifications. A frequent version lacks the final falling notes and may be written: *we we we we we we we wheer*, of which the last two syllables rise conspicuously in pitch. A still simpler version consists of similar, sharp notes rapidly repeated. At times, a harsh, nasal drawl, or a series of them, terminates the performance. To list all the variations would be tedious. When several Bicolored Antbirds, gathered around a swarm of army ants, are singing and calling on all sides, in varying tones and cadences, the effect is most amusing. Sometimes the members of a pair sing responsively.

When foraging with the ants, these antbirds frequently utter, especially when disturbed by an intruding human, a throaty, drawled, complaining note. They also repeat a peculiar whining note, and a low *churr*. At times one bird flies at another with a harsh, rasping call. When disturbed at their nest, Bicolored Antbirds utter a low, scolding *churr*, and a churred *per-r-r-r-r*, at once plaintive and protesting. As they approach their nest undisturbed, or look down at their eggs or nestlings, they sometimes give a whispered *p-p-p-p-p*.

FOOD AND FORAGING

Foraging with army ants.—A square mile of forest on the mainland of tropical America contains many species of birds, but most of them are represented by fewer individuals than is true of the birds of clearings and plantations. Although southern Central America has, for its area, one of the richest avifaunas in the world, one may walk a long while through its lowland forest without seeing many birds. With growing disappointment, the bird watcher may peer into the dark undergrowth or gaze upward into the trees that tower high above him until his neck aches. If he is a newcomer in these forests, he may before long conclude that those who have written so glowingly about the wonderful bird life have been guilty of deliberate and unpardonable misrepresentation. But if he walks far enough he will finally, unless his luck is unusually bad, be attracted by a medley of harsh and liquid voices—trills, churrs, squeaks, whistles, and even snatches of beautiful song—coming from the neighboring undergrowth, or perhaps from a point ahead of him on the trail. Prominent among these voices will be the gently mocking tones of the Bicolored Antbird.

As the wayfarer approaches stealthily, the aspect of the forest suddenly changes. Whereas a minute ago its life seemed to consist almost wholly of the silent processes of vegetative growth, reproduction, and decay, now there is no dearth of the noisier, swifter, more dramatic and violent activities of animals. Small birds of many kinds are flitting back and forth, calling, feeding, at times chasing each other. The more timid hover in the background, indistinctly glimpsed through the low palms, ferns, and other undergrowth. The bolder may carry on their activities within a few yards of an observer who stands quietly in one spot. Some perch on slender, erect stems near the ground, others cling upright on thick trunks, still others perch on horizontal branches above the level of the watcher's head. From time to time most of these birds drop to the ground, then quickly rise with an insect or spider in their bills.

His attention directed downward by the movements of the birds, the watcher notices that the ground is covered with ants, which may be small or of medium size, brown or blackish in coloration. Over a space of 5, 10, or more yards in extent, they spread in countless thousands, hurrying over and under the fallen leaves and other litter, while others file up and down the trunks of saplings, palms, and even

massive trees. If the weather has been dry, the tiny feet of countless ants falling on the dead leaves that cover the ground, the scurrying and jumping of the small creatures which desperately strive to escape them, produce a continuous low rustling, which is the background of sound for the varied cries of the birds. The insects, spiders, millipedes, and isopods, of many kinds but mostly dull in color, along with an occasional small frog or lizard, driven by the hunting ants from their hiding places in the ground litter or from crevices in the bark of trees, are seized and devoured by the birds, who by accompanying the ants save themselves the incessant labor of stirring up the fallen leaves with their own bills or feet, or of scanning and probing countless crannies in the bark.

With so many birds eager to pounce upon the first small creatures that the ants set in motion, one wonders how the ants themselves manage to capture enough food to support their restless activity. But if one can find the narrow column which connects the deployed hunting swarm with the temporary nest in a hollow log or beneath a projecting rock, he will see that the homeward-bound ants bear small insects, or segments of the legs, wings, abdomens, or other parts of the larger insects and other invertebrates that they have caught and dismembered. These lines of communication, in which the foragers returning with their booty pass an outward stream of fresh hunters, are rarely molested by the birds, which collect only around the outspread swarm. Although I have watched domestic chickens devour many army ants, and probably some of the larger terrestrial birds of the forest do likewise, the small birds of many kinds, mostly passerines, which follow the ants, prey not on them but on the creatures that try to escape from them.

In the humid forests of southern Central America, from sea level up to 4000 feet and sometimes even higher, the white-breasted, loquacious Bicolored Antbirds are nearly always conspicuous in the motley flocks of birds which accompany the army ants. More fearless of a human observer than are most other ant-followers, they often come within a yard or two of him and provide an excellent opportunity to study their behavior. This is especially true in the valley of El General, where I have found Bicolored Antbirds far more easily observed than they were in the lowland forests of Costa Rica and Panamá. Although sometimes they rest on a horizontal twig or vine, far more often they cling to a slender, upright stem, where each holds its body more or less level by stretching out its lower leg and flexing the upper one. Usually they perch only a foot or two above the swarming ants and scan the ground with their large, brown eyes. When an insect rushes out from its hiding place to escape the ants, an antbird jumps down, seizes it, and rises at once to a perch to devour it. If the insect scuttles back into the ground litter, antbirds may move the leaves with their bills in an attempt to disclose it.

The rapidity of the antbirds' return to a perch suggests that they possibly fear the bite or the rather mild sting of the army ants, but this is probably an erroneous inference. One sometimes sees a Bicolored Antbird resting on a stem or vine along which the ants are filing. The insects either turn back or pass around the bird's toes, or sometimes they crawl over them, but apparently they do not attempt to bite, and the antbird pays little attention to them. I have also watched Ocellated Antthrushes perching calm and unperturbed while army ants passed over their feet. Likewise, a Barred Woodcreeper, clinging to a trunk along which ants were filing and crawling over its toes and even upon its plumage, did nothing except to pluck one of them off from time to time with its strong bill.

In this connection, an observation made by Huber (1932:225) is of interest. While collecting birds in Nicaragua, he shot a Fasciated Antshrike and it fell in front of advancing army ants, which soon surrounded it and prevented the collector from retrieving it. Next day he returned to the spot, expecting to gather up the skeleton from which the ants had cleaned the flesh, but to his great surprise he found the corpse intact. The ants had not even eaten the exposed skin around the eyes. Similarly, when I threw a dead snake into the midst of a foraging swarm, the ants passed over it and moved on without biting into it. Even birds of kinds which do not follow army ants seem not to be attacked by them, at least after such birds are adult, and I have watched a Variable Seedeater continue to cover her eggs while raiding ants swarmed over her nest (Skutch, 1954a:24). African driver ants, however, appear to be more aggressive toward birds. Elliott (1950:320) reported that a slightly wounded *Cossypha natalensis* which fell among them was immediately attacked and killed. Perhaps the struggles of the injured thrush stirred up the ants, which might have ignored a bird calmly perching or sitting in its nest. However, from all accounts, the African driver ants of the genus *Dorylus* are fiercer and more aggressive than the American army ants of the genus *Eciton*, the ferocity of which has been absurdly exaggerated in uncritical writings.

Although sometimes a single pair of Bicolored Antbirds accompanies a swarm of hunting ants, frequently there are more. Because the birds are constantly in motion in undergrowth that often hides them from view, it is difficult to ascertain their number. With one vigorous swarm of ants that I watched in March, there were certainly six and probably seven Bicolored Antbirds, with the possibility that a few more lurked beyond my limited range of vision. At least two of these antbirds were immature individuals, whose central under parts were more or less extensively dull brown rather than pure white. In late December, I found, gathered about a swarm of ants, ten or 12 Bicolored Antbirds, including some that were immature. At times there are juveniles whose mouths have yellow corners and who beg with quivering wings for food.

Sometimes two of the adults dart toward the same fleeing insect, and occasionally one bird flies at another with angry notes. On the whole, however, the Bicolored Antbirds forage peaceably even when several families are present, and I have seen no fighting among them. Territorial boundaries seem to be disregarded while the antbirds accompany the hunting ants, although at other times territorial rights are asserted. Rarely one adult bird passes to another, probably its mate, the insect that it has caught. When immature individuals are present, their high, thin voices add pleasant diversity to the varied utterances of the voluble adults.

The associates of the Bicolored Antbirds in the mixed flocks which follow the army ants vary from region to region. On Barro Colorado Island, I most often found them with Spotted Antbirds, Gray-headed Tanagers, Plain-brown Dendrocinclas, and Ocellated Anthrushes, with occasionally even a Great Tinamou walking sedately about the outskirts of the swarm. In the valley of El General, the total number of associates in the mixed flocks of birds that accompany army ants is large. Among the more constant are Tawny-winged Dendrocinclas, Gray-headed Tanagers, and Bare-crowned Antbirds. Sometimes a Barred Woodcreeper, a Buff-throated Woodcreeper, or a Ruddy Dendrocincla clings to the trunks above the ants. At altitudes of more than 3000 feet, the Immaculate Antbird sometimes forages in company with the Bicolored Antbird. Nearly always the mixed flock contains some manakins,

chiefly the Yellow-thighed and the Blue-crowned and especially the females of these species, not because these diminutive birds are, like the Bicolored Antbirds, largely dependent on the ants to provide food for them, but because the manakins are so numerous in these forests that some are almost always close at hand to take advantage of the insects which the ants set in motion. Not infrequently a Black-faced Antthrush lurks on the outskirts of the motley crowd.

Among occasional associates, which stay with the ants for a while when they happen to meet them but usually forage independently, are Lowland Wood Wrens, Nightingale Wrens, Sulphur-rumped Myiobiuses, Golden-crowned Spadebills, wintering Swainson Thrushes, and, especially near the edges of the woodland, Blue-diademed Motmots and Gray's Thrushes. The manakins and flycatchers feed chiefly on the insects which attempt to escape the ants by flying or by creeping up saplings and bushes. They seldom snatch insects from the ground, as do the antbirds. Hence these two classes of ant-followers compete little.

One of the most amazing aggregations of birds that I have ever seen with army ants was in the forest near our house on the morning of July 31, 1947. While I stood watching Bicolored Antbirds and Gray-headed Tanagers catching the fugitives from the ants, a hawk of medium size suddenly dropped into their midst, causing them to disperse with various calls of alarm. My first impression was that the hawk, an immature Collared Forest-Falcon, had tried to seize one of the smaller birds, but continued watching cast doubt on this conclusion. Although I have seen adult forest-falcons catch domestic chickens that were nearly full grown, this hawk in immature plumage was content with smaller prey. After its first unexpected descent, it rose to a perch a yard or two above the ants that swarmed over the ground and remained there while the smaller ant-followers continued their activities much as before, at times coming within 5 or 6 yards of the resting hawk. Although the Bicolored Antbirds came much closer to me than to the hawk, the reverse was true of the Gray-headed Tanagers. Always wary of man, they seemed to be less afraid of the raptor than of me. The hawk itself was almost fearless of me, permitting me to watch it for long periods at a distance of only 4 or 5 yards.

For two hours, I watched this hawk forage with Bicolored Antbirds, Gray-headed Tanagers, a Barred Woodcreeper, a Tawny-winged Dendrocincla, a Ruddy Dendrocincla, a Black-faced Antthrush, and a Bright-rumped Attila, the last a follower of the ants almost as unexpected as the hawk itself. The raptor was using the ants to stir up its prey just as the smaller birds did, but it was interested only in the larger of the fugitive insects and spiders. As it perched low above the swarming ants, it often rested on one foot, usually the left, with the other foot drawn up and almost buried in the white plumage of its abdomen. Its unbroken silence contrasted with the constant chatter of its smaller associates.

From time to time, the hawk dropped to the ground, where it might hop around searching for an insect that it had momentarily glimpsed. Sometimes it shifted the fallen leaves a little with its feet, although it did not actually scratch in the manner of a gallinaceous bird. At times it hopped for a considerable distance over the ground, pushing beneath fallen branches and under logs in a manner surprising in a hawk. Often its quest was unsuccessful, but when it rose to a low perch with an insect or spider in its bill, it held the victim beneath a foot while it pulled it apart and devoured it piecemeal. Sometimes after rising from the ground the hawk gave attention to its feet, as though ants had attached themselves to them. Each longer

flight of the falcon, to follow the shifting swarm of ants or to seize a fleeing insect, caused some of the smaller birds to dart away with cries of alarm, but as soon as their formidable companion settled on another low perch, they resumed their insect-catching all around it. In two hours, the raptor caught and ate at least four large insects and spiders and probably some smaller ones that escaped my notice.

Although these noisy aggregations of small birds intent on snatching insects from the ground seem to offer to the few raptorial birds, chiefly species of *Micrastur*, that hunt in the lower strata of the Central American rain forests prey that is readily found and easily captured, I have on no other occasion seen a hawk near them. In eight weeks devoted to studying the followers of the army ants on Barro Colorado Island, Johnson (1954:55) saw a predator attack these birds only once. While he watched two pairs of Bicolored Antbirds foraging over swarming ants, a small hawk swooped down and pursued one of them, which fled screeching. The fugitive escaped, and soon afterward all four of the antbirds were again accompanying the ants.

Johnson (*op. cit.*) was the first to make a careful study of the relations of birds to army ants, and to correlate the behavior of birds with the several phases of the recurrent cycles of a colony of *Eciton* ants. On Barro Colorado, he found that the Bicolored Antbird was the most characteristic follower of the raiding ants. It was usually the first to appear in the morning, and its calls, together with those of the Spotted Antbird, helped to guide other birds to the swarm. One morning, he saw a Bicolored Antbird examine the tree where the ants bivouacked, before they started their raid. Hour after hour, through the day, the same Bicolored Antbirds followed the raiding army ants, feeding, courting, singing, and resting, but staying near their front as they traversed different parts of the forest. Far more birds of all kinds accompanied the ants when the colony was in the nomadic phase and conducted strong raids than when it entered the stary phase and the raids became weak. These weak raids were sometimes without attendant birds.

The army ants play a most important role in the life of the Bicolored Antbird, which depends so largely on them to make its food available that one wonders whether without them it could forage with sufficient success to remain alive and rear its progeny. I have never watched a Bicolored Antbird foraging independently. It seems to lack such efficient procedures for finding insects as are possessed by the Scaly-throated Leaf-tosser, the Black-faced Antthrush, the Buff-throated Automolus, and others of its insectivorous neighbors of the forest undergrowth, and it has never been seen to eat fruits of any kind. But when the Bicolored Antbird fails to find raiding ants, it may avail itself of substitutes.

Foraging with a man.—While I walked along a narrow roadway through the forest on the morning of February 21, 1943, I heard a lone Bicolored Antbird in the undergrowth to my left. Near the antbird was the stump of a stilt palm, in which I thought it might have a nest. While I examined the hollow center of the trunk and the crevices between the spiny prop roots, the bird stayed within a few feet of me. Finding nothing of interest, I started to walk away. But from the path I noticed that the antbird was still in the same spot, and I returned to resume my search for a nest, with the same negative result. This time, as I moved away, the antbird followed me. Noticing this, I walked slowly, to see what it would do. Of a sudden, it jumped down to catch a small insect that my passage had stirred up from the dead leaves that littered the ground. Soon it captured another, and another.

I was serving it by driving up the insects that hide, unseen and hard to find, amid the decaying vegetation on the floor of the forest. Now I walked deliberately, stirring up the dead leaves first with my feet and then with a stick, and the enterprising bird followed, sometimes coming within a foot or two of me, sometimes lagging a few yards behind me. Thus we proceeded to the crest of the slope. Finding that the bird would not follow me beyond this point, I paced off the distance back to the palm stump whence we had started and found that we had travelled together for nearly 250 feet.

Then I began to move noisily through the undergrowth, and soon I had the lone antbird with me again. This time, instead of leading it out to the narrow, leaf-strewn roadway, where my follower did not seem thoroughly at ease, I continued to move through the dense undergrowth, and the bird accompanied me as before. As it grew accustomed to its relatively huge companion, the brown-and-white bird became even less shy than at first. It would snatch up insects almost at my feet. While it perched, it would permit me to advance a hand or foot to within 10 or 12 inches of it, but a closer approach caused it to flit to a neighboring stem. I soon discovered that I could touch its bill or body with the stick that I used to stir up the leaves, although this was little over a foot in length. The rustlings and crashings that attended my movement through the saplings, vines, and fallen branches of the denser parts of the undergrowth seemed not to alarm the bird in the least degree; it would continue to rest on a vine or a fallen stick that was swayed by my passage.

My small companion always stayed near the ground, rarely rising higher than my knees. Usually it clung to a slender, erect stem of bush or sapling, and more rarely it rested on a horizontal twig, vine, or fallen branch. While it perched, it watched intently with large, dark eyes for the small insects stirred up by my feet or by the stick that I used to scatter the fallen leaves. When it saw a small fugitive, it either snatched the insect from the air or dropped to the ground to pick it up. The antbird's eyes were sharper than mine, and almost always I failed to descry the victim until it was already in the bird's black bill. Many a sharp, flycatcher-like *snap* announced a successful or an attempted capture.

At times the antbird dropped to the ground, or to a perch only an inch or two above it, and flicked aside leaves with rapid movements of its bill, in the manner of antthrushes, antpittas, and many other ground-feeders. On such occasions, I believe that it had just seen a disturbed insect take refuge beneath the leaves. Sometimes the bird rested momentarily on the ground, but usually it delayed there no longer than was necessary to capture its victim. It did not beat its prey against a twig, as the Spotted Antbird often does. I noticed that it ignored a number of fairly conspicuous insects that it might easily have captured, among them some whitish and grayish moths. It appeared to have definite preferences.

When we first met, my antbird uttered a few times, in a low voice, a peculiar half-mocking, half-whimsical call which its kind frequently uses. But after a time, it was silent save for a throaty note which it gave whenever I relaxed my industrious stirring of leaves in its behalf.

Advancing slowly, I again led my companion to the top of the slope, and again it refused to follow me beyond this point. But we had been together well over an hour. Toward the end of our walk, I talked to the antbird in order to familiarize it with my voice, so that I might call it to me on future occasions. I gave it a name, shortening *Gymnophithys* to "Jimmy." And since I had chosen a masculine name,

I henceforth used the corresponding pronoun, although I lacked any indication of the bird's sex. I cannot explain why it was alone, when Bicolored Antbirds are nearly always found in pairs or larger aggregations, usually in company with the miscellaneous assemblage of birds which follow the army ants. Perhaps its mate was incubating eggs.

Nearly a month passed before I again met Jimmy. I was standing in the forest, watching a Ruddy-tailed Flycatcher build her pensile nest, when, during one of her absences, a Bicolored Antbird suddenly flew up and clung near the ground to a slender sapling close beside me. Here it uttered a single low, questioning note, the same that on our first excursion together Jimmy voiced when I remitted too long my effort to keep him supplied with insects. Knowing now what was expected of me, I started to walk slowly, stirring up the ground litter, and the antbird followed just as on the former occasion. As we moved through the undergrowth, we heard the quaint call of a second Bicolored Antbird, and I had a momentary expectation of being honored by two followers. But Jimmy uttered a harsh, rasping, nasal note, which I heard only this once. This was apparently a warning, for the other bird promptly vanished and did not again approach us. My antbird evidently regarded me as his private property, not to be exploited indiscriminately by any bird of the forest.

I now led my feathered companion out toward the edge of the forest. He accompanied me until I reached the pasture on the hilltop behind the house. I wished to learn whether he could be enticed to forsake the dim light of the underwood for a foray into the bright sunlight of the clearing. There were many fallen leaves among the sparse grass at the pasture's edge; I walked slowly over these, rustling them noisily with my feet, and putting up an occasional grasshopper, which would provide a meal more substantial than most of the insects that I had seen Jimmy capture in the woodland. But he merely moved parallel with me through the bushes at the very margin of the forest, keeping himself screened behind the heavy foliage. Not one step into the *terra incognita* of the clearing would he advance.

Finding that my companion would not come with me into the pasture, I pushed back through the wall of bushes into the forest, and immediately I had Jimmy at my feet once more. I led him back to the Ruddy-tailed Flycatcher's nest, and finding that she had resumed work, I stayed to watch her. The antbird uttered the little, throaty, questioning note that he always voiced when I delayed too long in one spot; this time, finding that I was not so easily set in motion again, he rested on a low twig close beside me and gave his plumage a good preening. After 5 or 10 minutes, he completed his toilet and began to move away, voicing his quaint *we we we we we*, softly at first, then more and more loudly, with two falling, harsh notes at the end of the phrase. At this point, I began to move with intentional noisiness. Immediately Jimmy abandoned his search for his feathered companions and returned to my side.

These were the first of numerous meetings with Jimmy, which extended over a period of 16 months. Sometimes two or even three months would pass between our encounters, but nearly always he came to me at once with perfect confidence, as though we had parted only yesterday. A long separation did not lead to estrangement. Almost always he saw me before I noticed him. If I had paused in my walk to watch some bird amid the trees, he would wait quietly beside me until I moved onward again, or call my attention to him by his usual low note. The scattered points

where we met in the forest indicated that he ranged over a fairly extensive area, at least 1000 feet in diameter—and 1000 feet seems a far longer distance in the tangled undergrowth of the woodland than in an open field.

One morning in January, nearly a year after we had become acquainted, I decided to see how far I could lead Jimmy. We worked slowly southward through the forest, making many turns and twists, while Jimmy found many morsels along the way. If I moved too fast, my companion would fall behind, doubtless delayed by the good things that my passage over the dead leaves brought to light. But I had only to pause and look around, and in a few moments he would suddenly alight on the slender stem of a sapling close beside me. We passed over a column of army ants, travelling in single file and carrying many small white pupae, but these did not interest or detain my antbird. After about an hour's journey, we came to the edge of the woods beside an old maize field, now overgrown with bushes and weeds, forming a head-high tangle. Jimmy refused to follow me into this sunny opening but lingered at the forest's margin, where I soon rejoined him. This point was at least half a mile from any spot where I had previously met Jimmy, and I felt sure that I had led him beyond his home range. When I started homeward along a little-used cartroad, he would not come with me, preferring to go his own way through the undergrowth. Yet I did not doubt that he would find his way back without my guidance. In this I was not mistaken, for a few weeks later we met again in this familiar surroundings.

During the breeding season of the majority of the birds, which in this region extends from March to July, Jimmy sometimes kept me company while I hunted for nests. But nests are difficult to find in the heavy forest, and usually our expeditions were more profitable to him than to me, for his journey was rewarded by many a choice tidbit, while my only reward was his company. No nest could have pleased me more than his, but if he had a mate and a nest, he never betrayed its location.

Sometimes I met Jimmy in a tract of tall second-growth woodland that adjoined the primary forest. I soon discovered that he would accompany me only through the portion of the woods next to the forest, where the shade was heaviest and the undergrowth most dense and tangled—just those parts through which I found it most difficult to move. Where, beneath the high, open canopy of *Inga*, *Heliocarpus*, and *Croton* trees, there was relatively little undergrowth, and spots of sunlight lay close together on the litter of fallen leaves, my little friend held back and watched from the edge of some denser thicket, to join me again if I returned to the kind of vegetation that he preferred.

After the rains began and the woodland became wet, Jimmy often caught small frogs, not over an inch in length, that I stirred up for him. He would beat them vigorously against his perch before he swallowed them with an effort. At times he captured fairly large, dark-winged moths that arose from the forest floor, gulping them down wings and all. But to other moths he paid no attention, evidently having learned from experience that they did not taste good. Once I found him with a small tick attached to the side of his head near his left ear.

One day, after we had become well acquainted, it occurred to me to see whether Jimmy would be afraid of sudden loud noises. Neither clapping my hands nor shouting seemed to bother him. He never flew nor even gave a start when I made the loudest noises that I could produce.

Although Bicolored Antbirds are as a rule found in pairs throughout the year,

Jimmy was nearly always alone. Possibly he had left his mate to come and feast on the insects that I made available to him. Rarely I glimpsed, lurking in the background, another Bicolored Antbird that I took to be his mate; but it would fade away amid the underwood, and we two would go on alone. But one morning in March, a month after our first walk together, I encountered a pair of Bicolored Antbirds in the forest on the ridge behind the house. One, which I felt sure was Jimmy, promptly flew up to me and began to catch the insects stirred up by my feet; the other remained at a distance. I descended a steep slope toward a rivulet, Jimmy keeping me close company, the bird who seemed to be his mate following inconspicuously in the background. Beside the stream this second bird approached us more closely, whereupon Jimmy uttered a harsh note and flew at it as though to drive it away. Then one or possibly two other Bicolored Antbirds appeared and chased Jimmy's supposed mate. The low vegetation through which they flitted made it difficult to keep them in view. Apparently they were a pair on whose domain we had encroached. Jimmy, being so close to me, was safe from their persecution. Although Bicolored Antbirds follow army ants apparently without regard for territorial boundaries, away from the ants they seem to defend an area much as other birds do.

Next I moved downward along the forest streamlet, hunting birds' nests as I went. Jimmy accompanied me as before, and the bird which seemed to be his mate followed at a distance. Again it came nearer, and again Jimmy darted at it with an angry sound and caused it to retreat. But it always lingered near us, clinging to some slender stem near the ground. It was still unobtrusively with us as we worked obliquely up the steep slope, where there was only a sparse undergrowth of ferns and small shrubs, beneath tall, clean-boled trees and towering chonta palms with spiny prop roots. Jimmy was doing well for himself, catching two froglets and a number of small, brown or gray moths.

All this while the other antbird, gathering confidence, was working closer and closer to us, until it foraged only 8 or 10 yards away. It was catching things, too, sometimes from beneath the dead leaves that it flicked vigorously aside with its bill. Probably it was now close enough to seize some of the insects that had been stirred up by my passage and had not yet returned to perfect concealment. Jimmy did not again fly at the other bird, nor repeat his angry notes. Although in the past he had always followed me in silence, save for the slight, confidential note that he used to attract my attention whenever I neglected too long my self-imposed task of purveying to him; now that the second antbird was close by, the two not infrequently repeated their little, laughing song of low, slight notes running up the scale. This strengthened my belief that they were mated.

I led the pair up to the level ground on the back of the ridge. Here, doubtless feeling full after more than an hour of feasting on specially provided food, Jimmy lagged farther and farther behind me, and the one who appeared to be his mate stayed with him. Finally, I left them in the undergrowth. This episode led me to suspect that I had misnamed Jimmy, that perhaps "he," after all, was a female. A male, I believe, would have been far more tolerant of his mate and not tried to drive her away, as Jimmy at first did. Male antbirds of a number of species feed their mates. Still, from old habit, I continued to call my woodland friend "Jimmy," always keeping in mind the fact that I was far from certain of its sex. The observation of

Willis (1967) that male Bicolored Antbirds are frequently henpecked by their dominant mates makes it appear probable that Jimmy was a female.

My last meeting with Jimmy took place at the end of June, 1944, at the top of the ridge where I had left him with his supposed mate over a year earlier. I had stopped to examine the ferns and small orchids that covered a fallen branch. Suddenly, I heard a low, intimate note, and looking up I saw Jimmy clinging to a slender, upright stem close to me. I had not seen him in over three months. For an hour and a half, he followed me in his usual confiding manner. At first he was surprisingly voluble, often repeating his throaty note, as though impatient for me to move faster and stir up more insects.

From time to time, when he caught some larger creature, instead of eating it promptly, as he had invariably done in the past, he flew off through the undergrowth bearing it in his bill. He went in a direct manner, as though he had some definite objective, then paused and called *we we we we we*, then continued onward once more. Once he carried off a fairly large moth in this fashion, and again a fair-sized spider which he first killed, and also other objects which I did not recognize. He seemed to be feeding nestlings, or perhaps young birds that had already left the nest. Twice he was answered by calls that sounded weaker than those of an adult. Further, the fact that he did not always direct his course toward the same part of the forest suggested that the recipients of the food did not remain in the same spot, and hence had left the nest. But the visibility within a yard of the ground was so restricted by the low vegetation that, despite my efforts to follow Jimmy, I could not discover what he did with the food that I made available to him. At the end of an hour and a half, I abandoned the attempt. More than three years were to pass before I found my first Bicolored Antbird's nest, in this same part of the forest.

If anyone should ask how I can be sure that the Bicolored Antbird who followed me through the forest was always the same individual, I must candidly admit that I can offer no real proof. I placed no distinguishing mark on Jimmy, and he looked very much like any other adult of his species. Yet I have little doubt that the antbird whom I called Jimmy was always the same bird. The habit of following a man through the forest cannot be common in the species. In the Bicolored Antbird's range from Honduras to Ecuador, wild birds have exceedingly few human associates, and I suspect that few antbirds which attempted this mode of foraging would live in freedom to repeat the experiment. I have not known Bicolored Antbirds to behave in this manner in other localities where they were abundant, and there is, to my knowledge, no published report of such conduct. It is not impossible that, in forests with their original fauna unimpaired, the Bicolored Antbirds sometimes forage with quadrupeds such as peccaries or deer, just as anis follow grazing cattle in the open. However, we lack evidence on this point.

On my solitary walks through the forest during the years that followed Jimmy's disappearance, I missed his quiet companionship. I had never been so intimate with any other wild bird, and my association with him was one of the unique experiences of a lifetime. Although on various occasions I tried to entice other Bicolored Antbirds to accompany me, I was for a long while invariably ignored by them. But finally, on May 16, 1947, nearly three years after my last meeting with Jimmy, I was standing in tall second-growth woods when I heard a low note behind me, and looking around, I saw a lone Bicolored Antbird. When I moved, it followed, capturing the insects stirred up by my passage. While it clung to an upright stem, it permitted me

to touch it with the end of a yard-long stick but not with my hand. In this respect it resembled Jimmy. For nearly an hour it followed me through the woods, and it was easy to imagine that my old friend was with me again. Possibly the present bird was Jimmy's descendant, and in this belief, I called it "Jameson."

In the following month, I took several other walks with Jameson. On June 12 a second Bicolored Antbird, apparently Jameson's mate, followed us, but it stayed somewhat farther from me. Presently one member of the pair captured a particularly large moth and, instead of eating it at once, carried it away in a direct and purposeful manner, as though taking it to a nest with young. I followed its course but again I searched in vain for a nest. Perhaps the only reason why Jameson did not become as attached to me as Jimmy had been was that at this period I spent less time in the forest.

Two more years passed before, on July 23, 1949, I met along a forest path a pair of Bicolored Antbirds which seemed so tame that I encouraged them to follow me. As with their predecessors, I could come within a few inches of touching them with my hand and actually could touch them with a short stick. For several hundred yards we advanced, all three, through the forest, and they ate the food that I stirred up for them. Presently we came within sight of two other Bicolored Antbirds, and these and my companions started to chase each other. Apparently we had invaded the territory of another pair, who did not hesitate to assert their ownership. After this, the first pair would follow me no more. Two months later, I was again accompanied by two antbirds, doubtless the same pair, on a walk through the forest. Some Bicolored Antbirds, like Jimmy, assert exclusive possession of the human who provides for them, and at best grudgingly permit their mate to follow. Others freely share this valuable asset with a mate.

While I set a blind in view of the burrow of White-whiskered Soft-wings on April 29, 1953, a lone Bicolored Antbird hovered close around me, probably attracted by the insects shaken from the forest undergrowth by my movements. I suggested to my wife, who had come to see the soft-wings' burrow, that the antbird would follow her if she would move slowly and stir the ground litter; my prediction was correct. Returning from this excursion, the antbird watched me complete the setting of the blind. After I entered the blind on the following morning, the antbird hovered around it for about a quarter of an hour, catching the insects which had evidently been disturbed by my arrival. Then it drifted off through the underwood, and I did not see it again that morning.

On several occasions, a young Bicolored Antbird, distinguished by the dark patches on its breast and the yellow corners of its mouth, has flown up close to me while I stood in the forest, and watched me intently from a perch hardly a yard away. When I moved, the young bird followed, then paused to gaze at me from another upright stem. Sometimes the young bird would permit me to advance a hand to within 10 or 12 inches of it, although it never waited to be touched. I have never been able to induce one of these immature birds to forage with me, as the adults have often done. The parents, who were nearby, and probably still fed them, were a stronger attraction than I.

TERRITORY AND PAIR FORMATION

On Barro Colorado Island in the Panamá Canal Zone, Willis (1967) color-banded 109 Bicolored Antbirds and spent about 1400 hours observing them at ant swarms.

He found that unmated birds wander through the forest without apparent attachment to any locality, but breeding pairs have definite nesting areas, in which they tend to raise their families in successive years. The resident pair do not exclude other Bicolored Antbirds who follow foraging ants into their territory, but within this area they are definitely dominant over all intruders. By threats and supplanting attacks, the residents drive the trespassers from the most coveted positions over the front of the swarm, so that the latter must often forage in less remunerative spots. The prompt establishment of a social hierarchy or "peck order" among the attendants of an ant swarm makes grappling fights between the antbirds extremely rare. Since a nesting territory does not every day contain an active swarm of ants, the breeding pair frequently seek food beyond it, but they usually forage within 1300 feet of their nest. Their excursions often take them into the territories of neighboring pairs, where they in turn become subordinate and give way to the very individuals whom, in their own area, they dominated. Thus territoriality in the Bicolored Antbird is manifested, not by the fierce exclusiveness characteristic of certain other territorial birds, but by the reversal of dominance as an individual crosses the poorly defined border region that separates its own area from that of a neighbor. Stricter territorial defense would be incompatible with the Bicolored Antbirds' heavy dependence on army ants that wander irregularly through the forest and may for a considerable period be absent from an antbird's territory.

On Barro Colorado, Willis found males more numerous than females in the ratio of about 1.7 to 1, in consequence of which there were many wandering, unmated males. Females generally pair between the ages of four and six months, and they may lay their first set of eggs when little over six months old. Males, however, rarely win a partner until they are over a year old, and some perforce remain bachelors for five or six years, or even more. Young females whose parents have ceased to feed them are usually timid and occupy low positions in the social hierarchy at an ant swarm, making it difficult for them to catch enough escaping insects to satisfy their hunger. Males of high social rank, on the contrary, often forage so successfully that they become satiated and dally with the additional insects they catch instead of swallowing them immediately. A hungry young female often solicits food from a well-fed bachelor, and she may even snatch it from his bill. If she persists in begging from him, the unmated male may form the habit of feeding her. At first his behavior toward her is ambivalent, and after she has taken his insect he may drive her away with a hiss and a snap. Gradually, however, he becomes more tolerant and permits her to forage near him. If this continues for several weeks, the pair bond is established. Occasionally a male feeds a young individual of his own sex, and two mature males may exchange gifts of food.

Before each nesting, even of long-established pairs, the male feeds his mate for several days or even weeks, during which she comes to rely heavily upon him for her meals. Toward the end of this period of nuptial feeding, the pair go hunting for a nest site together. When he finds a suitable hollow stub, the male perches on the rim and attracts his mate's attention to it by a display similar to that of a number of other hole-nesting birds.

NEST AND EGGS

The earliest description of the nest and eggs of the Bicolored Antbird appears to be that published by Van Tyne in 1944, seventeen years after he found the nest

on Barro Colorado Island. This nest "was placed in the conical cavity formed by the petiole [that is, sheathing base] of a large dead palm frond which had fallen to the ground but stood there upright, the blade still caught in the branches of a tree" (Van Tyne, 1944:2). Long before this description was published I had supposed, from reading an account of the nest of the South American *Gymnopithys (Anoplops) rufigula* (Beebe, Hartley, and Howes, 1917:228-231), that the Bicolored Antbird builds in a hollow tree. But despite much searching for many years, I found no nest until 1947, when I discovered one in the forest near our house. It had recently collapsed, spilling out the nestlings. The difficulty of finding nests of this species is understandable when one considers their sparse population. Johnson (1954:48) estimated that the nearly six square miles of forest on Barro Colorado supported no more than 24 individuals. Willis (1967:112), however, found about 15 pairs and 11 unattached males in his study area of four square kilometers in August of 1961, and he calculated that the whole island supported about 160 Bicolored Antbirds, including 60 pairs and 40 wandering, unmated males. In later years, the population was even lower.

On May 12, 1948, I discovered my first intact nest of this species. It was in the hollow stump of a feather palm (*Euterpe*) in the forest on the ridge behind our house. The top of this low stump was strongly oblique, 12 inches high on one side and only 7 inches high on the opposite side. Its external diameter was 2½ by 2 inches, and since the shell was only about ⅓ inch thick, the hollow interior had almost the same diameter. The eggs rested 4½ inches below the lowest point of the rim surrounding the cavity, the bottom of which had been filled with a double handful of leaf fragments. These consisted chiefly of strips of palm fronds, but there were also pieces of dicotyledonous leaves. On top of these was a thin mat of rootlets and other fibrous materials, on which the eggs rested. This stump was shaded by a few leaves of a small sapling that grew close beside it, but there was nothing to keep the rain out of the upward-facing opening.

On August 14, 1947, I had found two naked nestlings lying on the ground in the forest on the same ridge, about 250 feet from the site of the nest just described. They had apparently been hatched inside a palm stump that was about 6 inches high and had been reduced by decay to a papery shell. One side of this small shell had broken away, spilling the nest and its occupants on the ground. The nest consisted of large shreds of decaying palm fronds which formed a thin mat, upon which was a slight lining of coarse, fibrous roots and similar materials. The nest described by Van Tyne (1944:2) had much the same composition.

I discovered a third nest on August 30, 1959, not far from the site of this collapsed nest. It was also in the exceedingly frail shell which was all that remained of the stump of a feather palm. This stump was 34 inches high, but the opening in its top was oblique, and the lowest part of the rim was only 28 inches above the ground. The central cavity was about 3½ inches in diameter, and the eggs rested 3½ inches below the lowest part of the opening. The nest was composed of strips of palm fronds, with a slight lining of fibers. Part of the nest material bulged out through a gap in the thin, frail shell that enclosed it. The stump was well covered with hart's-tongue ferns, a small-leaved aroid, and much moss. This nest was successful, and in April of the following year another brood was raised there.

On the same forested ridge where the foregoing nests were situated, I found, on April 29, 1965, the only nest that I have seen in the stump of a dicotyledonous tree

rather than of a palm. The rotten stump was 2 feet high and about 4 inches in diameter. The thin, fragile shell surrounded a central hollow 3 inches in diameter, in which the eggs rested only $2\frac{1}{2}$ inches below the lowest part of the rim. Again, the nest was composed chiefly of pieces of palm fronds, the largest of which was 8 inches long. There were also a few dicotyledonous leaves.

Each of the intact nests contained two eggs. The ground color was whitish or cream-colored, covered with many crowded speckles and streaks of reddish brown or cherry-color. Most of the streaks were parallel to the long axis of the egg. In one set the pigmentation was heaviest in a wreath around the thick end of each egg, but in the other set the streaks were almost evenly spaced over the whole shell. The eggs found on May 12, 1948, lay in a cavity too narrow for exploration, but the eggs found in the wider hollow on August 30, 1959, could be removed. They measured 23.8 by 17.5 and 23.0 by 17.5 mm. On April 15, 1960, this nest again held two eggs. Both measured 23.8 by 17.5 mm. The nest found by Van Tyne contained two eggs measuring 24.5 by 18.0 and 23.5 by 18.0 mm, and weighing 3.8 and 3.5 gm, respectively. He described them as streaked and blotched with Prussian Red and dark Prussian Red on a background shading from nearly white to Light Vinaceous Fawn (color names from Ridgway, 1912).

From the dates of these nests and from observations of juveniles in transitional plumage, it appears that the breeding season in the valley of El General extends from at least early April until January; this excludes only the driest months, February and March. On Barro Colorado, according to Willis, nesting continues through the wetter months from April to November, when ant swarms and the arthropods of the leaf litter are most abundant.

INCUBATION

While walking along a little-used woodland path on May 12, 1948, I happened to glance down into a low palm stump and saw a Bicolored Antbird sitting in the shallow hollow and returning my gaze. After about a minute, the antbird jumped out and landed on the ground, where it spread its wings and grovelled on the dead leaves. After this brief distraction display, the bird rose and started to circle around me a few yards away, clinging near the ground to slender, upright stems and repeating over and over a slightly churred *p'r-r-r-r*, *p'r-r-r-r*. At intervals it punctuated this reiterated complaint with a higher, sharper note.

During the whole time that I was engaged in examining the nest and making notes, the antbird continued to hover around me, calling and watching me intently. Rarely have I known a bird to evince so much concern over what was happening to its nest and eggs. Finally, becoming bolder, the antbird advanced within arm's length of me while I bent over the stump, then it moved away for a few inches with mincing steps, as though trying to lure me to follow, but it did not spread its wings. When at last, having finished making notes, I walked away, the antbird followed me for several feet. Then it promptly returned and looked down into the stump, to see whether its eggs were still there. It peered in once more, then withdrew a short distance. I stood several yards away, watching. Within five minutes the antbird entered the hollow to incubate. I did not see the other parent, but the antbird's complaints had attracted a Yellow-thighed Manakin and an Orange-billed Sparrow.

On the following day, I set up my blind about 20 feet from the palm stump that contained the nest. At dawn on May 14, I entered the blind and remained until

midday. At 5:38 a.m., when the light was still very dim, an antbird left the stump and flew silently away. At 6:01, a parent came in silence with a fiber in its bill and entered the cavity, headfirst. Seventeen minutes later, the other parent approached through the undergrowth, called *p-p-p-p-p* in a low voice, and looked into the hollow. Thereupon the sitting bird emerged and clung to a neighboring slender stem. The latest arrival flew off and the other bird followed. At 6:36, one of them came silently with a fiber in its bill and entered the nest. It stayed out of sight in the stump for 4 hours and 4 minutes. Finally, at 10:40, it jumped out, called several times *we we we we we we we wheer* with ascending final notes, then flew away low above the ground. The eggs were unattended for the next hour and a half. At 12:10 p.m., an antbird at last returned to take charge of them, and I left.

On the following morning, I again watched the stump from daybreak until past noon. At 5:45, an antbird silently left the nest, as on the preceding morning. The eggs were neglected until, at 6:25, a parent approached in silence and entered the hollow headfirst. The morning passed with nothing worthy of note, except the passage of a pair of Chestnut-backed Antbirds, the female of which alighted for a moment on the stump's rim. The incubating Bicolored Antbird remained out of sight during this time. After sitting uninterruptedly for 5 hours and 39 minutes, it emerged at 12:04 p.m., flew off, and called in the distance. The eggs were still unattended when I left at 12:10 p.m.

On the following day, May 16, I watched the nest during a cloudy afternoon. The eggs were covered for two periods of 168+ and 85 minutes and neglected for two intervals of 41 and 27 minutes. Again a rootlet was taken into the nest by a parent coming to incubate. At 5:41 p.m., when the light was growing dim in the forest, an antbird entered, headfirst, for the night.

I had now spent about 19 hours watching this nest without seeing a changeover. It was interesting to know that so small a bird spent 4 or even 6 hours on its eggs without food. I wished to learn whether both sexes incubated, as in other antbirds, and, since I could not distinguish the sexes, I decided to try to place identifying marks on these birds. Remembering that Jimmy and other Bicolored Antbirds had permitted me to touch them with the end of a stick, I cut a slender wand, attached a tuft of cotton to its end, and soaked the tuft in vermilion enamel. Approaching stealthily, I lowered the end of the stick into the cavity above the incubating antbird, and as it jumped out it brushed against the cotton and acquired a bright spot on its left wing. Then, while the bird hopped, complaining, through the surrounding bushes, I managed to touch it two or three times more, leaving small but conspicuous stains on its white breast and abdomen. Later, after I found that this bird sometimes came or left without giving me a view of its identifying marks, I placed by the same method a white spot on the nape of the other member of the pair.

I again entered the blind at 12:20 p.m. on May 18, when the nest was unattended. At 12:48, hard rain began to fall, but the eggs were left exposed to it until 1:25, when the unmarked bird (which was later given the white mark) silently entered. At 3:51, the parent with the vermilion spots on its breast came in the steady rain, perched on the stump's rim and looked down at its incubating partner, then flew away. Four minutes later, this bird returned and clung to the sapling beside the nest, looking down into it. The unmarked bird slowly emerged, and then the two darted off through the wet undergrowth, one apparently chasing the other.

After 5 minutes, at 4:00 p.m., the vermilion-spotted bird entered the cavity, and I had proof that both sexes of the Bicolored Antbird incubate.

I made no more long watches until after the eggs hatched, but on a number of visits I found now the vermilion-spotted, now the white-naped antbird in the nest. I did not hesitate to make them leave and give me a better view of themselves, because usually they returned after a few minutes, even while I stood, watching, a few yards away. Often, after jumping out of the hollow, the sitting bird would drop to the ground, spread its wings, and "feign injury." But it would soon "recover" and return to the eggs.

According to Willis, the male takes the long morning session on the eggs, while his mate forages at an ant swarm. This investigator found that the incubation period was 15 days at one nest and 16 days at another.

THE NESTLINGS

In the early hours of May 26, I went by moonlight to visit the antbirds' nest. Looking into the hollow stump with a flashlight, I found a parent sleeping with its plumage so widely spread that it appeared to be a heap of detached feathers rather than the plumage of a living bird. From one side of this loose mass of feathers emerged a tail, held erect against the wall of the cavity, and on the opposite side a small part of the bird's hindhead was recognizable. Such disarrangement of the contour plumage is typical of antbirds sleeping on their nests.

The flashlight's beam did not awaken the parent bird, and although I looked in again from time to time, it continued to sleep while many other birds began to call and sing, and the daylight slowly seeped into the undergrowth of the forest. Even after it awoke and pulled its feathers together, the antbird was reluctant to depart, and it continued to sit while I tapped gently on the outside of the frail shell and waved my hand over the opening. I knew the reason for this increased attachment to the nest when I heard the weak peeping of newly hatched nestlings filtering through the plumage of the brooding parent. Yielding at last to my gentle urging to come forth and give me a good view of itself, the antbird jumped out and dropped to the ground, where it grovelled and vibrated wings widely spread over the fallen leaves. It repeated this demonstration again and again at various points near the nest, some within arm's length of me, and in the intervals between displays it clung low on erect stems and complained with a sharp, distressed *per-r-r-r-r*.

Remembering the danger of attracting hostile eyes, I soon put an end to this performance by withdrawing a few paces. The parent then promptly returned to its nestlings in front of me. It was the one on whose nape I had placed a white mark. Since in those antbirds which exhibit sexual differences in coloration I had always found the female on the nest at night, I had little doubt that the white-naped parent was the female.

The nestlings' skin was dark flesh-color, with the feather tracts distinctly darker than the intervening areas of skin. The young birds were quite devoid of down or projecting feather sheaths. Their eyes were tightly closed. The inside of the mouth was orange-yellow, and at the corners were wide, conspicuous white flanges. The empty shells had not yet been removed, a circumstance which suggested that the eggs had hatched during the night. When I returned at 8:30 a.m. to set up the blind, the shells were no longer present.

On the following day I watched the nest from daybreak until past noon. Again

the white-naped parent passed the night on the nest, and she left at 5:49 a.m., when her vermilion-spotted mate arrived with food and called softly. In the next six and a quarter hours, the two day-old nestlings were fed seven times by the male and four times by the female. Each time a parent came to feed them it approached by flitting from upright stem to upright stem, holding in the end of its bill a single insect. To deliver the food, the parent clung to the rim of the cavity in an inverted position, with its head lowered into the hollow and its tail projecting into the air. After feeding, the parent sometimes swallowed a dropping, and then it often brooded. In the course of the morning, the vermilion-spotted parent brooded three times, for 62, 19, and 80+ minutes (the last session continued after I left); the white-naped parent also brooded three times, for 31, 5, and 85 minutes. Between 5:49 a.m. and 12:06 p.m. the nestlings were covered for a total of 282 minutes and were left exposed for 95 minutes.

When the nestlings were 5 days old, their pinfeathers were becoming long and they could open their eyes, although most of the time they drowsed with closed eyelids. On the following day, their nest was empty. Since the frail shell of the stump was not torn open, I inferred that the nestlings had been carried off by some slender animal, probably a snake. Before and after the eggs hatched, the parents had simulated injury dozens of times—more than any other birds whose nest I have studied. Yet when a predator arrived, this ruse failed to save their nestlings, possibly because the despoiler of their nest had come by night.

On the afternoon of August 14, 1947, I was walking slowly along the narrow trail beside which the nest with eggs was found in 1948, when a Bicolored Antbird flew up and clung to a slender, upright stem close in front of me. It held in its bill a large, fat insect and repeated a low, scolding *churr* over and over. When I turned around to look for the nest that I suspected was close by, the antbird darted past me, so near that its wing brushed my leg. Again it clung in front of me and scolded. When I started to search through the bushes beside the trail, it dropped to the ground and beat its half-spread wings against the fallen leaves, repeating this display in various spots a yard or two from me while I moved around.

Presently I discovered two nestlings lying close together on the ground, as though they had been tumbled there. They had open eyes, lead-colored pinfeathers sprouting from body and wings, great white flanges at the corners of their mouths, and they seemed to be about 5 or 6 days old. Both were cold and sluggish, and one had fresh blood on its flank, from a slight abrasion of its skin. About a foot from where the nestlings lay, I found the palm stump that has already been described. It was so fragile that it might have collapsed under the slight weight of the attendant parents.

The behavior of the single parent then present was most extraordinary. Soon it gulped down the insect that it had been holding when I first saw it, and with the clearance of its mouth its utterances changed; it now repeated incessantly a churred *per-r-r-r-r* that seemed to be an angry complaint. Its distraction displays continued. Each was performed in a single spot, where with stationary body the bird beat its partly spread wings against the ground, and it lasted for a few seconds. I placed the cold nestlings in the palm of my hand, which I lowered to the ground in front of the antbird. It advanced and bit one of my fingers, not once but three or four times. These nips were not hard enough to be painful, and they brought memories of the male Slaty Antshrike that had bitten my hand when I placed it on his nestlings. Now I spread my handkerchief on the ground and laid the nestlings on it, while I

pondered what to do with them. The adult antbird then lay or sat on the ground, at a point less than a yard from the handkerchief, facing it, and remained there motionless, watching or guarding the nestlings, for 10 minutes or more.

I cut the sheathing basal portion from a great fallen frond of a stilt palm and set this stiff, hollow cylinder, open along one side, upright against the spiny prop roots of the palm, close by the collapsed palm stump. I covered the top of this yard-long cylinder with a green leaf to keep out the rain, and in the bottom, on a stuffing of leaves, I placed the nest which had fallen out of the palm stump. Then, while the parent, still lying on the ground less than a yard away, intently watched what I did, I laid the nestlings, one by one, on the nest. I could do no more for them.

Would the antbirds attend and keep alive their nestlings in this new position? I watched for nearly an hour, but neither parent approached with food, although I heard the voices of Bicolored Antbirds off in the forest. Early on the following morning, I found both of the nestlings dead, one in the palm sheath, the other on the ground close by it. Doubtless it would have been better to have placed them in a shallow hollow that opened upward, but at that time I had seen no intact nest of the Bicolored Antbird.

The nest found with two eggs on August 30, 1959, fared better than the earlier ones. One egg vanished a few days later, but the surviving egg was pipped at 7:45 a.m. on September 11 and had hatched by 6:10 a.m. on the following day, when the shell had already been removed. This nestling resembled those of the earlier brood. Its skin was dark flesh-colored and utterly naked; its eyes were tightly closed; the inside of its mouth was orange-yellow; and there were wide white projections at the corners of the mouth. The young bird already held itself erect, on its abdomen and tarsi, and gaped persistently. When it was seven days old, its eyes were open and the feathers in the center of its back were just emerging from the ends of their long sheaths. At the age of 9 days, the nestling's back and shoulders were fairly well covered with expanded feathers, but only the tips of the remiges and wing-coverts had emerged from their sheaths. The head was still without expanded feathers, and the nestling's tail was rudimentary. When 12 days old, the young antbird was fully feathered. Its bill was black, and its legs and feet were plumbeous. It left the palm stump between 1:00 p.m. on September 24 and 1:00 p.m. on the following day, when it was 13 or 14 days of age.

On April 15 of the following year, this same palm stump, which seemed too frail to have survived so long, again held two eggs; these hatched on April 22 and 23. The two nestlings were successfully reared and they left between 8:20 a.m. and 1:30 p.m. on May 7, when 14 and 15 days old. A few weeks later, I found that the exceedingly rotten stump had collapsed.

In both years, as I approached this nest soon after the eggs hatched, an adult jumped out and gave a low intensity distraction display. But on all my other visits to the palm stump, the parent, if present, merely complained out of sight in the dense undergrowth. Perhaps these antbirds never gave a convincing distraction display because they found no suitable spot for performing, since the area around their nest site was densely overgrown with seedlings of the milk tree and with other low vegetation. Also these parents were always more timid, and seemed less concerned about the nest contents, than were the adults at my first two nests. Those parents were possibly the same individuals which followed me through the forest. It is

puzzling that the less zealous parents should have reared two broods whereas the very solicitous parents failed. Perhaps distraction displays are more effective in saving fledglings which can take cover while the adults divert the attention of the predator. In passerines whose young often remain well concealed during the first few weeks after they leave the nest, and in many species that live near the ground, the observer witnesses distraction displays by adults attending nests far more often than he sees them given by adults attending mobile fledglings. Yet the only time that I saw a parent actually save its progeny by simulating injury was in the case of a fledgling Black-striped Sparrow that could fly (Skutch, 1954a:115-116).

Willis (1967:86-87) watched Bicolored Antbirds flutter their wings from low saplings and from the ground in front of a coatimundi (*Nasua narica*) which approached their nest. Once one of the adults landed on the coati's back and pecked it, causing the animal to snap backward blindly at its assailant. Despite this determined defense, the coati might have plundered the nest had it not been deterred by huge stinging ants that emerged when the animal sniffed at the base of the nest cavity. Of 18 nests watched by Willis on Barro Colorado, only five (28 per cent) produced fledglings.

On May 29, 1956, I found a full-grown young antbird with its parents. It had prominent yellow mouth corners (rather than white flanges as in nestlings) and there was scarcely any blue skin around its eyes. Its whitish breast was crossed by an almost continuous band of dull brown. It gave the "laughing" song of the adults, but its voice was thinner than theirs. This young bird must have hatched from eggs laid no later than mid-April. I have also seen young whose mouths had prominent yellow corners at the end of December. Even in late March, one finds young antbirds whose white breasts still bear dark patches that reveal immaturity. But July and August is the period when juveniles are most frequent.

According to Willis, after the young leave the nest at the age of about 2 weeks, the male takes exclusive charge of one and the female of the other, if both survive. Even if one adult loses its fledgling it seldom, if ever, helps to feed the other. The male and female, each with its young bird, may forage with different ant swarms for a day or more, after which the family is reunited. The young are fed by the adults until they are 8 to 10 weeks old; then they separate from the parents and wander nomadically from one ant swarm to another. At an age of between 7 and 10 weeks, the young acquire the white ventral plumage of the adults.

SUMMARY

The Bicolored Antbird inhabits lowland rain forest from sea level up to at least 5000 feet in Costa Rica. Occasionally it ventures beyond the forest into tall second growth, banana plantations, and even shady dooryards and pastures. It appears to remain mated throughout the year, but when from four to ten or 12 individuals are foraging together with army ants, it is difficult to distinguish pairs.

The Bicolored Antbird has a great variety of songs and calls. At best, its utterances are pleasant rather than musical. The most elaborate song consists of a series of clear, thin notes which become shorter, faster, and higher in pitch until a climax is reached, after which they fall in pitch as they become longer and more widely spaced.

This antbird's diet appears to consist wholly of insects, spiders, and other invertebrates, varied by an occasional small frog. Although it sometimes pushes fallen

leaves aside with its bill to disclose the small creatures that hide in the ground litter, it usually depends on other animals to make its food available. In southern Central America, at lower altitudes, it is one of the most constant, and likewise one of the noisiest, of the attendants of foraging army ants. It watches the ants from a perch, usually on a slender, upright stem, a foot or two above them, jumps down to seize an insect or spider that has been driven out of the ground litter, then promptly rises to a perch, where it devours its prey. It does not, except perhaps accidentally, eat the ants. When several pairs attend the same ant swarm, one individual at times flies at another with angry notes, but actual clashes are very rarely witnessed. The Bicolored Antbirds appear to follow the army ants without reference to territorial boundaries, although when ants are not present territorial rights are asserted. Just as the antbirds do not attack the ants, the ants do not attack these and other birds, even when they pass over the birds' feet. On one occasion, the Bicolored Antbird and several other species of small birds foraged with ants in company with a young Collared Forest-Falcon.

Occasionally, Bicolored Antbirds follow a person who walks slowly through the forest, stirring up leaves for them. Then they come very close to their human benefactor, permitting themselves to be touched with the end of a short stick, but not by a hand. Sometimes these antbirds will follow a person for over an hour, traversing half a mile of woodland, but they will not follow him into sunny fields or light, open vegetation. Intermittently over a period of 16 months, one individual followed me and foraged as I walked through the woods, stirring up the leaves. Three years passed before I found another antbird that would forage in this manner. Later a pair of Bicolored Antbirds followed me and foraged as I walked through the woods. When I led them into the territory of another pair of antbirds, they were pursued by them. Immature birds sometimes approach very close to a human and seem to examine him, but they do not forage in his wake.

In El General, one nest held eggs in early September and it also held eggs in the following April. Two other nests were found in May and August. These nests were placed in palm stumps which were not over 3 feet high and had been reduced by decay to fragile, hollow shells. The cavities opened upward, and the eggs rested about 4 inches below the lowest part of the rim. The nests were composed of fragments of leaves, chiefly those of palms, on which was a thin mat of rootlets and other fibrous materials. In Panamá, a nest was built in a sheathing base of a fallen palm frond.

Each of five nests contained two eggs or nestlings. The eggs are whitish or cream-colored, heavily marked with spots and longitudinal streaks of reddish brown.

At one nest, incubation was performed by both sexes. Diurnal sessions were long, up to nearly 6 hours, but usually each partner left the eggs before the other arrived and changeovers were not witnessed. The periods of neglect lasted from a few minutes up to an hour and a half. At night, the parent on the nest slept with her contour feathers so widely spread that they appeared not to be attached to a bird. The parents brought fibers to the nest when they came to incubate. The incubation period is 15 or 16 days.

The nestlings are hatched with dark flesh-colored skin wholly devoid of down. The mouth is orange-yellow inside, and it has wide white flanges at the corners. The young are brooded and fed by both parents, who bring a single insect on each visit.

In six and a quarter hours, two nestlings, 1 day old, were fed 7 times by the male parent and 4 times by the female.

At one nest, the parents showed exceptional solicitude for their eggs and young. They simulated injury with great frequency, usually close to the observer. They watched intently whatever he did at the nest, and they entered it while he stood nearby. Another parent, whose nestlings had fallen from a collapsed palm stump, bit the hand in which they were held. When they were temporarily placed on a handkerchief, the parent sat beside the cloth and watched the nestlings. But at the third nest, the parents remained aloof and never gave a convincing distraction display; yet these parents reared two broods, whereas the more zealous ones failed.

One nestling was fully feathered when about 12 days old, and it left the nest at the age of 13 or 14 days. Two young departed from another nest when 14 and 15 days old.

STREAKED-CHESTED ANTPITTA

Grallaria perspicillata

This stout, long-legged, terrestrial antbird differs greatly in appearance and habits from all the other members of the family that are treated in this book. The statement that this bird is about five inches in length will convey an erroneous impression of its size, if I fail to remind the reader that this measurement includes a relatively long tail in the other antbirds that we consider here, but the Streaked-chested Antpitta has a very short tail, little over an inch in length. The sexes cannot be distinguished by their plumage. In both, the crown and hindneck are slate-color. The rest of the upper plumage is olive or grayish olive, with the wings browner and having two rows of small, buffy spots on their coverts. Each large, dark eye is surrounded by a conspicuous, broad, buffy orbital ring. Other prominent facial marks are a buffy loreal spot separated by a dusky line from the eye ring, a buffy line on the cheeks and ear-coverts, and a blackish malar stripe. The ventral plumage is white, immaculate on the chin and throat, heavily streaked with black on the breast and the buff-tinged sides. The under tail-coverts are buff. The eyes are brown. The upper mandible is blackish and the lower mandible is horn-color. The legs and toes are grayish flesh-color.

From Nicaragua to Ecuador, the Streaked-chested Antpitta is found in lowland forests. In southern Costa Rica, I have seen it as high as 2500 feet above sea level and heard its unmistakable song about 1500 feet higher. In my experience, it associates with birds of other kinds even less than does the Black-faced Antthrush, and it is usually solitary, although once in April I met two who kept company and seemed to be a mated pair. As it stands on the dimly lighted, leaf-strewn forest floor, the antpitta has a unique and unforgettable aspect. Its legs are so long and slender that its roly-poly, seemingly tailless body appears to be propped up on two thin sticks. As though it were not already sufficiently plump, it rhythmically puffs out and contracts the streaked feathers of its white breast, and at intervals it half spreads, then closes, its short, brown wings. The light ring around each dark eye gives the bird a startled expression. Finally, it hops away over the ground, moving its legs together, rather than alternately in the manner of the antthrush, the only truly ambulatory antbird that I know. From time to time, it flicks the fallen leaves aside with vigorous sideward motions of its bill. Apparently, much of its food is found in this manner, but I have not succeeded in keeping the elusive antpitta in view long enough to learn what it eats.

Rarely, especially if alarmed, the antpittas fly up to a low perch, at most a yard or two above the ground. Once, while I stood in the forest near my home, an antpitta, which had been singing in the vicinity for days, suddenly alighted on a great, mossy, fallen trunk in plain sight. Here it puffed out its streaked breast, stretched up its neck, and delivered its far-carrying song. Then it hopped rapidly down the inclined log and went off through the dense undergrowth. Presently it returned and perched on a slender, slanting stem, about as high as my head and 5 yards away. After we had stared at each other for a fraction of a minute, it flew off and was not seen again. Probably a weasel, which at about the same time I glimpsed scurrying over the ground nearby, had caused the antpitta to fly up to a perch.

VOICE

For years I had conjectured about the authorship of a hollow, far-carrying, oft-repeated whistle that floated through the forests of Costa Rica and Panamá, but I was not successful in tracing it to its source until I watched an antpittas' nest from concealment. This utterance consists of about seven to nine mellow whistles, loud yet soft, in a most peculiar, melancholy tone, which makes them sound far away even when the antpitta is close by. The notes are repeated with increasing rapidity until about the middle of the series, then they become somewhat more widely spaced toward the end; they follow each other so quickly that they are most difficult to count. *Cow—cow-cow cow cow cow-cow—cow* is the best paraphrase that I can make of this memorable song. It somewhat resembles the song of the Black-faced Antthrush, but the latter is sharper and more metallic, without the hollow quality of the antpitta's notes. Moreover, the antthrush only exceptionally utters so many whistles together, and then the series does not slow down toward the end. The Chestnut-backed Antbird's whistles also bear some resemblance to those of the antpitta, but there are rarely more than three in a series. If a few good showers soak the forests of El General in March, the antpitta may then begin to sing, and it continues until July or August. Occasionally I have heard it through the last quarter of the year, and even until the end of January.

One morning, while I watched from a blind a "court" where an Orange-collared Manakin performed, an antpitta hopped into the center of the circle of bare ground, and standing there, voiced a rapid series of soft, clear notes which diminished in volume and were not as loud as those of the usual song. Another utterance that I have occasionally heard consists of whistles higher in pitch, clearer, and more cheerful in tone than the ordinary song, and if possible more rapidly repeated. Once I watched an antpitta deliver this brighter song from a perch about a yard above the ground. In addition to these notes, there is a loud rattle, dying away at the end, which I heard from an antpitta that I took to be a female, just after she left the nest.

NESTING

In the afternoon of April 30, 1940, the boy who was hunting nests for me in El General came to report that he had found one of "a tailless bird which resembled a dove." When he led me a short distance into the high forest to see it, the bird was absent, and I did not know to what species or family to attribute a nest so different from any that I had ever examined. The site was 5 feet above the ground, among the slender stems of an aroid that grew over a thin, upright, basal branch of a small tree, beside a broad but unfrequented, leaf-covered trail. Here on the aroid was a small platform, 4 inches in diameter by 2 inches in thickness, composed of coarse twigs and dry petioles, on which rested a few partly decayed dead leaves, whose edges, bent upward against the supporting stems, made a low rim around the top. Above the leaves, a few coarse, dark, fibrous roots formed a scanty lining. The nest resembled a double handful of decaying fallen vegetation, caught up among the stems of the aroid. Dead leaves that had lodged elsewhere on these stems strengthened the impression of its randomness, and made it less likely to attract attention.

On this loosely constructed, scarcely concave nest rested two blunt eggs. They were light gray in color, very heavily and coarsely mottled with dark brown, which

was deepest and most nearly continuous in a wreath about the thick end. On one of the eggs, the brown pigmentation covered more than half of the entire surface. The two eggs were identical in size, both measuring 25.4 by 20.6 mm.

Surmising that this structure might belong to an antthrush, whose nest I then knew only from an erroneous description, I was not prepared for the sight which greeted my astonished eyes when I returned next morning. There on the eggs sat a stout grayish olive bird, the exposed portion of whose breast was heavily streaked with black on a white ground—the first antpitta that I had seen in Costa Rica. Since I found the eggs on two visits uncovered and cold at about 6:30 a.m., I chose this hour to set up my blind without disturbing the birds. At 5:45 a.m. on May 4, I began to watch on a dark, overcast morning after a rainy night. As daylight increased, I saw that the nest was unattended. Some Crested Guans in the big trees above me kept up a loud din for a long while. Finally, at 7:21 I noticed an antpitta hopping rapidly over a log a short distance beyond the nest. From this it flew up to the nest and settled on the cold eggs. After incubating only 44 minutes, it flew to the ground and hopped rapidly away. Sixteen minutes later this bird, or more probably its mate, silently returned to the eggs, which it covered for the next 194 minutes. At 11:35, it jumped to the ground and hopped away, leaving the nest unattended until my departure at 1:20 p.m.

Since this long vigil failed to yield an answer to a number of questions, I waited a few days for the antpittas to grow more attached to their nest, then resumed my watch at daybreak on May 9. This time, the growing light revealed that the nest was occupied, and at 5:48 a.m. I saw a bird leave it. Then the eggs were neglected for 30 minutes, until at 6:18 one of the parents came to take charge of them. Soon after settling down to incubate, the antpitta in front of me uttered the weird, hollow whistles that I had so often heard without guessing their source. For the next 50 minutes, the sitting antpitta, which I took to be the male, repeated this song over and over. At last becoming silent, he sat patiently for the rest of the morning. Finally, at 11:16, 2 minutes less than 5 hours after his arrival, he flew down as his mate silently approached over the ground. Alighting on a fallen branch, he stood there for a minute or two, with his long legs quivering as though they had been strained by his long period of uninterrupted sitting. The female then flew up to the nest, but instead of resting quietly she stood up and pushed her bill down into the platform. After about 10 minutes of this, she flew to the ground and delivered a long rattle that died away at the end, repeating it many times as she hopped off. I then went home for lunch. My morning's watch had been gratifyingly productive. Not only had I learned that both sexes of the Streaked-chested Antpitta share incubation, but I had also identified a memorable bird song that had long baffled me.

In the afternoon of the same day, I shifted my blind a short distance to watch a nest of the Tawny-crowned Greenlet. As I approached to move the blind, an antpitta jumped from the nest and gave the rattling call as it hopped away. From this utterance, and from the fact that this bird was easily disturbed while the one that I took to be the male continued at his post on the eggs even while I set up the blind, I inferred that it was the female.

From my new position, I had a more distant view of the antpittas' nest. Toward the middle of the afternoon, one of them returned to the eggs, but it sat restlessly, continually rising up to preen and to tug at the nest with its bill. A large dead

leaf, which was included in the nest but stood up well above the others on the side toward me, seemed particularly to annoy the bird. It tugged so hard at this leaf that once it lost its balance and fell to the ground. Returning to the nest, the antpitta continued to tussle with the leaf until finally it was pulled out and dropped. Its removal from the nest left the incubating antpitta far more exposed on the side toward the blind, which was the direction that the birds usually faced even before the blind was set up; possibly the antpitta had removed the leaf in order to have an unobstructed view. Even after discarding the leaf, the bird continued to rise up to preen the feathers of its breast or to probe at the nest.

I made a final watch at this nest from 10:55 a.m. to 2:38 p.m. on May 13. Fifteen minutes after I entered the blind, now set farther away, an antpitta approached, hopping rapidly over the ground and at times pausing to flick aside dead leaves. Soon it flew up to incubate. After sitting for nearly 2 hours, it began to call in a low, mellow voice, from which I judged it to be the male. At 1:08 p.m., it hopped from the nest and vanished in the undergrowth, whence for a considerable period the mellow whistles continued to emanate. After the nest had remained unattended for an hour and a half, I took down the blind. The eggs were afterward abandoned. I did not, to my knowledge, hear the whistle and the rattle from the same individual; if I am correct in attributing the whistle to the male and the rattle to the female, we may draw the further inference that the male was quite willing to continue his attendance, but his mate, possibly disturbed by my interference, refused to carry on.

In the same patch of woodland, close beside the Río Pacuar at the western end of the basin of El General, we found in the following month a second nest of the antpitta. Only 26 inches above the ground in a low bush, it resembled the first in construction but was broader. Not including the long, projecting ends of the twigs which it contained, it was about 8 inches in diameter; its thickness was 2 inches. When the nest was found on June 10, it held two eggs; one had a puncture which revealed that incubation had hardly begun. The intact egg measured 26.2 by 20.6 mm. No further study was made of this nest.

More than 19 years passed before, on August 29, 1959, I found my third nest of the antpitta. It was in the forest on our farm in El General and was situated 40 inches above the ground in a tangle of the climbing fern *Salpichlaena volubilis* that grew over a small, spiny palm. This nest differed greatly from the first two. It was a dark-colored, thin-walled cup, composed of fine vines, rootlets, thin petioles, and similar materials. In the bottom were a few dead leaves, above which was a sparse lining of rootlets, fine petioles, and tendrils. The nest measured 4 inches in overall diameter by 3 inches in height. The interior was 3 inches in diameter by 1½ inches in depth.

Apparently this nest had not been built by the antpittas. Two years earlier, a Thrush-like Manakin had a nest in almost exactly the same position. After the manakin's eggs vanished, I removed her nest for examination. Later, another nest was built in this site, probably by Gray-headed Tanagers or Blue-black Grosbeaks, but it did not seem to be finished and I never found an egg in it. After this slight, open cup had remained there, neglected, for a long while, I found in its bottom some pieces of dead leaf, which might have fallen in. The antpittas' building had apparently been limited to placing a slight lining above the leaves. Possibly the

antpittas had done little more than this at the first two nests, which in this case would consist of fallen leaves that had lodged in the undergrowth, and the scanty mat of fibrous materials which the birds arranged on the leaves.

When found on August 29, this third nest contained two eggs which resembled the earlier sets in their broad, blunt shape and heavy pigmentation. The eggs measured 26.2 by 20.6 and 27.0 by 21.4 mm. I disturbed the nest as little as possible during the incubation period, for I was very eager to see the nestlings and watch the parents attend them. As the days passed, this old structure, weakened by decay, tilted more and more strongly to one side. I tried to straighten it, but my efforts were rather ineffectual. At about the time the eggs were pipped, they were abandoned by the parents. When, two days after the first fracture appeared in the surface of the shells, the eggs had failed to hatch and were always cold when I visited them, I opened them to see the chicks. Their dark skin was wholly devoid of down, as in all other nestling antbirds that I have seen, with the exception of the anthrush. With a magnifying glass, I could see feather rudiments beneath the skin on the body and wings. The interior of the mouth was orange. After two days of neglect, the chicks still moved, but they could not be reared without their parents.

SUMMARY

The terrestrial Streaked-chested Antpitta inhabits the lowland rain forest up to about 4000 feet above sea level in Costa Rica. It rarely associates with other birds. It progresses by hopping rather than walking over the ground, and it flicks fallen leaves aside with its bill. At times, apparently when alarmed, it rises to a perch a yard or two above the ground. It has the curious habit of continually puffing out its plumage, thereby increasing the apparent size of an already stout bird.

The song consists of a rapid sequence of about seven to nine mellow whistles of a most peculiar tone, which makes them sound distant even when their source is nearby. In El General, this song is heard from March to August and occasionally later. A loud rattle is attributed to the female.

In El General, a nest with eggs was found at the end of April, and another, probably a replacement nest, was discovered near the site of the first in early June. Years later, a third nest with eggs was found at the end of August. All of these nests were in heavy forest, at heights ranging from 26 inches to 5 feet. The first two nests were untidy, loosely made platforms of coarse twigs, petioles, and large dead leaves, with a scanty lining of dark, fibrous roots in the shallow concavity. The third nest differed greatly from the first two. It was a thin-walled open cup that apparently had been made by a tanager or a finch, and the antpittas' building seemed to have been limited to placing a slight lining above some small dead leaves in the bottom. Probably at the first two nests the antpittas had done little more than arrange a lining upon an accumulation of fallen leaves.

Each of the three nests contained two eggs, which in shape were broad and blunt. In color, they were light gray, heavily and coarsely mottled with dark brown, which almost obscured the ground color on the thick end of some eggs.

At one nest, both sexes incubated, taking long sessions, which in one instance continued without interruption for nearly 5 hours. One member of the pair, apparently the male, sang repeatedly while covering the eggs.

The nestlings are hatched with no trace of down on their dark skin. The interior of the mouth is orange.

BLACK-FACED ANTTHRUSH

Formicarius analis

The Black-faced Antthrush is a stout, long-legged, short-tailed, terrestrial bird, about six and a half inches in length. In both sexes, the feathers on top of the head are black with brown tips, which give the prevailing color tone to this region. The remaining upper parts, except the hindneck, are deep brown or olive-brown, which becomes more chestnut on the upper tail-coverts. The lores, cheeks, chin, and throat are black, with a small spot of white on the lores. The hindneck, sides of the neck, much of the auricular region, and (in some races) the throat are chestnut or cinnamon-rufous. The under parts are dark gray mixed with olive, which brightens to light brown or tawny on the under tail-coverts. Behind each large, dark eye in a crescent of bluish white bare skin. The short, straight, fairly thick bill is black. The long legs and toes are pinkish with a dusky tinge. The colors of the unfeathered parts refer to the form found on the Pacific side of southern Costa Rica and neighboring parts of Panamá, *Formicarius analis hoffmanni*, with which this account chiefly deals.

The Black-faced Antthrush ranges from southern México to Amazonia. An inhabitant of humid forests, it occurs throughout the length of the Caribbean lowlands of Central America, but on the Pacific side it is absent from El Salvador and Guatemala. In southern Costa Rica, it extends from sea level up to no less than 5000 feet, at least on the Pacific slope near the Panamanian border. In the Coastal Range of Venezuela, another race extends upward to the lower edge of the Subtemperate Zone, at about 5600 feet (Schäfer and Phelps, 1954:100).

The antthrush is a solitary bird which, except when breeding, rarely keeps close company with other individuals of its own or other kinds. Wary and retiring, it is far more often heard than seen. When by good fortune or patient stalking one succeeds in watching an antthrush in the subdued light which has penetrated the whole vertical extent of the heavy forest, he beholds a bird of unique and unforgettable attributes, a passerine with the aspect of a rail. Its erect head and large, dark eyes set off by whitish crescents give it an appearance of keen-sighted alertness. Deliberately, the long-legged bird walks over the leaf-strewn ground, tilting forward at each step. Its short tail is held erect above its brown back, exposing the brownish or tawny under tail-coverts. No other antbird that I know walks in this fashion; even the terrestrial antpittas move over the ground by hopping with their feet together. If the observer stands quite still, the antthrush may circle around him as it continues to search for food on the ground. More often, the little "cock-of-the-woods," as this bird is called in Trinidad, walks quietly off and vanishes in the shadows. Unless hard pressed, it prefers not to use its short wings. Yet it can fly strongly for considerable distances, and it usually does so when leaving its nest in a hollow stump.

I have only twice seen an antthrush perch in a tree. As I walked along a trail through the forest near Cañas Gordas on March 19, 1964, an antthrush suddenly flew up from the ground and landed on a slender, horizontal branch above my head. Here it perched for about 15 minutes, seeming not to notice me as I stood a few yards away. Sometimes it twitched its short tail up and down, and sometimes it wagged its tail from side to side, but mostly the bird rested quietly. After a while

it flew to a still higher branch, stood for a few minutes, and then flew to a third branch about 15 feet above the steep, wooded slope. Finally it dropped to the ground and walked away. Three years later, in the forest on our farm in El General, an antthrush perched about 5 yards up on a thin, horizontal branch while it continued to answer whistled imitations of its call. Between calls it preened. Finally it flew off on a long, descending course.

FOOD

As it walks sedately over the forest floor, the antthrush flicks aside the fallen leaves with its short, black bill and devours the small creatures thereby exposed. Often it moves in circles as it hunts. While watching army ants, I have glimpsed an antthrush lurking on the outskirts of the attendant flock of birds often enough to be convinced that it frequently forages with them. But whereas most of the followers of the hunting ants perch in a bush or cling to a trunk above the thick of the swarm, alighting in its midst just long enough to snatch up an insect or spider, the terrestrial antthrush, perhaps avoiding the ants, hovers about the edge of the fray, capturing those fugitives which seem to have the best chance of escaping. Johnson (1954:57) also found the Black-faced Antthrush following army ants.

Insects form the bulk of the antthrushes' diet, as I infer from having watched them feed their nestlings. Occasionally they catch a small lizard, and according to Van Tyne (1935:28), they also eat terrestrial snails. Once, while I sat in a blind in the forest before a nest of a Ruddy Quail-Dove, I heard the mellow whistles and then the sharp call notes of an antthrush. Presently, through a side window of my wigwam of brown cloth, I glimpsed the shy antbird struggling with a snake, which was brownish above and bright coral-red below, and seemed to be slightly less than a foot in length. With its bill, the antthrush was pecking and knocking the serpent as it writhed on the ground. After this had continued for a good while, a second antthrush, probably the mate, walked hurriedly up, as though to take the prize. To my great regret, intervening foliage screened from my sight what then occurred, but in view of the frequency of nuptial feeding in the antbird family, I suspect that the newcomer received this very substantial meal. I could see, imperfectly, that the snake, still squirming, continued to be pecked and shaken for some minutes longer, but whether by the first antthrush or the new arrival I could not tell. At last both the bird and its victim vanished amid the undergrowth.

VOICE

The call, or song, of the Black-faced Antthrush is one of the characteristic and unforgettable sounds of the lowland forests of southern Central America. In a full, mellow voice, the antthrush delivers an emphasized opening note followed by a variable number of shorter notes, rarely one, sometimes ten or more. Perhaps most often a sequence of three whistles is given: *whoo who who*. By imitating this whistle, a man may obtain the response of the bird and finally bring it toward him, as it walks hesitantly through the undergrowth. In El General, the antthrush's appealing notes are heard chiefly from February through August or September, more rarely through the remainder of the year. The song is readily confused with that of the Chestnut-backed Antbird, but the latter gives two notes together more often than three, and its tone seems less "cheerful" than that of the antthrush.

The alarm note is a sharp, almost explosive *tleet*, which may be rapidly repeated a number of times.

THE NEST

In El General, 2500 feet above sea level, breeding starts in March and may continue until early October; sometimes three broods are reared in the same season. I have seen six nest sites, in one of which seven sets of eggs were laid, and all were in deep, tubular cavities in slender trunks in the forest. Two were in palms, three in small, dead dicotyledonous trees, and one in the hollow trunk of a small, living dicotyledonous tree. One nest was placed in a stub of a stilt palm (*Iriartea*) that was propped up on long, spiny aerial roots. The top of this trunk had been broken off irregularly, so that the highest part was 14 feet above the ground, whence the opening extended obliquely downward to a point 11 feet above the ground. The eggs were 13½ inches below this lowest point of the aperture, in a well-like hollow about 4 inches in diameter.

The other nest in a stilt palm was in a surprising situation. A piece had broken from the upper part of a tall palm trunk and stood, inverted but nearly upright, on the slope below it, held in this position by a single thin loop of a dead frond of the twining fern *Salpichlaena volubilis*, which permitted it to sway precariously whenever it was touched. Reduced by the decay of its internal tissues to a thin and somewhat flexible shell, this segment of trunk formed a tube nearly 7 feet long and about 5½ inches in internal diameter, so that in width and in the thickness of its wall it reminded me of a stove pipe. In the side of this tube which faced uphill, 5 feet above its base, was an irregular opening with jagged edges, 7 inches in height by 2¼ inches in greatest width, which served as the antthrushes' doorway. Nearer the ground were several smaller holes, less than an inch wide, which were useless to the birds. The nest had been built on the ground in the lower end of the tube. Approaching or leaving their nest, the antthrushes had to descend or ascend through about 4½ feet of this wide, nearly vertical tube.

Another nest was in the slightly leaning trunk of a dicotyledonous tree, far advanced in decay, about 12 feet high and 7 inches thick. The trunk was covered with green moss, and a few aroids and small ferns grew upon it here and there. In the side of the trunk was a large gap, the lowest point of which was 74 inches above the ground, and this gave access to a deep central hollow. Beside this was a smaller gap that extended 2 inches lower and was the preferred doorway of the antthrushes. The eggs rested approximately 24 inches below this opening, or about 4 feet above the ground. This was the only nest which I had seen when I wrote my earlier account of the antthrush (Skutch, 1945*b*). It was likewise the only nest site which afforded shelter from rain because it had no opening at the top.

The fourth site was in the hollow, decaying stub of a dicotyledonous tree about 9 feet high and 5 inches in diameter. The top of this stub was open, and there was a long, narrow lateral slit which began 7 feet above the ground, extended upward for 13½ inches, and for most of its length was about 1½ inches in width. Both the terminal and lateral openings were used by the antthrushes for ingress and egress. An aroid and a species of *Carludovica*, both with small leaves, crept over the side of this slender trunk. In three years, the antthrush laid seven sets of eggs here and

reared broods from the first five. The distance from the lower end of the lateral aperture to the eggs fluctuated slightly from brood to brood. When the nest was first found on April 10, 1958, the eggs lay 36 inches below the doorway. Before the second set of eggs was laid, in July of the same year, the nest had been built up, and the eggs rested only 22 inches below the aperture. In April of the following year, this cavity again held eggs, which were 29 inches below the lowest point of the doorway. Apparently because of decay the nest sank down, and the second set of eggs in 1959 was laid, about the middle of June, 36 inches below the opening, the same as the egg level of the first clutch.

Not only may the antthrushes sometimes build their nests at ground level, as in the pipe-like segment of palm trunk, but they may even attempt to rear a brood underground. In early June of 1967, in the northeastern lowlands of Costa Rica, I found a nest in a hollow stump, apparently of a wild papaya (*Carica* sp.), beside a forest path. The thin-walled stump, about 3 inches in diameter at the top, was only 18 inches high. But the tubular central hollow, about 3 by 2 inches in diameter, was so deep that the eggs rested 14 inches below the surface of the ground. If this subterranean nest had not been situated on a well-drained slope, it would doubtless have been flooded by the heavy seasonal rains. A few days after incubation began, some passerby pulled up the flimsy stump, leaving the nest and eggs intact in the bottom of the resulting hole. As I approached, an antthrush that had been incubating in the altered nest rose up through the litter on the forest floor and flew away. The next day the nest was abandoned.

Whenever there was a prospect of finding a later brood in a cavity I did not disturb it, and I have examined in detail the contents of only three cavities. After my first nest had been pillaged by some mammal which tore open the cavity, I completed the work of demolition and found that the bottom of the cylindrical hollow had been filled to a depth of about 14 inches with a loose mass of dead leaves of many kinds, chiefly dicotyledonous, although there were also a few strips of palm fronds. The largest leaf was 5 inches long by 3¾ inches broad. At the top of the filling, the leaves were mixed with flower stalks and slender petioles. On this filling rested the nest proper, a thick mat consisting largely of petioles and flower stalks, mixed with which were a number of long, slender, yellowish flowers, too far decayed for identification. There were also a few ventral scutes of a large snake.

In the fallen segment of palm trunk, the filling of leaves rested on the ground and bulged out from the bottom of the tube. It was 6 inches high and consisted of dicotyledonous leaves, whole or in fragments, the largest of which was 6 inches long. On top of this was a fairly thick layer of fine petioles, on which the eggs and nestlings had rested. Since I did not open this cavity for examination until over two months after I had found it, it is probable that the filling of leaves had settled because of dampness and decay. Termites had invaded the sodden mass.

The bottom of the subterranean cavity in which the antthrushes nested was also filled with decaying dicotyledonous leaves and leaf skeletons. At a higher level, these leaves were mixed with slender secondary rachises of *Pentaclethra macroloba*, a tall mimosaceous tree abundant in this forest. At the top was a great mass of these rachises with scarcely any admixture of other materials, on which the eggs rested. Most of the rachises were from 2 to 4 inches long.

THE EGGS

Each of 11 sets consisted of two eggs. When freshly laid the eggs are white, with little gloss, but as a rule they promptly become soiled with mud from the birds' feet, and they are stained brown by contact with the decaying vegetation on which they lie. Not until many years after I found my first antthrushes' nest did I hold one of their eggs in my hand. Since it is hardly possible to reach them without breaking open the nest cavity, I inspected them by means of a mirror inserted through the entrance and illuminated by a flashlight. So consistently did the eggs appear to be white, finely speckled or flecked over the whole surface with dark brown, that I long believed that this was their original color. Only when I removed a set from an abandoned nest did I find, by washing off the brown spots, that these were not shell markings but blotches of caked mud. These two eggs were oval and measured 33.9 by 24.8 and 33.4 by 24.8 mm.

In the valley of El General, 10 sets of eggs were laid as follows: March, 2; April, 1; May, 3; June, 1; July, 1; August, 1; September, 1. The sets laid in June, July, and August were second and third broods following successful earlier broods.

INCUBATION

Both sexes incubate. As I entered the blind before my first nest in the dim light of dawn on May 22, 1942, I heard the sharp *fleet* alarm call of an antthrush. Evidently the bird left the nest as I approached. From my arrival at 5:15 a.m., the eggs remained unattended until 5:33, when an antthrush flew up silently and entered through the smaller of the two openings in the side of the hollow stub. The bird went in with a hardly perceptible pause without the careful inspection of the cavity and its surroundings that woodpeckers, trogons, and many other hole-nesting birds habitually make. It stayed out of sight in the hollow trunk until the mate, arriving silently through the undergrowth at 7:22, flew up and entered the smaller gap with no sound save that of its whirring wings. Almost at once an antthrush (doubtless the one that had been incubating) appeared in the small gap and stood there facing outward. Here it called, giving the emphasized first whistle and about ten following whistles, and then it flew away to the south.

At 8:15 a.m., an antthrush entered the trunk exactly as the one had at 7:22. Two minutes later a bird appeared in the cavity behind the entrance and stood there, looking out. After a while it went down out of sight, but soon it appeared again. Twice more it vanished and reappeared. Finally, at 8:28, an antthrush flew out through the large gap. Evidently the member of the pair that had been on the eggs since 7:22 was reluctant to relinquish its post to the newcomer. Whether the changeover was finally effected I could not tell. Nearly 3 hours later, or at 11:27, the antthrush that had left at 8:28 entered in silence as on previous occasions, and then one bird promptly flew away. Without much doubt, the partner which had been in the nest so long now went off to forage. If there was no changeover at 8:15, one bird incubated continuously from 7:22 until 11:27, a period of 4 hours and 5 minutes. If there was a changeover at 8:15, the longest session was about 3 hours. The next longest session lasted an hour and 49 minutes. Except for a brief interval before sunrise, the nest was attended continuously throughout the morning.

As I approached the blind set before my fourth nest in the dim light of dawn on April 12, 1958, I heard the loud call of an antthrush. But I saw no antthrush until soon after 6:00, when one hopped upon a fallen branch in front of the blind

and stood there for several minutes, preening. Then it flew up and silently entered the hollow stub through the gap in the side. No bird then emerged, whence I inferred that the nest had been unattended. When an airplane passed overhead, the antthrush looked through its doorway, but it did not show itself when a squirrel scolded close by and then jumped on the stub that held the nest. Late in the morning, it again looked out when a large lizard ran over the dead leaves on the ground close by the stub. Finally, at 11:07, the mate silently entered through the open top of the cavity, and then an antthrush left through the lateral slit. The outgoing bird was doubtless the parent that had sat for 4 hours and 53 minutes.

On the following morning, I repeated my watch at this nest. Again I heard an antthrush call as I entered the forest in the dim light of daybreak. At 5:37 a.m., an antthrush silently entered the nest, but none emerged. At 7:51, I heard a rustle of wings close by the blind. The bird that had been in the nest since dawn emerged through the top of the trunk and, standing there, delivered a series of about eight whistles before it flew off beyond sight. Then the newcomer promptly entered through the top. At 10:07, an antthrush entered through the slit in the side of the stub, and almost immediately one left by the same orifice. There was no further activity until 11:15, when I ended my vigil. On this morning the antthrushes had taken two sessions of nearly equal length (2 hours and 14 minutes, then 2 hours and 16 minutes) instead of the single very long session which covered the same period of the preceding day. Possibly the antthrush had then remained on the eggs so long because its mate was kept away by the squirrel which spent much time in sight of the nest, but it is also possible that the presence of the blind had been a contributing factor. After the blind had remained in place another day, the antthrushes were apparently no longer suspicious of it.

On one morning at my first nest and on two mornings at my fourth nest, I had heard an antthrush call as I approached in the dim light, but I had failed to witness its departure from the hole. It is most unlikely that these birds had left the nest because they had seen or heard me, for I approached the blind with caution, and moreover antthrushes sit steadfastly and are not easily frightened from their holes. To gain further evidence on this point, on April 14 I entered my blind at 5:20 a.m., while it was still dark in the forested dell where nest 4 was situated. At 5:30 an antthrush emerged from the stub and stood on its top for about a minute, a dark figure dimly seen in the weak dawn light. Then it uttered eight full whistles, after which it flew off through the dusky underwood. Thirty-eight minutes later, this bird or, more probably, its mate silently entered the nest.

It appears that antthrushes habitually leave their eggs in the dim light of dawn, calling before they leave or as they fly off. The nest then remains unattended for a short while—about 12 to 44 minutes in the observed instances. Thereafter, it is constantly occupied through the forenoon by the two parents sitting alternately. In the early afternoon, however, I have often found the eggs unattended, as they were in the early mornings. The antthrushes' sessions of incubation are rarely under 2 hours in length and may be as long as 5 hours. The oncoming partner usually enters the cavity before the other emerges, although occasionally the partner that has been on duty flies out when it hears its mate's approach. The changeover is effected without vocal sounds that are audible a few yards away, but occasionally the bird that has been relieved stands in the orifice and whistles loudly before it flies off.

The oncoming partner arrives by walking over the ground until it is near the

base of the stub that contains the nest, a mode of approach which provides the best opportunity to discover lurking enemies before betraying the nest's position by entering it. The outgoing partner flies swiftly from the doorway on a long, descending or nearly horizontal course, which takes it out of sight before it alights on the ground.

Antthrushes sometimes fly from their nest, voicing their sharp *tleet tleet tleet*, as a man walks close by. All of my nests were revealed to me by this startling movement close by my head. With the advance of incubation, or as the antthrushes become more familiar with their visitor, they sit more steadfastly. At times, even tapping on the side of the stub fails to make them reveal their presence. On several occasions, an antthrush remained on its eggs while I lowered a lighted electric bulb above its head; then it rushed out past the bulb and my eyes. The same reaction has occurred with parents brooding young nestlings.

Antthrushes show a good deal of discrimination in revealing themselves in their doorway. As already related, one of them did not look out when a squirrel scolded close by and then jumped on the stub within which the bird was hidden. Since squirrels sometimes pillage nests, the bird did well to remain out of sight. On another day, the antthrush did not leave this nest when an agouti rushed by it with three howling dogs in pursuit, and I shouted at the trespassing dogs to drive them off. Yet this bird looked out when an Orange-billed Sparrow hopped over the ground near the stub, and its mate peered through the doorway when a lizard crawled by. Slight, rustling sounds arising near the nest are more likely to make the antthrushes look out to see what is producing them than are loud noises and the passage of large animals.

At one nest, an egg was found on the afternoon of August 25 and by 1:15 p.m. on the following day two eggs were present. Both hatched between 1:20 p.m. on September 14 and 1:30 p.m. on September 15, after approximately 20 days of incubation. At another nest, both eggs hatched 18 days after I first saw the completed set.

THE NESTLINGS

Appearance and behavior.—The shells from which the nestlings emerge are promptly removed by the parents. The newly hatched antthrush displays much pink skin, but as soon as its natal down has dried and the long filaments have spread out, the nestling becomes a featureless mass of dark gray down. The length and density of this down, far surpassing that of most passerine nestlings, are the more surprising when one recalls that the nestlings of other antbirds are, as far as I have seen, hatched in utter nakedness and have at no time a downy covering.

Except for the possibly slightly greater diameter of the mound, two nestlings present almost the same appearance as one, for they huddle together as closely as possible. Hence to learn the number in the brood is not easy. But if you watch closely, after a while you will see a nestling move slightly. The other nestling, if there are two, then makes a swift compensating movement to bring itself once more into closest contact with its companion. These shifts of position often reveal flashes of pink skin on the neck and perhaps also a momentary exposure of the ventral surface. But as soon as the adjustment has been made, the nestlings again become a featureless ball of down. Occasionally one or both bills project from this fluffy mound.

As they grow older, the nestlings cover more completely the bottom of the deep well, but otherwise their appearance changes surprisingly little. At one nest, I found two five-day-old nestlings lying with much bare skin exposed on their necks and backs. Short, dark pinfeathers were clearly visible in the center of their backs and on their wings. At neither this nor any other nest did I on any other occasion see nestlings reveal so much of their skin. Usually I have been able to detect no pinfeathers amid their down until the young are 15 days old, when the sheaths of their remiges are sometimes visible. Even on older nestlings, it is at all times difficult to distinguish any sheaths or expanded feathers of the juvenal plumage.

The most conspicuous features of an older nestling are the wide, flaring, whitish flanges at the corners of its mouth. The flanges at the base of the upper mandible do not fit tightly against those at the base of the lower mandible, but on each side there is a gap between them which resembles the horizontal pupil of an eye. As one peers down into the dark tube, each nestling seems to be staring up at him with great white eyes. The effect is sometimes startling, and it seems possible that, in addition to guiding the parents to the mouths in which they must place food, the projecting corners may frighten predators, and so be doubly useful. The true eyes are far less prominent than these false eyes which project in front of them. I once glimpsed partly open eyes on a nestling 10 days old, but I have rarely seen the eyes of nestling anthruses of any age.

Not only are the nestling anthruses nearly featureless, they are nearly always silent and inactive when one visits them. At all but one of the nests, it was almost impossible to elicit any vocal or other response from them. The exception was the nest in the pipe-like section of palm trunk, which swayed whenever it was touched. When I looked in at these nestlings 3 days after they hatched, they stretched their heads far upward, with widely opened mouths that revealed a yellow interior between the prominent whitish flanges. They also made a buzzing sound, which as they grew older changed into a sort of chiming-sizzling chorus. I believe that these nestlings stretched up for food when I shook their palm trunk because they could not distinguish this motion from that imparted to it by the arrival of their parents. But at the other stubs, which were less mobile, the nestlings evidently learned to respond to a stimulus which I could not reproduce, such as the whirr of approaching wings and possibly the scratching sound made by their parents' toes as they climbed down the shaft. On many visits of inspection to nest 3, I heard only two low notes, when the young were about two weeks old. At nest 4, a nestling of about the same age uttered several low, frog-like grunts when my mirror knocked loudly against the sides of the aperture. But I could not later elicit this grunt by the same means.

As the nestlings lying on the bottom of a dark cavity seem likely to escape the notice of a predator that hunts by sight, so their habitual silence, which contrasts strongly with the loquacity of certain other nestlings, provides slight guidance to one that hunts by sound. When a parent brings food the nestlings are noisy, but the parent goes to the nest only after careful scrutiny of the vicinity has failed to disclose an enemy. A ten-day-old nestling greeted each parental visit with a continuous whirring sound, which began when it heard the rustle of approaching wings and continued until the parent flew from the doorway. When about ready to leave the cavity, nestlings received their food with loud, liquid *chip*'s, which they also uttered if they heard a parent's voice in the distance.

Parental care.—I watched nest 3 in the early morning, when the two nestlings

were 6 and 7 days old. This nest was in the midst of tangled vegetation, in an opening in the forest made by the fall of a great tree that broke off the top of the palm and transformed it into a nest site. The parent always arrived on the wing, from some point beyond my range of vision, and darted into the palm trunk with never a pause at the opening. After about 15 or 20 seconds, it would appear in the orifice, delay there for a few seconds, and then fly rapidly outward and downward until lost to vision in the understory. There were five visits between 6:52 and 8:52 a.m., and each was made in silence except for the slight, dry sound produced by the bird's impact against the hollow shell. On no occasion could I distinguish anything in the bill of the approaching parent.

Nest 4 was far more satisfactory for observation, because it was situated where there was little undergrowth, beneath magnificent tall trees. Here, where the ground was fairly free of obstructions, the parents often approached by walking until they were near the base of the hollow stub, when they flew up to one of the openings. Possibly they always approached in this manner, but on one side foliage screened them from my view until they appeared in flight a few yards from the nest. At times, one of them continued to walk slowly around the stub for about 5 minutes, before it rose sharply to the doorway. Once a parent, arriving with food, walked around and around the blind, frequently within a yard of it, and eyed it intently, at first repeating at short intervals a loud, full, double note, but afterward in silence. For nearly 20 minutes it walked around me. No other bird that I have watched from a blind has exhibited so much obvious curiosity.

The antthrushes' terrestrial approach provided an excellent opportunity to see what they brought for their nestlings. Unfortunately, the food was nearly always badly mangled before the birds came into view. The most recognizable object was a single small lizard. Usually the food appeared to consist of insects, but their mutilated state made it impossible to determine their kind or the number brought on a single visit. Sometimes a wing or two dangled below the amorphous mass in the parent's bill. Once this mass was whitish, with dark wings hanging loosely from it. This observation suggested that the whitish mass, with nothing to reveal its provenance, which I more often saw in a parent's bill, came from the interior of insects. Even with a laden bill, the parent sometimes continued to push aside fallen leaves, searching for more food as it walked toward the nest. With rare exceptions, it came and left in silence.

Feedings were infrequent. From 5:30 to 9:30 a.m. on April 26, 1958, a single nestling, 10 days old, was fed seven times. From 6:00 to 10:00 a.m. on August 17 of the same year, the single nestling of the second brood in this nest, now 18 days old, received nine meals, but there was an interruption of nearly an hour while I caught, examined, and returned to its nest the young bird, which had accidentally fallen through the doorway. From 5:35 to 10:00 a.m. on May 21, 1959, two nestlings of the first brood, now 17 days old, received only five meals, the first of which was delivered at 5:39. Each meal appeared to be very substantial, and perhaps this is the reason why so few were brought.

After the nestlings were a week old, brooding was not observed. Although I never saw a parent remove a dropping, the fecal sacs were evidently swallowed by the adults. When three days old, if not before, the nestlings attach these large white sacs to the wall of the cavity beside them. As the nestlings grow older, they deposit the sacs higher on the wall, well above the bottom where they rest. The

parents continue to remove this waste matter until, a day or so before their departure, the nestlings climb up and take their meals through the doorway. No longer obliged to enter the cavity in order to deliver food, the parents relax their attention to sanitation, and the white sacs may remain sticking to the inner wall near the opening.

The nestlings' departure.—The nestlings of my first nest were taken by some predator when they were a few days old. In the third nest, only one young was reared, and it vanished from the hollow palm stub when it was about 18 days old. There was no indication that it had been taken by a predator, but on the day before its disappearance, it appeared as downy, as lacking in flight feathers, as when it hatched. Did it have, concealed beneath its long, loose down, developed wing feathers to bear it from the nest? Or did it simply drop from the top of the stub and walk away? These questions remained unanswered until I found my fourth nest, five years later.

I entered my blind before this nest at daybreak on May 4, 1958. I expected that the single nestling would leave on this day, because on the preceding day I had found its droppings stuck to the wall near the doorway, indicating that the young bird was climbing up to take its food at or near the aperture. At 5:45 a.m., I heard the whistles of an antthrush approaching through the still dusky forest. Looking around for the parent, I almost missed the event which I most desired to see; at this moment the fledgling emerged from the hollow stub. It flew well, on a long descending course. Alighting on the ground a good distance from the nest, it called loudly *chip chip chip*. It looked much like its parents. When I tried to catch it for closer examination, it moved unsteadily over the rough, leaf-strewn forest floor by a combination of walking and hopping, and when I came almost within reach, it flew fairly well. A parent followed us, calling sharply *tleet tleet*. Finally, the fledgling walked into a tangle of bushes, vines, and fallen boughs, and I knew that my attempt to catch it was futile.

My questions had been answered sooner than I had anticipated when I began to watch at daybreak. When first seen by me at 7:30 a.m. on April 16, the young antthrush had so recently hatched that its down was still plastered against its skin. Now, at 5:45 a.m. on May 4, when almost exactly 18 days old, it flew and walked competently. Beneath its shielding cloak of long, dark down its flight-feathers and other plumage had gradually expanded. But the only alteration evident to me, as I looked down on it from above, was a slight change in color from dark gray to olivaceous.

In the following year, the first brood in this stub was hatched on May 4, and both nestlings were successfully reared. At daybreak on May 22, when they were 18 days old, I entered my blind to watch for their departure. At 5:50 a.m., I noticed a parent standing silently on the ground in front of me. It had approached so quietly that I had not been aware of its arrival. There was still too little light to see whether it held food in its bill. At 5:52 it flew up to the top of the stub. Then I saw three shadowy figures fly down to the ground in swift succession, and I heard a rapid *chip chip chip*, followed by the loud, full notes of the parent. These notes grew fainter as the family moved off through the dimly lighted undergrowth, where I could not see them. Going to the nest with light and mirror to confirm my observation that both fledglings had flown from it, I found it empty.

The second brood of 1959 hatched on July 2, and both nestlings were reared. When I looked into the stub at noon on July 18, one became frightened, pushed out

past the electric bulb, fluttered to the ground, and promptly walked off through the forest. The other remained, and at daybreak on July 20 I began to watch for its departure. Neither parent came near the nest until 6:08 a.m., when one silently approached over the ground. Flying up to the stub, it fed the nestling just inside the doorway, while the young bird fluttered its wings and uttered a sharp *chip chip chip*. The parent then flew down. After delaying in the opening for a few seconds, the young bird flew to the ground and started to walk away a short distance behind the parent. They soon passed beyond sight, and the fledgling's *chips* grew rapidly fainter in the distance.

The third brood of 1959 hatched on September 15. One nestling vanished between noon on October 1 and the following noon, apparently having left spontaneously when only about 17 days old. At daybreak on October 3, I began to watch for the departure of the remaining young antthrush. I neither saw nor heard an adult or nestling until 6:03 a.m., when a parent silently flew up and fed the young bird at the doorway. The adult then flew down to the ground, and after hesitating a few seconds the fledgling followed, calling *chip chip chip* in the usual manner. At first, the young bird moved around on the forest floor as though bewildered, and it started to walk in the direction opposite that taken by its parent, which was calling loudly to my left. But in less than a minute the young one got its bearings and started to follow its parent. The latter was now behind me, and the fledgling passed right through the blind, within 2 inches of my foot. Behind the blind it found its parent; the two then walked away and were soon lost to view.

Although both eggs of the second brood hatched in 1958, one nestling died and the development of the other was retarded, perhaps as a consequence of the very hard rains of early August. On August 17, when the survivor was 18 days old, I watched for its departure. It called with loud, liquid *chip's* when it heard the whistles of its parents in the distance, and it climbed up the shaft to take its meals just inside the doorway. At 6:55 a.m., as a parent flew to the open top of the stub, the young bird fell from the slit in the side, quite accidentally, it seemed. It tried to stop its descent by clinging to the epiphytes growing on the stub, but in vain. The parent was obviously puzzled by the young bird's sudden exit through one opening while it was entering through the other. Twice the adult descended into the cavity and then returned to the top, still holding the food it had brought. Once more it entered the hollow; then it looked out through the opening in the side. Finally, it saw or heard the young bird calling on the ground at the base of the stub, flew down, and fed it.

After receiving a second meal at the base of the stub, the young antthrush hopped after its departing parent, but it did not follow far. It rested on the ground beneath a fallen palm frond and uttered loud *chip's* at the rate of 56 per minute. Each time that it called it bobbed up, and the prominent white projections at the corners of its mouth caught my eye. Otherwise, the fledgling was hard to distinguish in the dim light beneath the palm frond. After another meal, it again followed its parent over the ground, until I lost sight of it, although its continuing calls proclaimed that it had not gone far. Guided by these cries, I tried to catch it for a closer inspection. As I drew near, it became silent. I stood motionless, and soon it resumed its calling, thereby revealing its position to me. The young antthrush was standing on its long legs, and when I approached it moved away, hopping where the ground was rough and walking with short steps where the surface was smoother. It did not attempt

to fly, and I soon captured it. After examining it carefully, I replaced it in the hollow stub, where it remained for the rest of the day. Its behavior after it fell from the doorway differed in so many points from that of the other young antthrushes, which flew out after a parent's first visit of the morning, that it was obvious that this nestling was not yet ready to leave.

Watching from concealment the following morning, I heard the whistles of a distant antthrush at 5:30 a.m. At 5:50, the young bird suddenly emerged from the side entrance and flew to the ground on a steeply descending course, alighting near the base of the stub. It at once began to call loudly and rapidly. At 6:00 a parent approached, and the fledgling moved over the ground toward it until out of sight. It continued to voice its sharp *chip* while the parent called *tleet*. Fifteen minutes later, its calls had grown faint in the distance. Although this fledgling was 19 days old, hence a day older than the others whose departure I witnessed, it flew more weakly from the nest and walked away more slowly than they.

To summarize these observations on the spontaneous departure of six fledglings belonging to five broods: The young antthrush leaves its nest in a hollow stub when it is 18 days old, rarely a day earlier or later. It departs in the early morning, before sunrise, and the immediate stimulus for its departure seems to be the arrival of a parent. If the parent calls as it approaches the nest with food, the fledgling flies forth to meet it. If the parent arrives in silence, the fledgling, probably after receiving its meal, flies down with its departing parent, or sometimes it follows the parent after hesitating a few seconds. The fledgling flies from the nest, often rather strongly, but it alights on the ground and walks away with its parent. The departure is always accompanied by continuing loud *chip*'s. Although the parent's presence stimulates the young bird to leave the nest, the parent does not obviously try to induce it to depart, even when the young one has delayed in the nest beyond the usual time for leaving. The nestling's emergence in the dim light of early morning seems related to the incubating parent's habitual departure from the nest at the same time.

Description of a fledgling.—The eighteen-day-old antthrush that I caught still bore much down on its upper parts, especially on the back of the neck and the shoulders. This down was dark gray in color, and it consisted of long, branched filaments about an inch in length. Beneath this, the contour plumage was well developed and completely covered the body. The young bird resembled its parents in coloration, being olive on the upper parts, with the nape and sides of the neck rufous-brown, of a duller shade than the corresponding parts of the adults. Its cheeks and throat were blackish, but the feathers, still incompletely expanded, had grayish bases. Its breast was olive like its back, and its abdomen was gray. Its dusky remiges were fairly well expanded, but its tail was very short. Its bill was black with a white tip, and there were prominent white flanges at the corners of its mouth. Its eyes were deep brown. Its long, strong legs and toes were dark flesh-color, and its toenails were grayish horn-color.

THE SEQUENCE OF BROODS

At the hollow stub in which five broods were reared in two years, the date of hatching of each brood is known and the departure of at least one member of each brood was witnessed. Assuming that an interval of 2 days separates the laying of the first and second eggs of a set and allowing 20 days for incubation, the dates of

the beginning of laying for these five broods can be calculated with a small margin of error. The sequence of broods in this stub was as follows: In 1958, laying of the first set of eggs began about March 25, the eggs hatched on April 16, and the young departed on May 4; laying was resumed about July 8, the eggs hatched on July 30, and the young of the second brood left on August 18. In 1959, laying began about April 12, the eggs hatched on May 4, and the first brood left on May 22; laying was resumed on June 10, the eggs hatched on July 2, and the second brood left on July 20; laying for the third brood began about August 24, the eggs hatched on September 15, and the third brood left on October 2 and 3. In 1958, 65 days elapsed between the departure of the first brood and the beginning of laying for the second brood. In 1959, the corresponding interval between the first and second broods was 19 days, whereas that between the second and third broods was 35 days.

In view of a number of recent studies which indicate that older, experienced birds care for their broods more efficiently than do young parents, it seems significant that in 1959 the antthrushes laid six eggs and reared six fledglings in the same stub; whereas in the preceding year, when the stub was presumably occupied by the same pair of birds, which were then a year younger, only three of four eggs were hatched, and only two fledglings were reared. The weather did not seem less favorable in 1958 than in 1959.

During the last nesting in 1959, a gap, about 2 inches high by an inch in width, had opened in the side of the hollow a few inches above the eggs, apparently a result of decay. I tied some large leaves over this opening, and on each visit I removed them in order to inspect the nest more satisfactorily than was possible through the birds' doorway high above it. A strong odor of must and decay emanated from this aperture. Accordingly, I was surprised to learn that the antthrushes were carrying new nest material into this hollow in early March, 1960. On March 15, I found an egg which had been laid recently, and on March 16 there were two eggs, both of which vanished before they hatched.

I then lost interest in this stub, but as I approached it on September 9 of the same year, an antthrush flew out. The stub was now in the last stages of decay. The top had broken off at a point 7 feet above the ground, and the covering of leaves which I had formerly kept over the lowest gap in the side had fallen. But the birds had filled the central hollow with leaves to above this aperture, and their two eggs now rested 19 inches below the open top of the stub. Between this and the nest a number of holes, too small for an antthrush to pass through, had appeared in the fragile wall, the lowest only 5 inches above the eggs. A week later, there were larger gaps in the sides of the cavity and the eggs had gone. Some large fragments of irregularly broken shell, which I picked from the ground, appeared to have been originally white and to have become stained by contact with decaying leaves. Thus, after having reared five broods in the same stub in two successive years, the antthrushes twice failed to hatch their eggs in the third year.

SUMMARY

The Black-faced Antthrush inhabits lowland forest, from sea level up to at least 5000 feet in Costa Rica. It is a solitary bird which walks over the ground like a rail. Although it can fly strongly, it seems rarely to use its wings except when approaching and leaving its nest, or when hard pressed by a pursuer. Rarely, it is seen perching in a tree.

Its food consists largely of insects, which it finds by flicking fallen leaves aside with its bill. Snails and an occasional lizard or small snake vary its diet. It often hovers about the outskirts of a swarm of army ants with their avian followers, picking up fugitive insects and other small creatures.

The antthrush's usual call or song is a full, mellow, emphasized whistle followed by a variable number of similar but shorter whistles. The sequence most often consists of three notes, but ten or more may be given. The alarm note is a sharp *tleet*, often rapidly repeated.

In El General, the antthrush breeds from March to early October, sometimes rearing three broods in the same hole. The nest is placed in the tubular center of a slender dead, or, rarely, living trunk of a palm or dicotyledonous tree. The cavity is often open at the top, permitting rain to enter. Sometimes the opening is in the side of the trunk, or there may be openings in both the top and side. In six instances, the height above the ground of the doorway used by the antthrushes varied from 1.5 to 11 feet. The nests themselves were from 13½ to 55 inches below the lowest part of the doorway, in tubes from 3 to 5½ inches in diameter. If the tube is deep, the antthrushes bring their nest nearer the entrance by filling the bottom with coarse dead leaves. In one instance, this accumulation was 14 inches deep. Above this is built the nest, which is a thick mat of slender petioles, or of petioles and flower stalks. One nest was 14 inches below the surface of the ground.

Each of 11 sets consisted of two eggs. Newly laid eggs are white, without much gloss, but in many cases they promptly become so uniformly flecked with earth from the parents' feet that they appear to be speckled all over with dark brown shell marks.

Both sexes incubate. The parent that has spent the night on the eggs leaves in the dim light of dawn. The nest then remains unattended until this bird or its mate returns, after an interval ranging from about one-quarter to three-quarters of an hour. Thereafter, each parent sits until relieved by the other; the eggs are constantly incubated through the forenoon. In the early afternoon there is another period of neglect. Usually the oncoming bird enters the cavity before the other leaves. When the surroundings permit, the parent approaches the nest by walking over the ground until it is near the base of the stub; it leaves by a long flight that takes it beyond view. Diurnal sessions range from nearly two to five hours in length. Antthrushes sit steadfastly and are not easily driven from their nests.

At one nest, the incubation period was 20 days.

Unlike other antbirds, which are naked when newly hatched, the antthrush is hatched with long, spreading, dark gray down, which completely covers its dorsal surface and continues to do so until the young bird flies from the nest. As one looks down on a nestling antthrush, its most conspicuous features are the wide white flanges at the corners of its mouth, which resemble staring eyes with horizontal pupils. The interior of the mouth is yellow. Nestlings lie quiescent when visited by a man but call loudly when a parent brings food.

The parents give the nestlings food which has usually been so mangled that it is difficult to recognize its kind, but insects seem to form the bulk of their diet. Rarely a lizard is brought to the nest. Feedings are infrequent; older nestlings received from 0.6 to 2.3 meals per capita per hour. The parents clean the nest, apparently swallowing the droppings, until the young climb up to the doorway for their food, when sanitation is neglected.

On the eighteenth day after hatching, rarely a day earlier or later, the nestling leaves when a parent first visits the nest with food in the dim light before sunrise. If the parent calls, the young bird may fly forth to it; if the parent goes silently to the nest, the young bird follows as the old bird leaves the stub. Although the young anthrush flies fairly well, it alights on the ground and walks away with the parent, repeating a loud *chip*. Its plumage is well developed, but it still bears much long down on its upper parts.

GENERAL SUMMARY OF INFORMATION ON THE FORMICARIIDAE

The antbirds are, after the American flycatchers, the largest family of the Tyranni or Clamatores and number about 250 species. They are confined to the American mainland with its closely adjacent islands, but they are not present in the Antilles. They scarcely extend beyond the tropics. Heat-loving birds, they are most abundant in the humid lowlands, being found especially in the vast forests of the Amazon basin and the Guianas. A few dwell high up in the cool Temperate Zone on tropical mountains, and a few others live among the cacti and thorny scrub of arid regions. In the forest where the majority of species is at home, the antbirds lurk in the undergrowth or at times forage 40 or 50 feet up, but none, as far as I know, frequents the sun-bathed crowns of the great trees. Beyond the forest, antbirds dwell chiefly in dense secondary vegetation that is often impenetrable to man, and only exceptionally do they enter the more open growth of plantations, shady pastures, and dooryards. Although in general they remain near the ground and seem rarely to fly far, only a small proportion of the species are more or less terrestrial. Of these, a number, including species of *Grallaria* and *Myrmeciza*, hop over the ground with their feet together; of those personally known to me, only *Formicarius* is ambulatory, advancing its feet alternately. It is unfortunate that this genus, which is in many respects one of the least typical of a fairly uniform family, should, according to the rules of zoological nomenclature, give its name to the whole great group.

The majority of the Formicariidae are of small or medium size for passerine birds, but a few are as large as jays. Because of superficial resemblances, and often real similarities in mode of foraging and the ecological niches they occupy in the tropical forest, various groups of antbirds have been given the names of other families of passerines. The smallest and most agile species are called "antwrens," although in their restless habits and manner of foraging among the foliage at lower and middle heights in the forest some of them more closely resemble wood warblers. The antvireos are small antbirds of slightly stouter form and more deliberate movements, somewhat vireo-like in their hunting. The antshrikes resemble the true shrikes in their stout bodies and strong bills, although, as far as known, they share none of the predatory habits of the Laniidae. The antpittas are long-legged, short-tailed forms which hop over the ground and somewhat resemble the true pittas of the Old World tropics, although they are never so brilliantly attired as many of the latter. Among the anthrushes are long-legged, terrestrial species, which in their mode of walking over the forest floor with short tail held erect suggest small rails far more than thrushes.

Brilliant colors are lacking in the plumage of these dwellers in the shadows of heavy tropical vegetation. Yet, for the most part, the plumage does not feature the nondescript olives and grays of many of the flycatchers and vireos; the antbirds are clad chiefly in attractive and often very striking combinations of black, white, slate-color, and brown of many rich shades. Bold cross-bars of contrasting hues are not uncommon in the family. A number of species are adorned with conspicuous erectile or even permanently erect crests, and some even have a beard to balance the crest. Others have areas of brightly colored bare skin, usually some shade of blue, surrounding the eyes or even covering most of the head; the intensely blue

bald pate of species of *Gymnocichla* displays one of the brightest colors to be found in the whole great family. Although in the terrestrial genera *Formicarius* and *Grallaria*, as well as in *Gymnopathys*, *Pithys*, and others, the sexes are alike in plumage, as a rule they are distinct, and often they differ so greatly that without seeing the male and female in close company one would never suspect that they belong to the same species. Indeed, in some instances the male and female of the same species were originally described under different names. In many antbirds, black or slate-color in the male is replaced by brown or chestnut in the female, either locally, as on the crown or under parts, or at times over most of the body. At times the deeply colored males of two related species are nearly alike in plumage, although the lighter-colored females are quite different—the curious phenomenon of heterogynism.

In numerous species of antbirds, the dark feathers of a restricted part of the dorsal surface have white, or in the female sometimes buffy, basal portions which are invisible except when these feathers are spread apart, as they are in times of stress and excitement. They then form conspicuous white patches in the center of the back, as in the Great Antshrike, Slaty Antshrike, Tyrannine Antbird, Spotted Antbird, and Velvety Antwren; or on the shoulders, as in the Plain Antwren and the Slaty Antwren; or on the crown, as in the Barred Antshrike; or on the forward edge of the wings, as in the Chestnut-backed Antbird. These areas of hidden white are functionally similar to the concealed patches of red, orange, yellow, or white on the crowns of some American flycatchers, which likewise are kept covered except when the birds are excited.

As far as I know, antbirds are never gregarious, but they live singly, or perhaps more frequently in pairs, outside the breeding season. Individuals of several species, along with numerous small birds of other families, may join in a loose flock which wanders through the forest or follows the hordes of army ants, but one rarely finds more than two or three pairs of the same species in one flock. Antbirds are not migratory, although Hudson (1920, 1:237) suggested that the Red-capped Bushbird of Argentina, one of the very few species which extends beyond the tropics, performs limited migrations, for he found it in the La Plata region only in the summer season.

The food of antbirds consists almost wholly of insects and other small invertebrates, with perhaps a few berries. At times the larger species may devour small frogs and lizards, and I have seen a Black-faced Antthrush capture a small snake. The smallest and most active antbirds hunt like wood warblers or vireos among the foliage; others search among dense tangles of vines and ransack the shrivelled leaves caught up among them, or in tangles which drape the stems of small palms and monocotyledonous herbs with giant foliage. The antbirds that hop over the ground flick aside fallen leaves with sideward movements of the bill but never, I believe, scratch with their feet like gallinaceous birds. Exceptional in its mode of foraging is the diminutive Rusty-breasted Antpitta, which, despite its resemblance to the terrestrial antpittas, does not hunt over the ground but flies out from a low observation post to pick small creatures from the forest floor or to seize insects in the air like a flycatcher (Schwartz, 1957:43–44).

Although perhaps the majority of antbirds give little attention to the swarming army ants, some, including species of *Pithys*, *Gymnopathys*, *Hylophylax*, and

Phaenostictus, depend largely on them as purveyors of food. They do not, except perhaps accidentally, devour the ants themselves, but they keep close to the hunting swarms, generally perching, or else clinging in characteristic fashion to a slender upright stem, a yard or less above the ground, while they keep watch for fugitives. When a cockroach, spider, or other small creature is driven by the ants from the spot where it is well concealed beneath the ground litter, the antbird drops down just long enough to seize it, then carries it up to a low perch and eats it. Sometimes a Bicolored Antbird has followed me closely through the forest, alert to snatch up insects and tiny frogs set in motion by my feet or by a stick that I used to stir the fallen leaves. This antbird was using me as though I were a horde of army ants and was almost fearless of me.

The voices of antbirds have slight range, as is to be expected from the relatively simple structure of their vocal organs. In the majority of species, the song consists of the more or less rapid repetition of the same or, at best, of closely similar notes. The rate of delivery may be rapid, in which case the utterance is a trill if the notes are soft and clear, a roll or rattle if they are dull, wooden, or harsh. With a slower delivery, the song is usually a series of more or less separated, similar whistles. The notes of a series, whether rapid or slow, may vary slightly in pitch and emphasis, but they are never complex, as in many of the true songbirds. Yet in spite of these limitations, the utterances of the antbirds are often attractive and at times beautiful. While calling, antbirds often move their tails up and down in time with their notes, and those with crests may erect them. The songs of the two sexes are similar, but often that of the female is weaker or higher in pitch. The male and female "duet" or sing responsively in a number of species, including the Black-crested Antshrike (Haverschmidt, 1953*b*:243), Barred Antshrike, Tyrannine Antbird, and Chestnut-backed Antbird. Sometimes an antbird of either sex sings loudly while incubating, either alone, as in the Streaked-chested Antpitta, or in response to its mate, as in the Barred Antshrike.

Courtship displays have been witnessed among antbirds on a few occasions. The male Velvety Antwren displays before the female by spreading the feathers of his back to reveal a patch of snowy whiteness in the midst of his velvety black plumage, at the same time voicing hurried, sharp, clear notes. White-flanked Antwrens display by rapidly lifting and dropping their wings one at a time, thereby momentarily revealing the long white feathers on the flanks of the male, which when the wings are folded are mostly covered over. As the antwrens flip up their wings, they turn rapidly from side to side or even about-face, at the same time uttering a weak call or song of two syllables. The females, although they have no conspicuous white tufts to display, go through these exercises as assiduously as the males. In other species, mated individuals preen each other's feathers, especially those on the neck, as I have seen in the Chestnut-backed Antbird and the Spotted-backed Antbird. Communal displays by males, of unknown significance, have been observed in the Black-chinned Antcreeper (Davis, 1949*c*).

Nuptial feeding is widespread in the antbird family. Haverschmidt (1953*b*:243) saw the male Black-crested Antshrike feed his mate, and Johnson (1954:57) watched one member of a pair of Ocellated Antthrushes feed the other. I have seen the male feed his mate in the Velvety Antwren, White-flanked Antwren, Plain Antvireo, Spotted Antbird, Bare-crowned Antbird, and apparently in the Bicolored Antbird, although in the last-mentioned species, as in the Ocellated Antthrush, the sexes are

alike in plumage. In each instance, the nuptial feeding occurred at a distance from any known nest. The Bare-crowned, Bicolored, and Spotted antbirds were foraging with army ants when food was passed from one member of the pair to the other; the male Spotted Antbird repeatedly passed choice morsels to his mate. On one occasion, a male Velvety Antwren, after presenting an insect to the female, mounted upon her back. Once I saw a female White-flanked Antwren give food to a male in adult plumage, apparently her mate.

The nests of antbirds are usually situated in a tree or bush, most often within 12 feet of the ground, although occasionally they are as high as 25 feet, as in the Velvety Antwren, or 36 feet, as in the Black-crested Antshrike (Belcher and Smooker, 1936:804), or even 50 feet, as in the Russet Antshrike. Very rarely is an antbird's nest placed on the ground. The nest is usually built in the horizontal fork of a slender branch, to the arms of which the rim is attached, so that the structure is suspended between its supports. At times, two parallel twigs close together may be chosen as the nest site instead of a fork. Some species of *Myrmotherula* and *Cercomacra* prefer a more or less pensile support for their nests. In form, the nest may be a cup or a deeper pouch with the opening facing obliquely upward, as in the pensile nests of the two last-mentioned genera. Nearly always well made, the antbird's nest may be composed almost wholly of fibrous materials or fine rootlets which form a strong fabric, thin enough for light to pass through the meshes; or it may contain few or many leaves, at times a great thickness of them, held in place by fine fibrous strands or, in some of the larger species, by a foundation of slender dead vines or the like. More or less green moss may be attached to the exterior of the nest. Some antbirds, especially the antwrens, employ cobweb to strengthen their nest's attachment to the supporting arms. If many leaves are used in the nest, there is nearly always an inner lining of fibrous materials or fine vines.

In addition to the nests of typical, vireo-like form, a number of aberrant structures have been recorded in the family. The substantial cup-shaped nests of the Chestnut-backed Antbird and related species are not attached by the rim but are supported from below, like the nest of a finch or a tanager. The White-winged Fire-eye builds a roofed, oven-shaped nest with the doorway in the side; in form it is much like the nest of the Vermilion-crowned and Kiskadee flycatchers. The materials used in this covered structure are straws and strips of the leaves of monocotyledonous plants, and the site is near, or even on, the ground (Euler, 1867:401-402). Species of *Gymnophithys* and *Formicarius* nest in decaying stumps or similar closed spaces. The former uses a shallow hollow, but the latter prefers a deep, well-like cavity. Whole or partly decayed leaves, a great number of them if the cavity is very deep, form the foundation of these enclosed nests, and there is a more or less ample lining of rootlets, petioles, flower stalks, or the like. The eggs of the Streaked-chested Antpitta have been found on shallowly concave platforms of dead twigs and leaves and in an old cup-shaped nest made by some other bird; its building appears to be limited to adding a slight fibrous lining to a foundation that it finds already made.

The nest is built, in all species of antbirds for which we have adequate information, by the male and female working in close cooperation. Often the male appears to be the leader in the undertaking.

The eggs are almost invariably two in a set, but three in a nest have occasionally been recorded for species of *Sakesphorus*, *Thamnophilus*, and *Taraba* (Marchant, 1960:369; Euler, 1867:198; Belcher and Smooker, 1936:804-805). In color, the

eggs are white, cream, buff, or light gray, more or less heavily spotted, streaked, blotched, or otherwise mottled with shades of brown, reddish brown, and lilac. Exceptionally they are pure white, as in *Formicarius*.

Incubation is performed by both sexes in all species (about 19 species representing 13 genera) for which we have information. The female covers the nest through the night, sleeping with her contour feathers so loosely spread that they appear not to be attached to a living bird. By day she alternates with her mate, who may then perform the greater share of incubation. In the tropical forest, where so large a proportion of all eggs and nestlings are destroyed by predators, many birds seem to reduce the chances of drawing hostile eyes to the nest by coming and going as infrequently as possible. Antbirds in particular follow the principle of minimum activity at the nest, and while incubating they replace each other at long intervals. Often a single session on the eggs by the male or female, even of the smallest species, lasts 2 or 3 hours. Larger antbirds continue on the nest even longer, up to 4 hours in the Great Antshrike, nearly 5 hours in the Black-faced Antthrush and the Streaked-chested Antpitta, and almost 6 hours in the Bicolored Antbird. As a rule, each member of the pair remains on duty until relieved by the other, or at least the intervals between the departure of one and the arrival of the other are short, so that the eggs are kept almost or quite constantly covered through the day. But the little White-flanked Antwrens neglect their nest for considerable periods and keep their eggs warm only from 50 to 75 per cent of the daytime. While sitting in the nest, antbirds nearly always face outward, away from the supporting crotch, thus differing from vireos, which build similar nests but usually sit facing inward, toward the crotch. Antbirds sometimes add material to their nest in the course of incubation, as has been observed in the Black-crested Antshrike (Haverschmidt, 1953b:247), Bicolored Antbird, Tyrannine Antbird, and Plain Antwireo.

Incubation periods of 15 or 16 days have been found in the very small antbirds of the genera *Myrmotherula* and *Dysithamnus*. In middle-sized antbirds, including *Sakesphorus* (Haverschmidt, 1953b:248) and *Thamnophilus*, the incubation period is 14 or 15, rarely 16, days. In the large *Taraba*, it was in one instance 17 or 18 days, and in the hole-nesting *Formicarius* it was 20 days.

The nestlings are hatched blind and helpless, with usually no trace of down. Quite exceptional in the family is the antthrush *Formicarius*, which on escaping from the shell is covered with down unusually dense for a passeriform bird. The interior of the nestling's mouth is typically yellow. Within 24 hours of hatching, or even sooner, the buds of the pinfeathers are visible beneath the nestling's naked, transparent skin. The pinfeathers push out rapidly and become very long before the horny sheaths break and allow the enclosed feathers to expand. After it starts, the process of expansion is very rapid, so that in a day or two a creature that bristles with spines like a sea-urchin is transformed into a well-feathered bird. The nestlings are brooded by both parents, at first in much the same manner as the eggs were incubated, but the amount of covering that they receive falls off rapidly from day to day.

Both parents feed the nestlings. The food is almost entirely insects and other invertebrates which the adults carry in the bill. Usually one insect is brought at a time. In accordance with the principle of minimum activity at the nest, meals tend to be large but infrequent, the average hourly rate rarely exceeding three feedings per nestling. The maximum rate that I have recorded for any member of the family over a period of several hours was at a nest of the Chestnut-backed Antbird, where

a single nestling, 8 days old, was fed 26 times in 6 hours, or at the rate of 4.3 times per hour. The male not uncommonly takes a greater share in feeding and brooding the young than does the female. At a nest of the Chestnut-backed Antbird the male did most of the daytime brooding and brought nearly all of the nestling's food. Parent antbirds keep their nests clean by swallowing droppings or carrying them off in their bills.

While incubating or brooding, antbirds as a rule allow a close approach by man and can sometimes be touched, but some individuals are shy and difficult to surprise on the nest. Those which sit closely often drop abruptly downward when finally they are forced to leave the nest. Often they flutter over the ground, simulating injury, and some of the best demonstrations of this sort that I have seen were given by antbirds. A Chestnut-backed Antbird that never gave a distraction display when I visited his nest did so repeatedly when an agouti approached it, but other individuals of this species displayed in front of me. Antbirds are devoted parents, and I have had my fingers nipped repeatedly by a Bicolored Antbird and a Slaty Antshrike whose nestlings I touched or picked up. While the male antshrike attacked the hand that I placed on the nest, his mate tried to lure me away by grovelling on the ground with beating wings. When taken in hand, nestlings of the Rusty-breasted Antpitta, 10 to 13 days old, roll up into a ball and become immobile as though dead (Schwartz, 1957:53), but this peculiar behavior has not been observed in other antbirds.

Very soon after they are clothed by the rapid expansion of their plumage, the young antbirds are ready to leave the nest. Recorded nestling periods of species with open nests range from 9 to 13 days, being longest for the larger antshrikes. Nestlings reared in cavities leave when somewhat older, at the age of about 14 days in the Bicolored Antbird and at 17 to 19 days, but most often 18 days, in the Black-faced Antthrush. In the latter species, fledglings usually fly from their hollow stub when a parent first arrives with food in the early morning of the eighteenth day after they hatched; descending obliquely to the ground, they walk off through the forest with the parent. In this family, the nestling period is usually substantially shorter than the incubation period, and the difference between the two is exceptionally great for nidicolous birds.

The plumage of the fledgling may resemble that of its parents, especially in species in which the sexes are alike, but often there are certain differences between the fledglings and the adults. In the Barred Antshrike, fledglings of both sexes resemble the adult male more closely than the female. Little is known about the details of the change to adult plumage; my impression, from seeing so few individuals in immature plumage, is that this latter is fairly promptly replaced by adult plumage. Exceptionally, as in the Slaty Antwren, a male may breed in transitional plumage.

The roosting habits of these retiring birds of dense thickets and heavy forests seem to be wholly unknown.

FAMILY FURNARIIDAE

SCALY-THROATED LEAFTOSSER

Sclerurus guatemalensis

A retiring inhabitant of the lowest and darkest levels of the heavy lowland rain forest, the Scaly-throated Leaf-tosser is clad in deep shades of brown which blend with the decaying leaves among which it hunts. Its throat is whitish, with dark, scale-like spots. The tawny-brown feathers of the chest are variegated with paler shaft-streaks. The sooty black tail is short, broad, and rounded. It is composed of stiff, harsh feathers, whose sharp-pointed shafts barely project beyond the usually frayed ends of the vanes. The eyes are brown. The blackish bill is slender and moderately long, and the strong legs and feet are dusky. The sexes are alike in plumage. The birds are about six and one-half inches long.

The Scaly-throated Leaf-tosser ranges from southeastern México to western Ecuador. In Central America it is found throughout the Caribbean lowlands as well as in the more southerly portions of the Pacific lowlands. In the basin of El General, it occurs upward to at least 2500 feet above sea level.

Little accurate information has been recorded on the Scaly-throated Leaf-tosser and numerous errors have been published.

I first became acquainted with this elusive bird in the forests of Barro Colorado Island in the Canal Zone in 1935. Here the leaf-tosser was perhaps not rare, yet it was seldom seen because of its retiring habits and its dark brown plumage, which made it difficult to distinguish from the dark litter that carpeted the ground where the shade was densest. My attention was most often drawn to a leaf-tosser by seeing dead leaves rising from the ground. If I approached with the utmost caution, I could sometimes watch the wary bird tossing them right and left with great vigor with its bill. On finding itself observed, the bird would sometimes rise to a low perch and deliver a sharp monosyllable of alarm, then dart rapidly through the undergrowth and vanish; often it stole away in silence. One day I found a pair of these ovenbirds flicking leaves side by side, hunting assiduously for the insects and other small edible creatures that live in the ground litter.

While searching for food, the leaf-tosser does not stand up like an antthrush or an antpitta but it squats with flexed legs. To change its position, it hops rather than walks. Rarely I have seen a leaf-tosser cling to the trunk of a tree, a few feet above the ground, upright, with its spread tail pressed against the bark. After possibly a minute in this position, it flew off through the underwood. I have never seen a leaf-tosser climb up a trunk or forage elsewhere than on the ground. It seems to cling to trees only when alarmed, and if it chooses a tree with brown bark, the bird blends with its background and is not easy to detect. Yet it is not evident that the leaf-tosser is safer in this position than it would be if it took refuge in a bush in the dim undergrowth of the forest.

In a little rill flowing through the forest, not far from the laboratory clearing on Barro Colorado, there was a pool where a pair of leaf-tossers used to bathe. Almost every evening in May when I passed that way after six o'clock, I found them splashing long and vigorously in the shallow water. Their ablutions over, they

would fly through the undergrowth to a roosting place which I could not find. If the leaf-tossers happened to see me, they voiced their sharp call.

FOOD

While I sat in my blind in the heavy forest on Barro Colorado, watching the nest of a pair of White-flanked Antwrens, a Scaly-throated Leaf-tosser foraged near me on two successive mornings. One day it hunted on the bank of the neighboring rivulet, pushing down big dead leaves and eating small objects that it found beneath them. Then it perched quietly for many minutes on a vine which hung low across the channel, only a few yards from where I sat concealed, and I had the best view of the bird that I had so far enjoyed. The next morning it made the dead leaves fly just in front of my blind.

In the forest on our farm in El General, the Scaly-throated Leaf-tosser seems to be less common but also less wary of man than on Barro Colorado. Late on a bright morning in February, while climbing a steep slope, so densely shaded by tall trees and stilt palms that there was scarcely any ground vegetation, I found one of these birds most busily engaged in tossing aside the dry fallen leaves, giving them such vigorous pushes with its bill that many went flying a foot or more. The bird was not at all shy, and while I watched a few yards away, it continued this activity for possibly half an hour with scarcely a pause. It appeared to be finding and eating some small creatures that lurked beneath the ground litter. The leaf-tosser was perfectly silent the whole time I watched. Finally, its hunger satisfied, it came to perch crosswise on a fallen log almost at my feet. Then it seemed to notice me towering above it and darted silently away. Later that same year, I watched a pair of these birds flicking leaves on the forested ridge behind my house. One morning, as I walked through the forest along a narrow, leaf-strewn roadway, I saw a leaf-tosser in action ahead of me. When I advanced closer, it flew forward a few yards and alighted to resume its searching among the dead leaves in the roadway. In this manner it continued to travel before me for possibly 50 yards, moving when I moved, stopping to scatter the leaves in the roadway when I paused to watch. Once it uttered its usual sharp monosyllable, and once it sang a little while standing in the road. Finally, as I continued to advance, it flew away through the undergrowth.

Years ago, Goeldi (1896:305) described the leaf-throwing habit of *Sclerurus umbretta* in Brazil. He believed that the bird "seized" the leaves one by one and threw them vigorously away; so far as I could see, the Scaly-throated Leaf-tosser merely flicks the leaves aside with strokes of its closed bill. According to the same author, the natives of the Serra dos Orgãos are familiar with this habit and call the bird *vira-folha*, that is, "leaf-overthrower." Other less careful observers have stated that *Sclerurus* scratches the leaves aside with its feet, like a gallinaceous fowl, but I have never seen this or any other tracheophone bird employ its feet in this fashion. In casting leaves aside with its bill, the leaf-tosser resembles the more terrestrial antbirds.

VOICE

In the forest on Barro Colorado Island, from time to time I heard an arrestingly beautiful song that seemed to arise from the underwood, but I never could discover the singer, until one day the song was delivered in my presence. On this

occasion, a Scaly-throated Leaf-tosser clung to the steep, bare bank of a deep ravine, and sang again and again. Its song was a beautiful, clear trill, delivered in two ascending movements, the second of which ended in a little silvery tinkle. As the leaf-tosser trilled the simple but pleasing melody, it vigorously moved its tail up and down.

In the forest on our farm in El General, the leaf-tosser sings at dawn in the wet season, from late April or May onward. It is vocal even in September, October, and November, when few birds sing. Although I have not often heard the leaf-tosser's song, the bird may perform with great persistence, continuing for many minutes with scarcely a pause. One to which I listened attentively at 8:00 a.m. in late September delivered verses consisting of about 12 notes, although it was impossible to count them accurately because they followed each other so rapidly. The series ascended in pitch until the final notes were rather chaffy, and the most beautiful sounds were in the middle of the sequence. The verse lasted 5 or 6 seconds. When the bird sang most vigorously, there was a scarcely perceptible interval between the high notes at the end of one verse and the full, deep notes that introduced the next. Yet despite the many repetitions, the song is not monotonous; on the contrary it is one of the most appealing songs in the forests of El General. While watching a nest, I learned that the male and the female have similar songs.

The call, already described, is a sharp, fairly loud monosyllable.

THE NEST

On Barro Colorado on March 28, 1935, I saw a Scaly-throated Leaf-tosser fly up the dark channel of a narrow forest stream with an insect in its bill, and later it returned carrying something white. This was unequivocal evidence that the bird had a nest with young, but I had no notion what kind of nest the leaf-tosser made, nor where it was placed. I searched in the vegetation along the banks of the stream, which had been reduced by continued drought to a series of dwindling pools scattered along the rocky bed, but I could find no trace of a nest. Finally, it occurred to me that the leaf-tosser might breed in a burrow, like some of the South American members of its family. There were a number of holes in the steep clay banks of the little watercourse, but only one, by the absence of cobwebs and the freshness of the earth along its bottom, gave signs of present occupation. Partly concealed by the bushes, I watched this tunnel, and presently a leaf-tosser flew up the channel with an insect in its bill and perched on a fallen branch in front of the hole. Here it delayed, flitting its wings silently; it would not enter the burrow while I was in sight. I set a short twig upright in the mouth of the tunnel and went away. Returning later, I found that the stick had been knocked over, evidence that something had passed in or out.

The length, curvature, and narrow diameter of the burrow made it impossible for me to see or reach what was at its end. Accordingly, I dug a wider and straighter tunnel to the right of the birds' burrow, and by good fortune intersected the latter near its inner end. Here I found a single nestling in pinfeathers, resting on a thick but shallowly cupped nest. I measured the burrow, which was $32\frac{1}{2}$ inches in total length. The entrance tunnel was $3\frac{1}{4}$ inches wide by $2\frac{3}{8}$ inches high; at its inner end it expanded into a rounded chamber. The tunnel curved to the right just enough to place the nest out of sight when I looked in at the front. The nest itself was a thick mat composed of the naked rachises of compound leaves from which the

leaflets had become detached. As far as I could learn by removing a sample of the loosely matted material, the structure was composed wholly of these rachises. My examination over, I replaced the nestling, then carefully sealed up my tunnel with stones, earth, and paper. The parents continued to use the original entranceway as before.

A nest of *Sclerurus umbretta*, examined by Goeldi (1896:306) in the Organ Mountains of Brazil, was placed in a burrow dug into a bank beside a forest path. It was composed of dry rachises like the nest of *S. guatemalensis*. The nest site appears to be fairly uniform throughout the whole genus. Nests of the White-throated Leaf-tosser found in Trinidad by Belcher and Smooker (1936:803) were in the tough clay of roadside banks. The tunnels measured a foot to 18 inches in length, were considerably wider than high at the entrance, curved strongly to the right or left, and terminated in a chamber floored with a few stripped midribs of leaves placed side by side. Apparently the leaves were all of one kind in any given nest, and they were loose and independent of each other rather than interwoven.

Sometime in 1944, a violent wind uprooted a tall campana tree (*Laplacea semiserrata*) growing close beside the cartroad through my forest. When the tree toppled over, the clay adhering to the shallow roots was lifted to form a massive vertical wall higher than my head. In the following year, three kinds of birds—a Blue-diademed Motmot, a Rufous-tailed Jacamar, and a Scaly-throated Leaf-tosser—dug their burrows into this root-bound mass of earth. It seems that in extensive areas of level forest where banks are rare, such masses of soil about the roots of prostrate trees are of the greatest importance to birds which nest in burrows, making it possible for them to breed in localities where otherwise they could find no sites for their tunnels.

Passing along this roadway on the afternoon of September 3, 1945, I saw a small brown bird fly out from the mass of clay between the roots of the fallen campana tree. Early the following morning, it again flew from the wall of clay as I approached. Next morning I watched from the undergrowth, and saw a Scaly-throated Leaf-tosser enter a tunnel 7 inches long, which had been dug into the mass of clay at a point four feet above the ground. But the bird was nervous and would not work while I looked on.

The tunnel in the earth between the roots lengthened slowly. By September 8 it was 12 inches long, and by September 11 it was 14½ inches in length. At this point the diggers struck a root and their work of excavation seemed to languish. But in October they turned their shaft to the right to avoid the obstacle and continued to lengthen it. When repeated visits of inspection failed to reveal that materials for a nest had been taken in, my interest waned. With the exception of hummingbirds, exceedingly few of the small birds of the region nest in the final months of the year. I expected that the leaf-tossers, like the Blue-diademed Motmots which also had dug a burrow in this mass of earth, would wait until the following February or March to lay in the tunnel that they had begun in August or September. Accordingly, I was greatly surprised when the light which I directed into the tunnel on November 7 revealed two white eggs resting in a shallow nest at the end. The burrow was now 21½ inches in total length, and the nest was composed of the slender petioles or rachises of small compound leaves. The eggs were already soiled by long incubation, and two days later they had hatched.

The nestlings from these eggs left the burrow on November 23, and then for several months the nest cavity remained deserted. During the early months of the following year, a number of fairly large, dead, dicotyledonous leaves were taken into the burrow, apparently not by the leaftossers. At about 7 a.m. on April 29, 1946, I surprised one of the leaftossers standing in the mouth of the old burrow, looking out, while its mate rested close by. One member of the pair sang, but I could not see which it was. Then the second leaftosser entered the tunnel and threw out a large leaf. Soon the pair flew away, and I waited in vain for their return. In the following days, they cleaned out all of the dead leaves, and then they began to form a new nest of slender brown petioles. This nest grew slowly, and when the two eggs were laid in mid-May, it was still so skimpy that in places the eggs rested on the bare soil. The birds continued to build up the nest while they incubated. I never opened this burrow but examined its contents with a small illuminated mirror attached to the end of a stick.

After the successful conclusion of this nesting in late June of 1946, I removed the nest. The burrow was apparently unoccupied until the following October, when I found two eggs on a new nest. These hatched on October 25. The circumstances attending the disappearance of the well-feathered nestlings early in November made me uncertain as to whether they had flown forth or had been caught by an animal which had enlarged the tunnel, leaving many sharp scratches on its sides. But in December the leaftossers incubated again in the same burrow, which they had lengthened slightly. By January of 1947 there were nestlings, the fourth brood to be hatched in this burrow since I had found it early in September of 1945. After these fledglings departed, the burrow remained deserted.

On September 4, 1947, I found that the leaftossers were digging another tunnel in this same root-bound wall of clay. The tunnel was already 11½ inches long. Watching this new burrow on three mornings, I enjoyed some intimate glimpses of the leaftossers, without seeing them do much work. On September 6, after singing responsively with its mate in the neighboring undergrowth, one of the birds entered the excavation. Presently it came to the mouth of the tunnel and flicked out loose earth with a muddy black bill. It was evident that the leaftossers did not, like kingfishers, motmots, jacamars, and other nonpasserines which dig tunnels, kick out the loosened earth with their feet. After a quarter of an hour, during most of which the leaftosser was out of sight in the burrow, it flew out and again exchanged songs with its mate. A few minutes later, one member of the pair went into the burrow. Standing in the entrance, it sang many times in an undertone, while its mate sang loudly outside. Presently the latter joined the first in the tunnel. They proceeded inward until I could no longer see them, and low notes emerged from the interior. Soon both flew away, and I waited in vain for their return. Next morning, I watched for an hour and a half without seeing them.

A week later, I left the farm for three months. Hence I do not know whether the leaftossers completed this nest and reared a brood, which would have been their fifth in this mass of clay. This was the last time that I saw a leaftosser take an interest in this nesting place. As the roots that bound it together rotted, the wall of clay slowly crumbled, until it was reduced to a low mound, of which a great many are found in this forest, each marking the spot where a tree grew tall and finally was uprooted by a gust of wind.

THE EGGS

Each of the four sets which I found in the clay around the roots of the fallen tree consisted of two eggs, which were pure white until they were stained with mud. With considerable difficulty I managed, without enlarging the tunnel, to remove one set for closer examination. These eggs measured 27.4 by 21.0 and 27.4 by 20.6 mm.

These four sets, apparently all laid by the same female, were found in October of 1945, and May, October, and December of 1946. Thus this pair of leaf-tossers nested chiefly in the last quarter of the year, when the rainfall is very heavy and few other birds of this region are breeding. The nesting season indicated by these few records resembles that of certain hummingbirds more than that of any other passerine bird of El General. As calculated from the date of departure of the nestling from the burrow that I found on Barro Colorado, the eggs were laid in this nest at the end of February or the beginning of March. In Trinidad and Tobago, the White-throated Leaf-tosser appears to breed at about the same time as its Central American congener; Belcher and Smooker (1936:803) found nests "from October onwards in most months till May, a somewhat unusual season if regarded as continuous." This species also lays two white eggs, as does *Sclerurus umbretta* in Brazil (Goeldi, 1896:306).

INCUBATION

After the leaf-tossers had been incubating for about a week at their second nest in the burrow in the root-mass, I spent a morning watching from the blind. Twice, after one of them had been sitting for nearly an hour, its mate entered the burrow, then a leaf-tosser flew out. I could not distinguish the male from the female and so could not be sure that the one which left was not the one which had just gone in, but I think it a fair assumption that the newcomer had replaced its mate on the eggs. Hence I would state that incubation was shared by both sexes. But, like other members of the ovenbird family that I have studied, the two leaf-tossers together failed to keep the eggs constantly covered, for sometimes the bird that had been on duty flew away before the arrival of the mate, leaving the nest unattended. From 5:35 to 11:02 a.m., I timed four sessions, lasting 71, 54, 53, and 59 minutes. The eggs were neglected for intervals of 34 and 38 minutes. The leaf-tossers always came and went in silence. But once when one of them entered to replace the other, I heard low *chip*'s during the few seconds when the two were inside together. Once one of the parents, arriving to begin its turn at incubation, carried a big sheaf of material into the burrow.

Often, as I walked down the roadway toward the nest, a leaf-tosser, hearing my footsteps, came to the entrance of the burrow and looked out. Here it stood until I approached within a few yards, then it darted forth and flew down the roadway in front of me, low above the ground. Finally it turned into the forest undergrowth and vanished. But sometimes when I followed it would alight in the road ahead of me, then move a little farther along when I came closer, repeating this several times before it veered aside into the undergrowth.

When discovered on May 16, 1946, the set of two eggs was complete but apparently newly laid. Their white shells became very dirty as the weeks went by. Both eggs hatched on June 6, after an incubation period of at least 21 days. Such slow development is characteristic of the ovenbird family.

THE NESTLINGS

The newly hatched leaf-tossers had pink skin which bore sparse gray down, and their eyes were tightly closed. The interior of the mouth was flesh-color. The empty shells were promptly removed by the parents. When the nestlings were 5 days old, their sprouting pinfeathers could be distinguished in the small mirror that I used for looking into the burrow. Two days later, the nestlings' eyes were open and their feathers were beginning to unsheathe. When 11 days old, the young birds were fairly well clothed with dark brown plumage, the color of which, blending with that of the earth which surrounded them, made them difficult to detect. Their pupils, milky blue in indirect illumination, appeared blood red when the beam of my flashlight fell directly on them. The pale yellow corners of their mouths were the most conspicuous features of the nestlings in their dimly lighted burrow.

On the morning of November 11, when the two nestlings of the first brood in this burrow were 2 or 3 days old, I watched from the blind from 6:10 to 10:11 a.m. The parents, flying low, would dart into the mouth of the burrow so suddenly that only rarely could I distinguish food in their bills. As far as I could see, it was always a small insect that they brought. Assuming that each time a parent entered the tunnel it carried food, the two nestlings were fed 10 times in 4 hours, by both parents. The two met inside the burrow three times, and each time I heard a rapid *chip chip chip chip* issuing from it while they were within together. Otherwise, the parents were silent; when a single one was inside with the nestlings, I could hear nothing. The nearly naked nestlings were brooded very little, only four times, for 22, 22, 32, and 10 minutes—a total of 86 minutes. I could not decide whether both parents brooded, but probably they did so, since both had evidently incubated. Before flying away, the parents sometimes delayed in the mouth of the tunnel, looking out and giving me the best views that I had of them.

Ten days later, when these same nestlings were feathered and almost ready to fly from the burrow, I again watched them during 4 morning hours. They were fed only nine times. Each time that a parent arrived it flew up the roadway and into the tunnel so swiftly that I could not tell what, if anything, it held in its bill. Then I would hear a chiming chorus of clear, high-pitched notes issuing from the burrow. In less than a minute, the parent darted out and away. Except when an adult entered, the young birds were silent in their nest.

On June 20, 1946, when the two nestlings of the second brood in the mass of roots and earth were 14 days old, I spent still another morning watching the burrow. These young leaf-tossers were fed much more often than the two of the first brood when the latter were only a day or two younger. Although I began my vigil at 5:40 a.m. as it grew light in the forest, the first meal was not brought until 6:20. By 10:00, the nestlings had been fed 20 times. For the period from 6:00 to 10:00 a.m., the average rate of feeding was 2.5 times per nestling per hour.

As far as I could see, the nestlings were nourished exclusively with small and medium-sized insects, brought in the parents' bills. Early in the morning, when the young birds were very hungry, they advanced down the tunnel almost to the entrance to receive their meal, and the parent could deliver it while clinging to the mouth of the burrow, without entering. After taking the food, the nestlings always promptly retreated deeper into the burrow, where it was not easy to see them from the front. Later, when they were less hungry, they remained farther back in the burrow, even at mealtime. Thus, the parents had to go farther in to deliver the meal,

but always they darted out and away very promptly. While the nestlings were younger the parents carried out their droppings, but with neither this nor the earlier brood did I see them remove waste after the young were feathered. As a consequence of this neglect, the inner end of the burrow became foul and swarmed with maggots.

Like their predecessors in this burrow, these nestlings raised a loud chorus of softly chiming notes each time they were fed, but their hearing was more acute than that of the slightly younger nestlings of the earlier brood. While the parents were still out of sight, the young leaftossers would hear the beat of approaching wings and begin their calling, which they continued until after they had received their meal and the parent flew off, when the chorus would gradually fade away. The rustle of the wings of birds of other kinds flying past the burrow would stimulate the nestlings to cry out in the same fashion; apparently, they could not distinguish the sound made by other birds in flight from that made by their parents. By clicking my tongue against the roof of my mouth, I could elicit the chiming chorus; but soon the young birds caught on to this deception and would no longer respond to it. Sometimes, too, they would call out for no apparent reason, perhaps deceived by some faint forest sound that resembled distant wing beats.

Sometimes, while I stood in the roadway looking into the burrow, a parent would fly up with food and almost bump into me. After the nestlings were older, such an approach of a parent would cause them to start a chiming clamor, despite the electric light that I had pushed into their nursery. Since my head filled the doorway, the young birds could not possibly see the approaching parent, but they could hear its wing beats. The surprised parent would usually drop down into the roadway at no great distance from me and utter its sharp notes of alarm. One day a parent, prevented in this fashion from entering the burrow, was carrying a long, limp, flat object which looked like a *Peripatus*.

The two nestlings of the earlier brood left the nest before 10:00 a.m. on November 23, when they were 14 or 15 days old. Those of the later brood departed before 9:00 a.m. on June 21, when they were 15 days of age. Guided by a loud, incessantly repeated cry, I found one of the newly emerged young birds resting about a foot above the ground in a tangle of undergrowth, not far from the burrow. It allowed me to come very close before it fled. Although it seemed able to fly fairly well, every few feet it would strike against a vine or some other obstruction and be knocked to the ground. When it had vanished into the dense undergrowth, it resumed its loud calls and continued them until I was beyond hearing. These calls were quite distinct in character from the notes that the young bird had uttered while it was still in the burrow on the preceding day. When they leave the nest, the young leaftossers resemble their parents. Their plumage, however, is even darker, especially on the throat, where it is rufescent, with poorly defined buffy shaft streaks.

On April 16, 1935, while I wandered through the forest on Barro Colorado Island, I met a Scaly-throated Leaftosser flicking leaves aside in its usual fashion. It was accompanied by a fledgling, and when it uncovered something edible it called the young bird with a loud *churr* and gave it food. The fledgling tossed aside leaves on its own account, but it seemed to depend chiefly on the parent for food. The point where I saw these birds was not far from the site of my first nest of this species, from which a nestling had departed ten days earlier. Probably the young leaftosser that I now watched had been reared in this burrow.

SUMMARY

The Scaly-throated Leaf-tosser lives on and near the ground in heavy lowland forest, from sea level up to at least 2500 feet in Costa Rica. The bird hops rather than walks, and when alarmed it sometimes clings upright to the base of a tree trunk. In the evening the leaf-tosser bathes in shallow woodland pools.

The leaf-tosser's food consists of small objects, probably largely invertebrate animals. These are found beneath fallen leaves, which the bird tosses aside with vigorous sideward movements of its closed bill. Male and female sometimes forage together.

The leaf-tosser's song consists of a long series of strong, clear notes, rising in pitch until they become chaffy at the end. The delivery of this verse requires 5 or 6 seconds, and when singing at full intensity the bird begins the next phrase after a scarcely perceptible pause. This beautiful song is continued for many minutes at daybreak and sometimes later in the day. Both sexes sing. The call is a sharp monosyllable.

The leaf-tosser nests in a burrow in a bank or similar wall of firm earth. In Panamá, a pair of these birds were feeding a nestling in a high streamside bank in late March. In Costa Rica, four broods were reared in a tunnel which the leaf-tossers dug in the wall-like mass of clay raised up when a great tree was uprooted. Later a new burrow was dug in another part of the same root-bound mass. Excavation of the tunnel was begun well in advance of the laying of eggs and proceeded slowly. Both sexes worked on the excavation of the tunnel. Loosened earth was pushed from the shaft with the bill rather than kicked out with the feet, as kingfishers do. Burrows varied from 21½ to 32½ inches in length and curved to one side, so that the chamber at the inner end could not be seen from the entrance, which was wider than high.

At the back of the burrow, the birds constructed a loose, shallow nest of rachises of compound leaves, from which the leaflets had fallen. When the eggs were laid, this mat was at times so thin that the eggs touched the earth beneath them. However, the birds continued to add material to the nest while they incubated.

Each of four sets consisted of two pure white eggs. In the first burrow in the root-bound clay, eggs were laid in October of 1945 and in May, October, and December of the following year. In September of 1947, a new burrow was being dug in the same mass of clay. The leaf-tosser has a peculiar breeding season, the causes of which are not understood.

Both sexes incubate, sitting for about an hour at a stretch. Sometimes the incubating bird leaves before its mate arrives and the eggs remain uncovered for half an hour or more. In one instance, the incubation period was at least 21 days.

Newly hatched nestlings have pink skin with sparse gray down and tightly closed eyes. Both parents infrequently bring small insects and similar objects to the nestlings. The most rapid feeding observed was at the rate of 2.5 feedings per capita per hour, for feathered nestlings, but at other times the rate was much slower. While the nestlings were young the parents removed droppings, but later they failed to clean the nest, which became foul.

When 11 days old, the young are fairly well feathered, and at the age of 15 days they leave the burrow. They then fly fairly well but lack control.

BUFF-THROATED AUTOMOLUS

Automolus ochrolaemus

The Buff-throated or Chestnut-tailed Automolus is a slender, long-tailed bird about seven inches in length. In both sexes, the dorsal plumage is dark olive-brown, brightening to chestnut on the rump, upper tail-coverts, and tail and to russet-brown on the wings. There is a conspicuous light eye-ring and a more or less distinct buffy superciliary stripe. The creamy buff feathers of the chin and throat are somewhat puffed out and conspicuous. The remaining ventral plumage is buffy brown along the center of the body, passing into olivaceous on the sides and light chestnut on the under tail-coverts. The moderately long and fairly stout bill is dark along the culmen and lighter below. The legs and toes are grayish.

The species ranges from southeastern México to Bolivia, Brazil, and the Guianas, and many races have been recognized. In Central America, it is found throughout the Caribbean lowlands, and on the Pacific side from the Gulf of Nicoya southward. Here it is resident from sea level up to at least 4000 feet. It is primarily an inhabitant of the lower levels of the rain forest, through which it travels in company with other small birds, including antbirds, ant-tanagers, Tawny-crowned Greenlets, and, at higher altitudes, Golden-crowned Warblers. With increasing human population and the consequent destruction of the forest, the automolus is adjusting itself to life in the taller secondary vegetation and shady plantations. These birds are found in pairs at all seasons; unless they have dependent young, one scarcely ever sees more than two together.

FOOD

The automoluses hunt their food chiefly among curled or clustered dead leaves, sometimes those lodged in the undergrowth near the ground, sometimes those caught among vine tangles or the boughs of taller trees well up in the air. Apparently they never forage in the high canopy of the forest. They are adept at clinging in an inverted position, or in any other orientation that the situation demands, while they assiduously probe the folds of the leaves with their strong bills. The dead foliage of the prostrate crown of a great fallen tree is a fertile hunting ground for them. If they capture a large insect, they may hold it against the perch with a foot while they tear it with the bill. When disturbed by man, they sidle up ascending branches with frequent about-faces, nervously twitching their bright reddish brown wings and voicing their harsh notes, then promptly dart out of sight. Sometimes they join a mixed flock of small birds foraging with army ants, but they and their usual associates in the forest are not habitual ant-followers.

One day while I sat in a blind in the forest, watching an antbirds' nest, an automolus foraged in front of me. It investigated the concavities of the curled brown leaves of a small dead tree, sometimes hanging head downward to reach them. Evidently in the course of this search an insect fell from a leaf to the ground, for the bird dropped down and hopped about on the ground-litter, flicking the leaves aside with its bill in the manner of an ovenbird or an anthrush. As far as I could tell, it was unsuccessful in retrieving the insect, and soon it ascended, climbing sideways up the slender trunk, to continue to hunt insects and spiders among the curled leaves hanging on the tree. From time to time, it voiced its loud rattle.

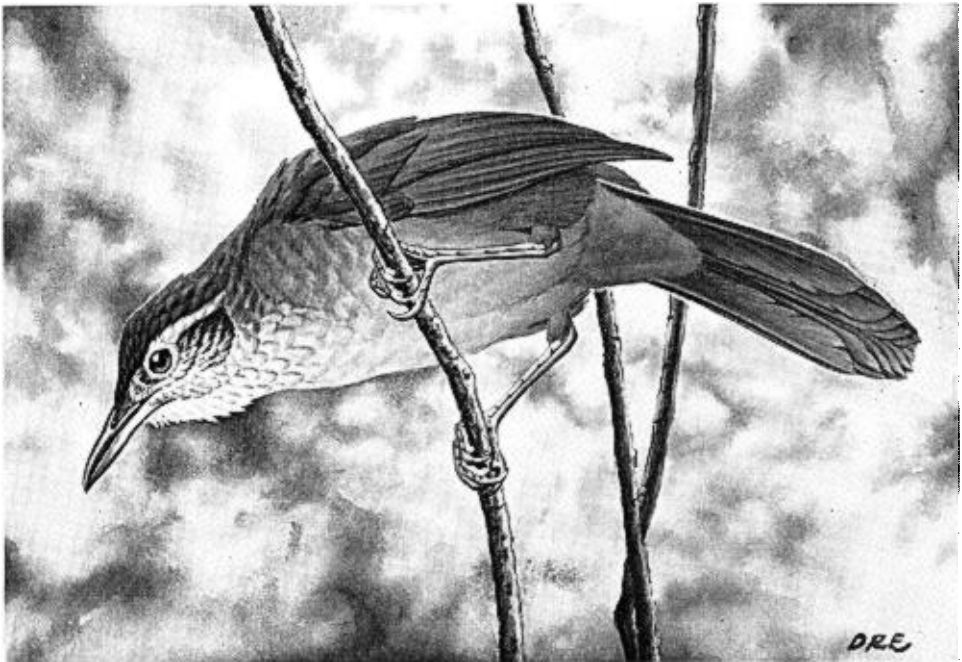


Fig. 16. Buff-throated Automolus.

Years ago, I used to see one or two of these birds, especially in the evening, in a small banana plantation adjoining the forest. Here they hunted among the brown, dry leaves which thickly draped the trunks of the neglected banana plants. As they investigated the long, curling segments of the wind-torn foliage, they usually clung sideways to the thick midribs, nervously twitching their wings, and again and again repeating their loud, harsh notes. Restless creatures, they never lingered long in one spot.

VOICE

In the valley of El General, where chiefly I have studied the automolus, it is a fairly common bird of the heavy forests, but it is shy, remains well concealed by the foliage, and is not easy to watch. One must become familiar with its voice in order to realize how abundant it is. Its most characteristic utterance is a loud, harsh, long-continued rattle. Through much of the year, this is given incessantly in the early dawn, when the birds first awake, and again as the shades of night begin to fill the forest. Strong and far-carrying, sounding from every side, this phrase proclaims the presence of the bird in fair numbers. During the hours of full daylight, the call is only infrequently voiced, except when the automolus is preparing to nest. Then the loud rattle is poured forth so tirelessly that one freely concedes it to be a song.

There is great variation in the length of the songs and in the rapidity of their delivery. One automolus sang at the rate of about 11 songs per minute, each song

lasting from 3 to 5 seconds. Another gave about 16 songs per minute, each of which lasted 2 or 3 seconds and consisted of seven or eight notes. At the other extreme, an automolus delivered 25 to 29 phrases per minute, each lasting about 2 seconds with a barely perceptible interval between the final note of one song and the opening note of the following one. The most rapid and sustained singing is heard before sunrise in March and April, when it may continue with hardly an interruption for many minutes.

Before sunrise on April 1, an automolus sang 21 songs in a minute. He sang very irregularly, and after a while he delivered a single song which continued without a break for 45 seconds. This performance consisted of a few emphasized opening notes followed by a long series of identical low notes, too rapid to be counted, and forming a monotonous rattle. After the briefest pause, a few emphasized notes introduced a similar rattle that continued for about 15 seconds. This rattling song was much softer than the shorter rattle of the Slaty Castlebuilder. Sometimes at dawn this male was answered by another bird which was probably his mate. Her songs were given more sparingly, about one for every three or four of his shorter songs, and she often remained silent while he continued to sing steadily. Her verses were also slightly shorter and drier than his.

In mid-April of 1961, an automolus sang irrepressibly in the fruit and shade trees around our house. He was to be heard at all times of day, even beneath an afternoon drizzle. Sometimes his mate answered with her slightly shorter and drier rattle. They seemed to be seeking a site for a burrow. They were very shy, and whenever I came within sight of the singing male he darted rapidly away. After singing around the house for a few days, this pair went elsewhere. These birds frequently shift their center of interest, singing a great deal in one area for several days and then, if it does not provide a satisfactory site for a burrow, moving away and resuming elsewhere.

An automolus sings with his tail beating time to his rapid notes, and the light-colored feathers of his throat puffed out so far forward that he appears to wear a fluffy beard. When not in song, mated birds keep in contact by means of much lower, throaty notes.

THE NEST

Like many other ovenbirds, the Buff-throated Automolus nests in a burrow. It does not demand a high, scarped bank, difficult for small animals to climb; any low, more or less vertical exposure of firm soil satisfies its needs. I have found burrows in low streamside banks, beside little-used roadways, and at the back of a shallow open pit at the foot of a steep slope. One tunnel, the most difficult to examine of all that I have seen, was in the vertical side of a deep, narrow pit dug by poachers to uncover the burrow of a tepiscuinte or paca (*Cuniculus*) in the forest. Often the mouth of the tunnel is more or less screened by vegetation, although sometimes it is exposed. Until 1956, the three nests that I found were either in or close by heavy forest. In this year, I discovered a pair nesting in the roadside bank behind our house. Their burrow faced light second-growth on the opposite side of the narrow roadway and was nearly 200 yards from the forest. In subsequent years, automoluses have nested even closer to the house and in more open situations, as in a bank in a pasture with scattered trees, 50 yards from the nearest second-growth

thicket. In five years I found eight nests, in contrast to the three which I had discovered in 17 previous nesting seasons in El General.

The burrow in which a pair of automoluses nests may be freshly excavated by the birds themselves, or it may be one which they have occupied in an earlier year. I have known three burrows to be used in successive years, and one of these tunnels was dug more than a year before I found eggs in it. Since the automolus often nests in burrows which have long been in existence, it is difficult to decide whether the tunnel has been made by some other bird or perhaps has resulted from the decay of a thick root in a cut bank.

Although in El General I have found no eggs before March, the excavation of the burrow may begin long before this. On October 21, 1958, I discovered a pair of automoluses working on a tunnel in the bank above the roadway in front of our house. The bank was screened by trees and shrubbery. At the foot of the bank was a narrow, shady pasture, beyond which were tall secondary woods. On this date, the tunnel was already 14 inches long, and despite the heavy rains of this season, the birds continued to lengthen it slowly. By October 25 it was 20 inches long, and in the next two days they lengthened it four more inches. Although in the following week more earth was pushed out, the tunnel became no longer, whence I inferred that the birds were enlarging the chamber at the inner end. By November 8, when digging had stopped, the burrow was still 24 inches long. I watched for nest material to be carried in, but none ever appeared. I also investigated the possibility that this burrow was used as a dormitory, but it was always empty when I inspected it by flashlight at night. After completion, the tunnel was neglected for many weeks.

On December 17, after a warm, cloudy night with a slow rain toward dawn, an automolus sang a long while in front of the house at daybreak. Although I did not see the bird, I could tell from the sound that it was near the burrow. However, the twigs that I had left standing upright in the mouth of the tunnel were still in place. At the beginning of February, this burrow, which had long been neglected, was cleaned of cobwebs and loose soil, and I expected that a nest would at last be built here, but by the middle of the month, the cobwebs stretched across the shaft showed clearly that it was again abandoned. In late April, I discovered that a pair of automoluses had eggs in another burrow, well concealed by herbage, in a bank behind the house. The bank was close to a guava tree in which chickens roosted. After the nestlings disappeared prematurely from this nest on May 19, the burrow in front of the house was again cleared of cobwebs, and on several mornings an automolus sang near it, but no nest was ever built there.

Although the automoluses sometimes dig a burrow months before the breeding season, they may also excavate during the breeding season. In early May I found, beside the road that leads down the hillside to our house, a tunnel that had obviously been newly dug, for below its mouth was a mound of loose soil covering herbs which were still green. A nest had already been started at the inner end of this burrow. From the late date, it is probable that this pair of automoluses had lost a nest earlier in the season.

One occupied burrow was only 18 inches long, but six others varied from 24 to 29 inches in length. At its mouth, the tunnel is about 3 inches wide by 2 inches high, and it varies little in diameter through most of its length, until at its inner end it expands into a low chamber wide enough to hold the nest. Most burrows are

nearly horizontal and fairly straight, so that the nest may be seen from the front with the aid of a light.

The broad, shallow cup which the automoluses build at the inner end of their burrow has so little cohesion that I have not succeeded, after the departure of the young, in removing one of these structures intact. By the time I have pulled it to the burrow's mouth with a stick, it has become a shapeless pile of material, nearly all of the same kind. The preferred building materials are the rachises of compound leaves from which the leaflets have fallen. A great many of these are gathered for a single nest. These rachises are slender, tapering, more or less curved, brown in color, and chiefly from 1½ to 5 inches in length. In El General, the automolus chooses chiefly the secondary rachises of the twice-pinnate, acacia-like leaves of a thorny liana, *Mimosa myriadena*, that climbs high into the tops of forest trees. Each rachis, which has lost its many tiny leaflets, is covered with fine pubescence and armed with minute retrorse spines on its basal half. In one nest I found, in addition to rachises, a few dry, unbranched pieces of some inflorescence from which the flowers had fallen.

Van Tyne (1926) described a nest of another race of the same species (*A. o. pallidigularis*) which he found on Barro Colorado Island in the Canal Zone. It was situated at the end of a horizontal tunnel, over 2 feet long, in a perpendicular cut bank beside a small stream flowing through heavy forest. The bulky, shallow structure was composed almost entirely of a single kind of slender leaf stalk, about 10 cm. in length. In Brazil, Euler (1867:399) found two nests of the White-eyed Automolus, likewise built in burrows beside streams in heavy forest. They were composed wholly of the fine inflorescence stalks of some plant of the verbena family, interlaced to form a compact fabric. One of these nests, built in a burrow which sloped outward at an angle of 45°, was made twice as thick at the front as at the rear, thereby giving the cup a horizontal position.

THE EGGS

My earliest date for eggs in El General is March 11. Here I have found five sets of two eggs and four sets of three eggs, and two nests with undetermined sets. An interval of at least two days separates the laying of successive eggs. I have closely examined only a single set, which I removed from the burrow when they failed to hatch. These eggs were bluntly ovate, pure white, and they measured 27.0 by 19.8, and 26.2 by 19.8 mm. In 11 nests, eggs were laid in March in three, in April in five, and in May in three.

INCUBATION

In an effort to discover the pattern of incubation of the automolus, I watched from a blind for 12 hours at my first burrow and for nearly 18 hours at the second. Seldom have I watched so long and learned so little of the habits of the incubating bird. I saw exceedingly little of the birds I studied; yet the necessity to keep my eyes constantly fastened on the hole in the bank, at the risk of missing the swift inward or outward dart of the automolus if my attention strayed, forbade my glancing now and then at other creatures that from time to time wandered into view. The record made at the second burrow on May 6 and 7, 1946, after incubation had presumably been going on for eight or nine days, is short enough to be given in full:

May 6, 12:30 p.m. I enter the blind; bright sun, clouding over. Shower falls at 2 p.m.

- 2:48. An automolus suddenly leaves the burrow, flying out across the edge of the pasture in front of it.
4:11. An automolus arrives through the thicket behind the burrow and silently enters.
6:05. I leave the bird in the burrow in the failing light. Rain fell hard during the late afternoon.

May 7, 5:10 a.m. I resume my watch at dawn.

- 5:21. An automolus leaves the burrow, flies silently out over edge of pasture.
5:53. An automolus enters, voicing only a few low notes.
6:55. The mate arrives with bill full of material (rachises of mimosa?), clings to vertical stem of sapling in front of the burrow. The one which has been incubating darts out and away. The new arrival is alarmed when I too suddenly raise my field glasses to the window of the blind. It retreats into the bushes behind the burrow and stays there for 25 minutes, moving around mostly out of my sight and constantly voicing rattling notes.
7:20. At length this bird enters the burrow.
8:23. It darts out and away.
9:37. A bird silently enters the burrow.
11:35. It darts out and away. I leave.

During my long watch I had proved, by seeing one member of the pair come to replace the other at 6:55 a.m., that both the male and female share the task of incubation. However, I could not distinguish the sexes nor learn how they divided the day between them, nor which bird sat through the night. On the afternoon of May 6, I timed one long session on the eggs lasting more than 138 minutes; next morning there were three sessions, lasting 62, 88, and 118 minutes. Morning and afternoon, the eggs had been left unattended for three periods, of 83, 32, and 74 minutes' duration. Such periods of neglect appear to be typical of the ovenbirds. The bringing of material to the nest in the course of incubation is also characteristic of the family and of other birds which build very bulky or loosely constructed nests.

A week later, on May 15, I again devoted a morning to watching this burrow. I thought that perhaps the automoluses would incubate more constantly now that their eggs were almost ready to hatch, but the contrary was true. The bird which had spent the night in the burrow darted out and away at 5:39 a.m., leaving the eggs uncovered until 6:14, an interval of 35 minutes. Then this bird or its mate came and sat for 89 minutes, or until 7:43, when an automolus approached through the thicket and darted into the burrow, and almost at once one shot out and away. Although I could not see the changeover at the nest far back in the tunnel, I believe it likely that the individual who had entered was not the one who came out so promptly, and that they did exchange places. The newcomer sat for 86 minutes and flew at 9:09; then for 2 hours and 2 minutes, or until 11:11, the nest was neglected. I was in front of the burrow, looking in to assure myself that one of the pair had not slipped in unnoticed, when an automolus darted out of the undergrowth and almost bumped into me.

To summarize: In 18 hours of watching at this nest, six diurnal sessions on the eggs ranged from 62 to 138+ minutes (the longest was begun before I started to watch). These sessions averaged 96.8+ minutes. Five periods of neglect ranged from 32 to 122 minutes and averaged 69.2 minutes. Computing from these figures, the eggs were incubated only 58 per cent of the time. The birds always approached the burrow through the dense undergrowth of the woods behind it; they invariably left the burrow by flying rapidly and low over the edge of the clean pasture in front and entering a tract of tall second-growth woods to the south.

At my first nest, which I found beside the Quebrada de las Vueltas in El

General in 1939, I failed in 12 hours of watching to witness a single changeover on the eggs. Later, however, I saw that both members of this pair brooded the nestlings, so without much doubt both had also incubated. At this nest I timed four sessions on the eggs, two not in their entirety, lasting 78, 183+, 124+, and 72 minutes. There were two periods of neglect, of 64 and 52 minutes' duration. Thus this pair of automoluses kept the eggs covered more constantly than did the second pair. They approached the nest through the undergrowth of the light second-growth behind the bank, and on leaving they flew down the river toward the neighboring heavy forest.

At this streamside burrow, the parents always flew out before I could approach and look in. Probably this was because, to reach the mouth of the tunnel, I had to jump or slide down the river bank close by, and the noise or vibration warned the automolus of my approach. The bird in the nest would move forward to the mouth of the tunnel, remain there for a few moments, with head and shoulders projecting but screened by the foliage of the creeper that draped over the edge of the bank, then dart rapidly and silently across the stream and away. At the second burrow, when I began daily visits of inspection to time the hatching of the eggs, I sometimes surprised a parent inside when I threw in the beam of my flashlight. Hearing my approach, the bird had apparently moved slowly and reluctantly toward the entrance to look out and see what was happening. When the beam of light fell on its face, it would retreat to the end of the burrow behind the nest and remain there. Then no moderate amount of stamping on the ground a few yards away would send it into the open. At later burrows, I have found both kinds of response to my visits.

At one nest, the eggs hatched between 21 days and 6 hours and 23 days and 8 hours after the last egg was laid. Probably the shorter interval is more nearly correct, because at two other nests I found the incubation period to be at least 21 days, and at two more nests it was no more than 20 days. In my experience, the two or three eggs have always hatched at about the same time, indicating that the ones laid earlier had been incubated little before the last was laid.

THE NESTLINGS

The newly hatched automolus has pink skin shaded by sparse gray down; its eyes are tightly closed. The empty shells are promptly removed by the adults. On the morning when the three nestlings in my first nest were two days old, I watched their burrow for 3 hours. I soon learned that both parents attended the nestlings. Between 5:30 and 8:30 a.m., the adults jointly fed the nestlings nine times. Assuming that only one nestling was fed per visit and that all the nestlings received equal shares of food, this was only one meal per nestling per hour. The articles that the parents brought, however, were big for such small nestlings. The food served to the young birds seemed to consist wholly of adult and larval insects. Both parents warmed the nestlings. Three times I saw one adult arrive with food and remain in the burrow after the departure of the mate, which had been brooding. In the 3 hours, the nestlings were brooded eight times, for intervals ranging from 2 to 17 minutes and totalling 75 minutes. Usually a parent did not continue to cover the nestlings until its mate arrived, but after a spell of brooding it flew away, leaving the young unattended. At dawn the parents rattled loudly as they approached the nest, but soon they came and went in silence.

These parents ceased to brood, even by night, when the nestlings were only 10

days old and were covered merely by their sparse natal down and sprouting pinfeathers, from which the plumage had not begun to escape. Surprised that nestlings so naked should be left uncovered through the night, I visited them again at daybreak on the following morning to confirm my observation, and again I found them alone. At a later nest, the young passed the night alone when they were only 6 or 7 days old. Apparently, in their protected nest, they remain sufficiently warm without a parent to cover them.

Each dawn, when I peeped into the burrow by the light of my flashlight, I saw a row of five or six, pure white, round, little objects lined up on the front rim of the nest. These were the nestlings' droppings, which the parents carried off during the early morning, one each time they visited the burrow with food, until all this waste matter had been removed.

To learn something of the nature of the food given to older nestlings, I watched my first burrow for a total of 4 hours on the mornings of May 24 and 25, when the young were 12 and 13 days old. At first I sat in the blind, but the parents coming with food flew directly into the burrow so rapidly that I could not distinguish what they carried in their bills. Finally, I took down the blind and sat in the open on the shore of the narrow stream opposite the burrow. My presence here caused the parents to hesitate and waver, but they would eventually enter the nest. This delay permitted me to recognize what they carried.

From 5:35 to 8:35 a.m. on May 24, the parents brought food to the three nestlings 12 times. On the following morning, they brought food five times between 5:45 and 6:45. Among the items recognized were insects, some of which were very large; caterpillars, one of which was hairy; a big, black spider; and four small lizards. Van Tyne (1926) saw the parents bring small lizards to nestlings on Barro Colorado Island. The food of all these nestlings resembled that of the related Streaked-breasted Tree-hunter of the highlands. I did not see the automoluses bring any frogs, which figure so prominently in the diet of their highland relative.

When the nestlings heard the voice of an approaching parent, they set up a loud, clear, little chiming or trilling of their united voices, which continued after the attendant entered the burrow. Or, if the parent approached in silence, the chorus did not begin until after the adult bird had flown into the tunnel. By directing a beam of light into the burrow and clucking with my tongue, I could cause the nestlings to trill in the same fashion. As all three faced me with their mouths open, expecting food, I could see clearly that the interior of their mouths was flesh-color, not bright red or orange or yellow as in many nestlings reared in open nests. Neither were there conspicuously projecting, light-colored corners to their mouths.

When 14 days old, these nestlings were nearly feathered. Now for the first time they shrank back in the nest, evincing fear, when I looked into the mouth of the burrow. All three left the burrow on May 30, when 18 days old, and promptly disappeared from the vicinity. In two other burrows, in which single nestlings were reared, each likewise left the nest at the age of 18 days. From another nest, three young automoluses disappeared when they were only 16 days old. There was no indication that their burrow had been disturbed, and they may have left spontaneously. After the young have flown, neither they nor their parents return to sleep in the burrow.

A burrow in which a brood was successfully reared and another in which three 16-day-old nestlings may have fledged were inspected periodically during the follow-

ing months, but they were not occupied again in the same year. Since the automolus may use the same burrow in successive years, it is probable that if it reared two broods in the same season it would do so in the same burrow. All the evidence points to the conclusion that in El General the Buff-throated Automolus rears a single brood.

SUMMARY

The Buff-throated Automolus is primarily an inhabitant of the rain forest, but in regions where this forest is shrinking before the inroads of man, it adapts itself to life in the taller secondary vegetation and shady plantations. Throughout the year, these birds are found in pairs which wander through the woodland in mixed flocks of small birds. In Costa Rica, the automolus occurs from sea level up to at least 4000 feet.

Its food consists of insects, spiders, small lizards, and the like, which it finds chiefly among curled or clustered dead leaves hanging from dying boughs or lodged in tangles of vines. The bird investigates these while clinging in the most diverse positions, often with its body inverted. Sometimes it descends to the ground to push aside fallen leaves with its bill. It holds large insects beneath one foot while it dismembers them with its bill.

The call or song of the automolus is a loud, harsh, long-drawn rattle, which is uttered very freely in the morning and evening twilight and also at other times of day when the birds are preparing to nest.

The automolus nests in a burrow, which it digs in a more or less vertical exposure of soil, such as a bank beside a stream or a little-used road, in the forest or in neighboring clearings. The excavation of the tunnel may start as early as October, five months before laying begins. Occupied burrows may be as short as 18 inches, but usually they are from 24 to 29 inches in length. At the inner end the birds build a broad, shallow cup, consisting almost wholly of a single kind of vegetable material, usually the curving brown rachises of compound leaves.

In El General, laying begins in March and the latest eggs are found in May. The set consists of two or three pure white eggs, which are deposited at intervals of 2 or more days.

Both parents incubate, each sitting continuously for a period usually longer than an hour and sometimes more than 3 hours. The sitting bird often flies away before its mate comes to replace it, with the result that the eggs are frequently left uncovered for intervals ranging from half an hour to 2 hours in length. At one nest, the eggs were incubated only 58 per cent of the 18 hours devoted to observation.

The incubation period, as determined at five nests, is 20 or 21 days.

Newly hatched nestlings have tightly closed eyes, pink skin, and sparse gray down. The interior of the mouth is flesh-color and at no age do the nestlings have conspicuous flanges at the corners of the mouth. Both parents brood and feed the young birds, bringing large insects, caterpillars, spiders, and small lizards at rather long intervals. Droppings are carried from the burrow. Nocturnal brooding ceases when the nestlings are about a week old and still lack expanded plumage.

At the age of about 2 weeks the nestlings are feathered. Five young left three burrows when 18 days old. A brood of three disappeared at the age of 16 days and may have left the nest spontaneously. Neither parents nor fledglings return to sleep in the burrow.

STREAKED-BREASTED TREE-HUNTER

Thripadectes rufobrunneus

The Streaked-breasted Tree-hunter is a large, stout ovenbird about eight inches in length. In both sexes, the top of the head and the hindneck are dark grayish brown. The back and wings are deep brown, which brightens to chestnut on the rump, upper tail-coverts, and tail. The chin, throat, and sides of the neck are ochraceous. The central under parts are light tawny-olive; the abdomen and under tail-coverts are brighter and more rufescent. There are more or less distinct ochraceous streaks on the chest. The under wing-coverts are bright tawny-ochraceous. The stout bill, of moderate length, is largely black. Although this genus resembles *Automolus*, it differs in having a stouter bill and in the rigid, protruding shafts of the tail feathers.

This northernmost species of an Andean genus is confined to the highlands of Costa Rica and western Panamá, where it is found chiefly between 4500 and 7500 feet above sea level. It inhabits dense stands of small trees and bushes, especially those in deep ravines and along mountain streams, which bear an abundance of moss and larger epiphytes. In this excessively humid environment, the tree-hunter searches in the mossy branches, and in the dead leaves caught up among them, for the insects, spiders, frogs, salamanders, lizards, and other small creatures on which it subsists. One day I watched a tree-hunter working at an epiphytic bromeliad of the "tank" type, the elongated leaves of which, arranged in an open rosette, hold much water between their overlapping bases. The stout-billed bird tore and tugged at the narrow leaves, often pulling away large pieces and dropping them to the ground. After I had watched, greatly puzzled, for about 5 minutes, the bird revealed the purpose of this strenuous activity: it extracted from among the bases of the leaves a small frog, which it promptly carried to the ground, doubtless to devour.

This bird was alone, like all the others that I met in the wet mountain forests between August and March. As it tore at the bromeliad, it repeated over and over a loud, harsh monosyllable, the only note that I ever heard from an adult of its kind.

NESTING

Nests and eggs of the Streaked-breasted Tree-hunter have been found in the Province of Chiriquí, western Panamá, by Worth (1939) and Hartman (1957). Both nests were in burrows in the volcanic soil of steep cut banks. The burrow found by Hartman was 7 feet above the roadway, 26 inches in length, 4 inches in width, and 3½ inches in height. At its inner end, it expanded into a chamber 6 inches in diameter. The burrow investigated by Worth was at the top of a bank about 6 feet high. It led upward at a gentle grade for 18 inches, then turned sharply to the right and slightly downward, to open at once into a chamber about 8 inches in all diameters. At the inner end of each of these burrows was a nearly flat nest composed of rootlets. In Worth's nest the rootlets, of medium size and wiry texture, were woven into a structure that was about 6 inches in diameter by 1½ inches thick; it was so compact that it could be drawn without injury through a passageway narrower than itself. Hartman's nest, situated about 4500 feet above sea level,

contained two well-incubated eggs on March 1; that of Worth, at 5400 feet, held two eggs, likewise far advanced in incubation, on August 4. All eggs were pure white. The earlier set measured 31.3 by 20.3 and 30.8 by 20.8 mm.; the later, 33.5 by 23 and 33.5 by 23 mm. Details of the birds' behavior are not given in these accounts.

At a point about 5600 feet above sea level on the muddy roadway leading down the wet northern side of Costa Rica's Cordillera Central from Vara Blanca to Sarapiquí in the lowlands, we found a tree-hunters' burrow on May 24, 1938. The tunnel was situated near the top of a steep, bare bank, about 20 feet high. A narrow, sloping shelf halfway up the escarpment made the burrow accessible. The tunnel, barely wide enough to admit my arm, slanted upward at an angle of about 45 degrees, and the nest, a rather bulky open cup composed largely of dark, fibrous rootlets, was placed 2 feet from its mouth. I could not decide whether the burrow had been dug by its present occupants, but I suspected that it had been otherwise formed, possibly by the decay of a thick root. Had the tree-hunters excavated the tunnel, I doubt whether they would have made it so wide.

By dint of much maneuvering of a mirror, while the burrow was illuminated by a flashlight, we convinced ourselves that the nest cradled two nestlings, already fairly well clad in brown plumage. While we were looking into the burrow, both parents arrived, each carrying a small frog. They flitted about in the distance, uttering at intervals loud, harsh, rather explosive monosyllables. We climbed down the bank and seated ourselves on a grassy mound across the road. The parents now advanced to the edge of the thicket which covered the steep slope above the bank, where they flew back and forth, still holding the green frogs in their bills and continuing to voice their loud, abrupt notes. At times they would pause on the horizontal branch of a bush at the top of the bank and nervously raise their wings, revealing the light buffy orange of the under wing-coverts. Presently one mustered enough courage to fly to the burrow's mouth. While it clung to the steep slope, the nestlings within set up a loud, resonant churring, somewhat like the hunger calls of nestling woodpeckers. This clamor reassured the adult that all was well within; it climbed up the steep incline with the frog, and in a moment it flew rapidly away bearing a white dropping. The other parent hesitated a little longer and then took its frog to the hungry nestlings. Its arrival at the mouth of the tunnel was greeted by the same churring chorus as welcomed the first parent.

To learn more about the tree-hunters' diet, I watched this burrow from 5:45 to 9:45 a.m. on May 26. In these 4 hours, the parents came 11 times with food. They brought four small lizards, one salamander, one little frog, one beetle, one small insect or spider, an object which I took to be a detached frog's leg, and two unrecognized items. I might add to this list a large green caterpillar which one of the parents took inside on the preceding afternoon. The appetite of these nestlings was enormous and I marvelled at their digestive power. Each time a parent reached the tunnel's mouth the young birds set up a loud churring, but this chorus became weaker as the morning grew older. The parents no longer brooded, but after delivering each meal they promptly and swiftly flew out of the burrow.

SUMMARY

The Streaked-breasted Tree-hunter inhabits dense stands of small trees and bushes, especially those in deep ravines and beside mountain streams. In these humid forests

the tree-hunter is found between 4500 and 7500 feet above sea level. Except in the nesting season, individuals were always solitary.

The food of the tree-hunter consists of insects, spiders, frogs, salamanders, lizards, and the like, for which the bird searches through the moss that covers the branches and in the dead leaves caught up among them. To uncover lurking prey, it may tear apart tank bromeliads with its strong bill.

The only note heard from the tree-hunter was a loud, harsh monosyllable.

The tree-hunter nests in a burrow, about 2 feet long, in a steep bank. At the inner end it builds, of dark fibrous rootlets, a broad, shallow structure, in which it lays two pure white eggs. In Costa Rica and Panamá, the breeding season extends from February to August.

Two feathered nestlings were attended by both parents. In 4 hours the adults brought the young 11 meals, including small lizards, frogs, salamanders, insects, and spiders.

PLAIN XENOPS

Xenops minutus

The curious xenops is a small bird of predominantly brown coloration, slightly over four inches in length. In both sexes, the upper surface of head and body is brown of varying shades, of which the brightest is the cinnamon-rufous of the rump and upper tail-coverts. The tail is longitudinally striped with black and cinnamon-rufous. The expanded wings reveal a conspicuous transverse band of ochraceous-buff on a brown and black ground. The brown sides of the head are marked with a narrow buffy streak extending from the upper eyelid to above the ears and a short, upwardly curved crescent of white below the cheeks and ear-coverts, the two together providing excellent marks for recognition. The throat is buff with darker spots, and the remaining under plumage is light brown. The short bill is most distinctive. The dark upper mandible has a nearly straight culmen or upper margin, whereas the pale lower mandible curves strongly upward toward the end, making the bill appear to be upwardly tilted. Viewed from above, the whole bill is narrow and pointed. The eyes are brown and the feet are dark.

The Plain Xenops ranges over the entire length of tropical America from southern México to Paraguay, excluding the West Indies. In Central America, it is found over the whole of the Caribbean lowlands and foothills. On the Pacific side, it is absent in the north, where the dry season is prolonged and severe, but it becomes abundant in Costa Rica, especially south of the Gulf of Nicoya. On the Pacific slope next to Panamá, it is still fairly abundant at 4000 feet and occurs sparingly up to 5000 feet, at which altitude it is also found in the Santa Marta region of Colombia (Todd and Carriker, 1922:294). Surprisingly, it has been recorded at 6200 feet on Volcán Chiriquí in western Panamá (Ridgway, 1911:175).

The Plain Xenops lives in the lower levels of heavy rain forest, but, at least in Central America, it is even more common in the older, taller, second-growth woods and along the borders of the forest. It forages among the vine tangles, in the crowns of the smaller trees, and in the lower branches of the giant trees of the forest. Often, especially in wet weather, these birds come into the low trees around our house, 50 yards from the woodland's edge; they also spend much time in the shade trees of our small coffee plantation. The xenops often roams through the woods with motley, straggling flocks of other small birds, including antbirds, woodcreepers, flycatchers, tanagers, and other kinds. Although they sometimes go in pairs, I see these ovenbirds singly more often than in the company of another of their kind, and I cannot convince myself that they remain mated through the year, as so many of their feathered neighbors do.

The ovenbird family is an exceedingly heterogeneous group of birds, which in form and mode of foraging may remind us strongly of members of other families. In its manner of climbing over the trees, the xenops has been said to resemble a titmouse, a chickadee, or a nuthatch. To the first two it does indeed bear some resemblance, but to liken it to the nuthatch is wide of the mark, for the nuthatch creeps over thick trunks and boughs, whereas the xenops hunts chiefly on slender dead branches and vines. Far more than any of these birds of the northern woodlands, the xenops resembles its neighbor the Olivaceous Piculet, smallest of the

Central American woodpeckers—smaller even than itself. Like the piculet, the xenops climbs over slender twigs without using its tail as a prop in the manner of the larger woodpeckers and woodcreepers; like the tiny woodpecker, it hammers vigorously on decaying branches and extracts food from their pith. In voice, too, there is a most unexpectedly close resemblance between these two diminutive birds of different orders. To complete the similarity, the xenops carves holes which resemble those of the piculet, and at times it nests in cavities made by the latter.

FOOD

An entry made in my journal on February 5, 1939, gives a good picture of the xenops' manner of hunting: "This morning I watched a pair foraging in the crowns of some trees growing amid the second-growth. They devoted attention chiefly to slender dead twigs, especially those, far advanced in decay, which had broken loose from the parent tree but were caught up in the vines that draped the trees, or else were clasped by tendrils and so prevented from falling to the ground. They climbed over and clung to these branchlets in all positions, erect and inverted, as best suited their convenience, and they hammered on them vigorously with their wedge-like bills, putting the whole body behind the blow, much in the fashion of a chickadee. I saw one of the birds extract an insect from the center of one of the slender dead twigs and fly away with it. Some days ago, in the forest, I watched a xenops break into the center of a hanging dead twig and then extend the gap upward with its bill, searching for creatures lurking in the central pith." The upward extension of the gap in the side of the twig was accomplished by inserting the bill and then forcing it upward, breaking away the soft wood with the sharp ridge of the upper mandible, which was used somewhat in the fashion of a canopener. The upward curvature of the lower mandible makes a bill which is at once sharp for pecking into wood, and reinforced for exerting the upwardly directed pressure used in enlarging the gaps.

On another occasion, I watched a xenops cling to the heavy petiole of a fallen dead leaf of a *Cecropia* tree, which had lodged on a lower branch of another tree, above a ravine in the forest. The brown bird pecked vigorously at the dry petiole, and when small ants swarmed out of the pithy center and over the outer surface, it snatched up and swallowed all that it could catch. Another xenops clung to a thick dead vine, and after enlarging with its bill a gap in the bark, it began to extract and eat white ant pupae, and possibly also the mature ants. In its fondness for ants and their pupae, and in its method of procuring them, the xenops closely resembles the piculet.

Still another xenops that I watched was pecking on a small dead branch, near its end. After hammering a while, it would go to the broken-off end and peer with one eye into the hollow center, an action very characteristic of the bird, which likes to keep watch over the movements of the prospective victim that it is trying to remove from its retreat in the center of a dead stem. After each inspection, the bird resumed its hammering on the side of the twig. After a while its vigorous exertion was rewarded and it drew a big brown insect from the end of the branch. In much the same manner, long, slender larvae are extracted from the hearts of thin, dead vines. If the prey drops out of the end of the dead stem, the xenops follows it to the ground, where otherwise this bird is never seen.

A xenops that I watched in the Caribbean lowlands of Honduras devoted much

attention to shrivelled dead leaves attached to the ends of slender twigs, often hanging head downward to explore their folds. I have not seen these birds eat fruit of any kind.

SLEEPING

In September, 1957, I found a lone xenops sleeping in an old woodpecker's hole, about 35 feet up in a dead avocado tree in a coffee plantation, close beside light second-growth woods. The small brown bird was most difficult to see as it entered the hole swiftly in the fading light or darted away at daybreak. It appeared to have more than one lodging, for if it saw me watching the hole in the evening it went off and did not return. In another branch of the same badly decayed tree slept a pair of Golden-naped Woodpeckers, which had evidently made and abandoned the hole used by the xenops. They went to rest much earlier in the evening and emerged much later in the morning than their smaller and far shyer brown neighbor.

A year and a half later, I discovered a xenops, possibly the same individual, sleeping in another tottering dead avocado tree in the same small coffee plantation. Instead of examining the cavity from the outside before entering, as woodpeckers and other birds which lodge in holes habitually do, often with a great display of caution, the xenops flew down from neighboring trees in the dim twilight and slipped through the irregular opening in the side of the trunk with hardly a pause, so that I rarely saw it well. Then neither tapping nor scraping on the trunk would make it look through its high doorway.

On the evening of March 18, 1959, several weeks after I found this second dormitory, the xenops, on arriving in the dim light, did not as usual go unhesitatingly into the cavity but clung in front of it for several seconds. Then another xenops, which I had not previously seen, emerged from the hole, and the two flew rapidly to neighboring trees, as though one pursued the other. After a while, one returned and entered the hole, so quickly that I hardly saw it. Soon the other bird returned, and while it clung beside the doorway the first emerged and flew off in the dusk. The new arrival then went in, and from the interior I heard the xenops' fine trill repeated several times. On other evenings, the bird was always silent after entering.

A few evenings later, a xenops came to the dead avocado tree and clung for possibly a minute in front of the hole, then slipped in. Soon another xenops alighted beside the doorway; but before it went in the first came out, and both flew rapidly away. Finally, one entered the hole swiftly in the twilight. The doorway which it used was one of three openings close together in a vertical row, but possibly all gave access to a single central hollow in the badly decayed trunk. It was evident that, like the woodcreepers and certain wrens, the xenops prefers to sleep alone and repels others of its kind that try to share its lodging. These two birds that coveted the same hole were perhaps mated, but I could not distinguish them.

VOICE

The song of the Plain Xenops is uttered by both sexes. It is a fine, sharp, very rapid trill, so similar to the trill of the Olivaceous Piculet that it is difficult to describe how they differ, but that of the piculet is softer. At daybreak in the breeding season, the xenops repeats this simple song over and over. In late March and throughout April of 1959, one performed in this fashion near our house. One morning I heard it singing within the dense tapestry of foliage at the woodland's edge, where I could

not see it. After the light grew stronger, it flew down into the ample crown of an old orange tree growing in the pasture, and here it pecked on the dead branches, voicing its trill at longer intervals. Already performing when I came within hearing, the xenops continued to deliver its song at irregular intervals for the next 25 minutes. The first note of the high, sharp trill was usually emphasized. This concentrated dawn singing, which in some years I have heard as early as the first week in December, corresponds to that of many flycatchers. Later in the day, I have not heard the xenops sing so persistently, although it utters the same bright trill.

The call is a fine, sharp note, in much the same tone as the song. It may be rapidly repeated as the xenops flies. A rather similar note is used to draw a mate to a potential nest site. At about sunrise on March 20, 1964, a xenops clung in front of a small round orifice in the top of a slender, decaying stub about 20 feet high, standing in a patch of forest. Here he remained for many minutes, rapidly repeating a sharp, clear note. From time to time he stuck his head into the hole, but he did not enter the cavity, which appeared to be an old one, possibly made by a woodpecker. After a long while, he varied his utterance with more nasal notes, reminiscent of those of the Black-capped Chickadee. He flew to a neighboring vine, where he clung and continued to call, then returned to the hole. At last his persistence was rewarded, and his mate flew up to cling to the stub beside him. But, without looking into the cavity, she soon flew away, and after a minute or so he followed. While she was beside him, he seemed to fluff out his white cheek stripes, making them more conspicuous.

A week later, a xenops carried two billfuls of finely shredded fibers into this hole. As late as the middle of April, I again saw the supposed male cling before the doorway, calling, but this time he continued for only 2 minutes. As far as I could tell, no egg was ever laid there. Special displays to attract a mate to a suitable nest site are used by a number of other hole-nesting species.

ANTING AND BATHING

Early one morning in November, I saw a xenops cling in an upright posture to a slender twig beside a silken nest of the ant *Camponotus senex*. This nest was attached to a hanging dead branch high up in a tree at the edge of the woodland. The bird appeared to pluck something from either the surface of the ants' nest or from a twig close beside it. Then, bringing a wing forward in front of its nearly upright body, it ran its bill rapidly over the lower or inner surface of its remiges. As it did so, its tail was bent forward beneath its body. The bird repeated this act about a dozen times in quick succession. Probably because of the considerable height, I could detect nothing in its bill, but doubtless it held an ant each time it rubbed the bill over its wing feathers. The bird was apparently anting, and as in some half dozen other species that I have seen engage in this curious behavior in the tropics, it did so in a tree and not on the ground, as is often true at higher latitudes. Some years later, I again watched a xenops anting beside a silken ants' nest hanging high in a tree.

In mid-August I noticed a xenops slip into a hole with a wide opening about 20 feet up in a tree trunk. Here it stayed for a minute or so with its head facing out, sometimes backing farther into the cavity and sometimes exposing more of its body. From the fine drops that flew from the hole, and from the matted appearance of the bird's plumage after it emerged, it was evident that it bathed in rain water that had

collected in the hole. Late in the afternoon, after a hard rain, a xenops came and bathed again in the same manner.

NEST BUILDING

In Costa Rica, the xenops breeds early. In the Pacific lowlands near the Golfo Dulce, I found a pair carving a hole on November 20, 1947. On our farm in El General, I discovered an inaccessible nest on February 4 of the following year. On February 12, I happened to see a bird emerge from this hole with part of an empty shell, apparently of an egg that had just hatched. This egg must have been laid before the end of January. In this locality, I have seen an occupied nest at the end of May, but none later.

The Plain Xenops nests in a neatly carved hole in soft, decaying wood. Four of the five nests that I have found were in slender, upright dead trunks, but the fifth was in an erect dead branch of a living burío (*Heliocarpus excelsior*), a rapidly growing tree with very soft wood. The sites of these nests were, respectively, at the woodland's edge, a short distance within primary forest, in tall second-growth woods, and in a clearing close beside the forest. The lowest nest was only 5 feet up in a decaying burío stump standing in a weedy, abandoned potato patch, 25 feet from heavy forest. Some months earlier, a family of Olivaceous Piculets had used this hole as a dormitory, and without much doubt these woodpeckers had carved it themselves, as I have watched them carve similar holes. The other nests were all considerably higher, from 15 to 30 feet up. Two of these were excavated by xenops as I watched, and possibly all four were the work of the occupants themselves.

It happened that the first xenops' nest that I found was that in the low hole where the piculets had slept, and for a long while I supposed that these diminutive ovenbirds always used holes that they had found already made. But soon after eight o'clock on the morning of November 20, 1947, a fine trilling drew my attention to two xenops clinging to a slender, decaying trunk just within the heavy forest near the Golfo Dulce. Training my binoculars on them, I saw that they were resting upright side by side, in front of a newly begun hole about 25 feet above the ground. The bird on the right was hammering at the hole and removing fine flakes of the soft, rotten wood, which it dropped to the ground. The partner on the left tried from time to time to peck at the hole, but it was too far to the side to work effectively. At 8:27 a.m. the bird at the left flew away, leaving the other alone. The latter continued for the next quarter of an hour to work very actively, removing many flakes of wood, which it threw away with a little flick of its head. It carved from the outside, for the hole was still shallow.

At 8:41 a.m., a xenops flew up to the hole and one flew away. The incident occurred so rapidly that I was not sure that the new arrival had actually replaced the other, but without much doubt this is what happened. The xenops that remained at the hole toiled continuously until 9:05, then flew off. While it worked, I occasionally heard faint tapping, but most of the time no sound reached me from the dead trunk. On later visits that same day, I found no bird present.

The following morning I began to watch at 7:45 a.m. Nine minutes later, a xenops came alone and worked steadily for nearly an hour, removing chips almost continuously. At times I heard faint tapping sounds as the brown bird pecked into the hole much in the manner of a pygmy woodpecker. Finally, at 8:52, the xenops stopped work, rested in front of the hole for about a minute, then flew swiftly away.

The mate was not seen while this bird worked. Neither member of the pair had returned by 9:30, when I left. Revisiting the site at 9:53, I found one at work, and it continued almost constantly until 10:43, when it suddenly flew away. Again the mate did not appear while it carved.

Before the middle of December, this hole was large enough to contain a xenops, and one morning I found one inside with its head in the doorway, trilling. On December 28, some loose shreds of fibrous material hung from the orifice, telling me that the birds had begun to line their nest. As far as I could learn, they had not started to incubate when I left this region at the year's end.

On April 20, 1953, I found a xenops working at a newly begun hole, 20 feet up in tall second-growth woods near our house in El General. Clinging outside the hole with its tail propped against the trunk, the bird pecked away for 15 minutes, reminding me very much of a woodpecker. The following day, a xenops carved at this hole for nearly an hour without stopping. Then it flew off and nothing was done for 23 minutes, when this bird or its mate arrived and worked steadily for 23 minutes. A week after I first found this hole, the birds were carving inside, where I could not see them. From time to time, however, the carver came to the doorway to throw out billfuls of wood particles, usually a number of billfuls in rapid succession. Then it would disappear, presumably for another spell of excavation, although I heard no revealing sounds. At this nest, I did not succeed in seeing one member of the pair replace the other at work, for after laboring for a while the xenops would fly off, and then a considerable interval would pass before carving was resumed. It was thus impossible to tell whether the same individual had returned or its mate had come to work. At the earlier nest, I had seen one bird replace the other only at the very beginning. On May 2, I noticed a fibrous strand in the doorway of the hole which I had found on April 20.

The nest cavity which had been carved by piculets and taken over by the xenops had a round doorway slightly less than an inch in diameter. A nest of the Plain Xenops found by Van Tyne (1935:28) in El Petén, Guatemala, was 12 feet up in a tree overhanging a dry stream bed in the heavy forest. It was 90 mm. deep and had a doorway about 35 mm. in diameter.

After carving a hole or taking possession of one which has been abandoned by piculets, the xenops lines the bottom with soft, shredded bast fibers, such as one never finds in holes of woodpeckers, whatever size they may be. The burío, whose soft wood often provides a favorable nest site, likewise yields in its inner bark fibers suitable for lining the cavity. The xenops continue to increase their lining while they incubate, and at this time I have seen both members of the pair bring fibers as they come to take their turns on the eggs.

THE EGGS

My attention was drawn anew to the dormitory which the piculets had abandoned by some shreds of fibrous bark hanging from the doorway. Looking in by inserting a flashlight and a tiny mirror through the narrow orifice, I saw that the bottom of the cavity contained the beginning of a nest, which certainly had not been left there by the woodpeckers. This was on February 21, 1937, and on the following day I watched in vain for the builders of this nest, whose identity I could not guess. By February 26 there was still no egg, and the ownership of the new nest remained a mystery. My next visit was on March 2, when I found two glossy white eggs resting

on the soft lining of burío fibers. No more eggs were laid. My second nest contained two white eggs when it was found on April 19, 1942. The nests that I found in later years were inaccessible and the number of eggs or young that they held remained unknown. Van Tyne's nest in El Petén contained two half-grown young on May 4.

INCUBATION

Incubation is performed by both sexes; they fail by a good deal to keep the eggs constantly covered. I devoted more than 11 hours to watching the low nest in the old piculets' hole in the clearing at the forest's edge. I began my vigil at dawn, when I could hardly distinguish the narrow round doorway in the side of the stub. At 5:44 a.m., when it was growing lighter, I heard the call of a xenops at the edge of the woods, and at the same time a face appeared in the round aperture in front of me. The owner of this face, probably the female, flew from the nest to the forest, and then the mate entered to incubate. Here he remained quietly for 72 minutes, until 6:56, when the supposed female suddenly flew out of the woods and clung to the stump below the entrance. The male thereupon left the nest and flew to the woods, rapidly repeating a sharp *chip* as he went. Then the female entered the hole.

The male clung to a dead twig within the margin of the woods and sang his clear, sharp, rapid trill over and over. Finally his mate began to answer, trilling in the nest. After she had sat for only 10 minutes, the male returned to the doorway and trilled, while the female responded with a more subdued trill from within. For 2 minutes the male clung outside the nest, singing, from time to time receiving an answering song from his mate. Then the female came out, and the male promptly entered to incubate.

After 29 minutes, the female returned silently to replace her mate, which came out and flew, chipping sharply, back to the woods. The female sat for 48 minutes, then the male returned and, clinging beside the doorway, called her out with soft trills. She flew away voicing low notes.

During the first 3½ hours of the morning, the male and female, sitting alternately and each remaining constantly at its post until the other came to replace it, had kept the eggs continuously covered. But at 9:10 a.m. the male looked out, then flew away, while his mate was out of sight. For 51 minutes the nest was wholly neglected. Then, at 10:01, one member of the pair came suddenly and entered the hole. After remaining out of sight for about a quarter of an hour, the xenops stuck its head through the doorway and gazed intently at the ground. After some minutes in this attitude, it slipped through the doorway and clung to the outside of the stub, still looking fixedly at the ground. With my own gaze directed downward by that of the xenops, I glimpsed a snake creeping through the weeds and brush at the base of the stump. To judge by the thickness of the part which I could see, it was a very large snake. I hastily emerged from the blind to look for the serpent, but it had already vanished, either into the tangled weeds or into a nearby hole in the ground, and I re-entered the blind. At 11:08 a xenops returned to the nest, taking in a big billful of finely shredded bark. It sat for 48 minutes and again flew away without waiting for its mate to replace it.

The radical change in the mode of incubation after the middle of the morning and my failure to witness another changeover, such as had been regular during the first three hours of the day, led me to fear that some accident had befallen one member of the pair while foraging in the forest. This suspicion seemed to be con-

firmed by a long afternoon watch on the following day, when between 1:00 p.m. and dusk the nest was occupied for two long periods of 57 and 118 minutes and left unattended for two alternating periods of 50 and 25 minutes. I never saw more than one xenops at a time, and I supposed that only one member of the pair survived.

But watching again at daybreak two mornings later, I saw the supposed male replace his mate in the nest as on the former morning. He sat for exactly an hour, then flew back to the woods and called persistently for his mate, while the eggs remained unwarmed. Now the periods of neglect began even earlier in the day than formerly. A brief watch that afternoon showed very inconstant incubation. I supposed that these woodland birds, accustomed to deep shade, found the interior of the stub, exposed to full sunlight in the clearing, warmer than they could endure, and for this reason they remained away so much of the time. But subsequent studies of other members of the ovenbird family, even those nesting in deep, shaded burrows, indicate that they neglect their eggs for long periods. Thus I was witnessing behavior widespread in the ovenbird family and probably not abnormal for this particular species.

In 11 hours of watching, I timed nine completed sessions on the eggs, ranging from 12 to 118 minutes and averaging 49.8 minutes. There were four periods of neglect, ranging from 25 to 51 minutes and averaging 43.5 minutes. The eggs were covered for 72 per cent of the period of daytime activity.

The pair which I found working at a shallow, recently begun hole on April 20, 1953, appeared to be incubating by May 10. On May 16, I watched this nest from 7:00 to 11:00 a.m. At 7:09 a xenops came with a billful of fibers, followed by another full-grown bird whose constant calling, in the manner typical of a fledgling xenops, suggested that it was the offspring of the nesting pair, which in this case would be attempting to rear a second brood. The member of the pair which had been incubating left the hole and the one bringing fibers promptly entered. The third xenops delayed beside the doorway for a few seconds, then flew off, still calling sharply.

After incubating for nearly 40 minutes, the xenops began to look through the doorway, continuing this for several minutes. Then it dropped almost straight downward from the hole 20 feet up, levelled its course, and flew off through the woods. This was at 7:50 a.m., and the eggs then remained unattended until 8:10. The partner then arriving incubated until 8:56, after which the nest was neglected until 9:45. Then followed another period of incubation which lasted until 10:20, when some Red Ant-Tanagers called excitedly nearby and the xenops left the hole, dropping almost straight down as before. By 11:00 neither parent had come to resume incubation. Thus this pair was no more constant in incubation than the pair which I had watched 16 years earlier.

At my first and lowest nest, one egg hatched in the afternoon of March 16 and the other on the following day. The empty shells were promptly removed. Because of the uncertainty as to the date of laying, it is impossible to give the incubation period with exactness, but it was between 15 and 17 days.

THE NESTLINGS

The nestlings in this low hole had pink skin, tightly closed eyes, and sparse gray down. When the young birds were 5 days old, their pinfeathers had become prominent, and 2 days later their feathers began to unsheathe. At the age of 9 days,

the young were well clothed with brown feathers. They now uttered a low, sharp, rhythmic *peep* while resting in the nest.

On the morning when the nestlings were 5 and 6 days of age, I watched their nest for 3 hours from the blind. Between 5:30 and 8:30 a.m., they were fed only six times. They were given fairly large insects and one very long and slender larva. Considering their lack of feathers, they were brooded very little, for 11, 4, 6, and 8 minutes, a total of only 29 minutes of the 166 minutes which passed after the parent which had brooded through the night left the nest at 5:44 a.m. I could not make certain that both parents brought food, for I never had both birds in sight at once, but since both had incubated, they probably shared the work of feeding the nestlings.

Early on the afternoon of March 29, I found one of the nestlings looking through its narrow, round doorway and uttering sharp, rhythmic *peep*'s. As I approached, it descended into the bottom of the hole. By the following day, both young birds had left, at 13 and 14 days of age.

My highest nest was situated about 30 feet up in a burío tree at the woodland's edge, close beside a clean pasture. When I passed beneath this nest while incubation was in progress, the parent dropped from its doorway almost to the ground, then dived into the bushes at the forest's margin. This happened repeatedly. Early on February 12, I watched a xenops fly from this nest with half an empty shell, as already related. By February 24, I often heard sharp, weak notes issuing from the nestlings in this high hole, the occupants of which seemed to spend much of their time calling in this manner. Both parents brought food, which was passed through the doorway. The adults rarely entered the cavity at this time. By February 27 the nestlings had gone, apparently spontaneously, as the hole had not been torn open. The one that emerged from the shell whose removal I had witnessed had been in the nest 15 days or less.

SUMMARY

The Plain Xenops inhabits the rainier parts of Central America from sea level up to 5000 feet. It is found in the primary forest and perhaps even more commonly in the higher second-growth woodlands. It is likewise found in the shade trees of door-yards and plantations near the woods. It hunts in vine tangles and in the lower boughs of trees. In its mode of foraging and nesting, and even in its voice, it bears a surprising resemblance to the Olivaceous Piculet of the same region.

The xenops subsists on adult and larval insects, including ants, which it removes from the center of slender decaying twigs, vines, and petioles, especially those caught up in vine tangles, and those which after breaking from the tree are prevented from falling by tendrils or roots of epiphytes attached to them. Clinging in whatever position is most convenient, the bird hammers vigorously until it pecks an opening in the side of the stick or length of vine; then it sometimes lengthens the gap by inserting its bill and pushing upward.

The Plain Xenops roosts singly in a cavity well above the ground in a decaying trunk. It enters the hole after the light has grown dim in the evening and flies forth in the morning twilight. When two individuals tried to roost in the same cavity, one chased the other away.

The song given by both sexes is a fine, sharp, very rapid trill, often with an emphasized first note. At daybreak in the breeding season, a xenops may repeat this trill for many minutes. The call is a fine, sharp note, which may be repeated rapidly

while the bird flies. A similar note is repeated incessantly while the xenops clings before a potential nest site, trying to attract a mate.

A xenops anted beside a silken nest of *Camponotus senex* high above the ground. One bathed in rain water that had collected in a hollow high in a trunk.

On the Pacific side of southern Costa Rica, the xenops breeds from December or January until at least May. The nest cavity is in a slender, upright, decaying trunk or branch, at the woodland's edge, within the woods, or in an adjoining clearing. Five nests ranged from 5 to 30 feet above the ground. The lowest hole had earlier been used by Olivaceous Piculets as a dormitory and had evidently been carved by them, but at least two of the higher ones were made by the xenops themselves. They excavate the chamber almost exactly as a small woodpecker does. Both sexes carve the hole, sometimes working for nearly an hour without interruption; except when beginning the excavation, one rarely continues at work until the other arrives to take over the task. After completion, the neatly carved chamber is lined with shredded bast fibers. Both sexes continue to bring this material while incubation is in progress.

Two glossy, pure white eggs are laid, and both sexes incubate. In the early morning, each may remain on the eggs until its partner comes to relieve it, but later in the day the eggs are neglected for long periods. When leaving a high nest, the xenops often drops almost straight downward until near the ground. At one nest, nine sessions by both parents ranged from 12 to 118 minutes and averaged 49.8 minutes. Four periods of neglect ranged from 25 to 51 minutes and averaged 43.5 minutes. The eggs were covered for 72 per cent of the 11 hours of observation. At one nest, the period of incubation was between 15 and 17 days.

Newly hatched nestlings have pink skin with sparse gray down and tightly closed eyes. Both parents bring them insects and larvae and doubtless also brood them. As they grow older, the young become noisy, uttering sharp, weak notes much of the time while they rest in the nest. When 9 days old they are clothed with brown feathers, and when 13 or 14 days old they emerge from their hole.

A xenops attending eggs was followed to the nest by a clamorous young bird, an observation which suggests that two broods may be reared in a nesting season.

BUFFY TUFTEDCHEEK

Pseudocolaptes lawrencii

The Buffy Tuftedcheek is a large, slender ovenbird, nearly eight inches in length. In both sexes, the top of the head and the hindneck are brown with buffy and dusky streaks. The back and shoulders are russet. The rump and upper tail-coverts are rufous-tawny, and the tail is cinnamon-rufous. The wings are blackish and tawny. The lores and auricular region are dusky brown with narrow streaks of buff. The lower cheek and adjoining side of the neck are buff, with the feathers elongated into a short tuft. The chin and throat are pale buff, which passes into yellowish buff on the central under parts and cinnamon on the sides, flanks, and under tail-coverts. The chest, especially at its sides, bears dark, scale-like marks. The projecting tuft on each cheek makes this exceptionally attractive ovenbird easy to distinguish from the many other brownish species which inhabit the high mountains where it lives.

The Buffy Tuftedcheek is found in the highlands of Costa Rica and Panamá, and closely related forms range through the Andean region to Bolivia. On Volcán de Chiriquí in western Panamá, it extends from 4000 to 10,300 feet above sea level (Ridgway, 1911:199). According to Carriker (1910:638), in Costa Rica it is most abundant on the high volcanoes for about 1000 feet below timber line (about 9000 to 10,000 feet above sea level), and it seldom descends below 6000 feet. In 1937 and 1938, I saw it occasionally in the heavy, epiphyte-burdened forest around 5500 feet on the stormy northern slope of the Cordillera Central of Costa Rica, and here I found a single nest. The few tuftedcheeks that I encountered between August and the end of the year were in pairs, which agrees with Carriker's experience with this species. The tuftedcheeks foraged for food, apparently chiefly insects and their larvae, in high vine tangles and on the moss that covered the trunks and branches of trees along which they crept. They also hunted in the large tank bromeliads that grew high in the trees. Sometimes they used their bills to push off the decaying outer leaves of these epiphytes, but I never saw them tear away the green living leaves, as the Streaked-breasted Tree-hunter sometimes does.

Although Carriker (1910:638) considered this to be "a very noisy bird, always chattering and continually moving about in the trees," at Vara Blanca I rarely heard it utter a sound. Early one morning, a tuftedcheek which seemed to be a male called sharply *wit wit*; then it gave a low, clear trill that became slower and ended with well-spaced, stronger notes. Later, I heard from a female attending a nestling a weaker version of this appealing song.

NESTING

Early in the morning of April 6, 1938, I saw a tuftedcheek throw a billful of debris from a cavity, apparently an old woodpecker's hole, in a barkless, decaying trunk that stood in a narrow clearing in the heavy forest. The bird threw a second billful from this hole, then descended to another cavity with a wider orifice, slightly lower in the same trunk, and began to remove particles of decaying wood from the bottom. After thrusting out its head and breast to drop this material to the ground, the bird climbed entirely outside, turned around, entered again, and brought up

another billful. Instead of staying inside while it cleaned out the hole, as a woodpecker does, the tuftedcheek continued this elaborate procedure without intermission until it had ejected many billfuls. Then the bird flew back into the neighboring forest. It was silent the whole time that I had it in view. If it had a mate, it failed to appear.

By April 18, a tuftedcheek appeared to be incubating in the cavity from which the decaying wood had been removed 12 days earlier. This hole was 30 feet up in a very rotten trunk. By standing on the topmost rung of my tallest ladder, I could barely put my hand into the doorway, but the hollow was so deep that I could not reach the egg or eggs, and I did not dare to set a longer and heavier ladder against a trunk of such doubtful stability.

On April 24, I watched from 5:30 to 11:33 a.m. I did not see the tuftedcheek until 5:52, when a pair of Hairy Woodpeckers alighted on the trunk where it was nesting and the bird looked out to see what was happening. At 6:00 it emerged and flew into the forest. After a recess of 36 minutes, it returned alone with an overflowing billful of brown material that seemed to be ramentum from a tree fern. Three minutes after the bird took this into the hole, another tuftedcheek flew to the top of a tall neighboring trunk and called or sang in the manner already described. The newcomer flew into an epiphytic bush growing on the next tree and repeated its song. The attendant of the nest thereupon came out and flew away, and the tuftedcheek that sang followed it. The singer had not gone near the nest. Seven minutes later, a tuftedcheek entered the cavity with another great billful of chestnut-colored fern scales.

The second tuftedcheek did not again come within view. Since I noticed no changeover on the nest throughout the morning, I concluded that only one parent was incubating, although in all the other ovenbirds that I had studied the male and female cooperated in this task. In a good deal of subsequent watching, before and after the eggs hatched, I never again saw two tuftedcheeks in the vicinity of the nest, and this strengthened my conclusion that only one bird was interested in it. Probably the solitary attendant was a female. The record that I made of the bird's movements that morning was imperfect, because once it darted into the hole unperceived by me. Its sessions became longer as the morning grew older; they lasted 3, 37, 40, 47, and 93+ minutes, in this order. It was absent for 36, 7, 22, and 22 minutes, and there was one absence the length of which I cannot give, because I missed the bird's return. It was in the nest for about 4 of the 6 hours that I watched. On leaving the hole, it always flew directly to the forest and promptly vanished among the vines and epiphytes. Except on the two occasions early in the morning when it brought material for the nest, it always flew from the forest's edge directly into the doorway, without touching the outside of the trunk. On a later morning, I again saw it bring fern scales on its first two returns to the nest.

Events at this nest moved very slowly. Although the tuftedcheek appeared to have started to incubate by April 18, I did not see it take food into the hole until May 12, 24 days later. Since I did not watch this nest every day and since the first small food items brought by the parent may have escaped my notice, I should hesitate to affirm on the strength of these observations that the incubation period was longer than 21 or 22 days, as in the Buff-throated Automolus and the Scaly-throated Leaf-tosser. But the nestling period was amazingly long for an ovenbird;

from May 12, or possibly a few days earlier, until June 10, the parent continued to take food into the hole, and to carry out white fecal sacs. If there had been two attendants, it is most unlikely that I should not from time to time have seen them together at or near the nest in the many hours that I spent watching it.

On returning with food, the parent invariably flew from a distance directly into the cavity, passing through the wide doorway without ever pausing in front of it or on the sill. These rapid entries made it difficult to distinguish what was brought; as far as I could see, it gave the offspring mainly small winged insects and larvae. After feeding the young, the bird often lingered for a few seconds with its head framed in the doorway, then darted out and flew rapidly across the clearing into the encircling forest. In great contrast to the nestlings of other species of ovenbirds and the loquacious young Spotted-crowned Woodcreepers that were growing up in a hole in a neighboring trunk, the occupants of this nest were so quiet that I never heard a sound from them, even at meal time, when many nestlings are noisy. I could not learn how many young the tuftedcheek's nest contained.

Just at sunrise on June 10, a young tuftedcheek flew from the hole without hesitating in the doorway or giving any warning of its impending departure. On a slightly descending course, it easily traversed the 50 feet which separated it from the forest's edge, where it came to rest in a dense tangle of vines draping a tree. The young tuftedcheek at once pushed into the massed foliage and vanished.

A few minutes after the fledgling's departure, the parent returned to the nest with a small insect in its bill. When it failed to find a nestling within, the tuftedcheek looked forth from the doorway, still holding the insect, and called *wit wit*. This call was followed by a clear trill that slowed down toward the end. This call or song resembled that which I had heard from the second tuftedcheek which had come into the nest's vicinity in April, but it was given in a much lower and weaker voice. After delivering the song, the parent went down into the cavity again, only to reappear in a moment and call as before. The bird did this several times more before it flew back to the forest, still carrying the insect. For a while its pleasant song continued to issue from the trees within the forest's edge, but soon I ceased to hear it. Apparently the parent bird had found the fledgling and led it deeper into the woods. I never saw them again.

SUMMARY

In southern Central America, the Buffy Tuftedcheek inhabits humid highland forests between about 4000 and 10,000 feet above sea level, but it is more abundant in the upper part of this vertical range. It finds its insect food in vine tangles, on moss-covered trunks and branches along which it creeps, and in tank bromeliads, the decaying outer leaves of which it removes with its bill. It stays high above the ground.

The tuftedcheek's call or song consists of several sharp notes followed by a low, clear trill that becomes slower and ends with well-spaced, stronger notes. A bird presumed to be a female attending a nestling gave a weaker version of this song.

In a narrow clearing in the heavy forest, about 5500 feet above sea level, a nest was found in a cavity which had apparently been made by woodpeckers, 30 feet up in a rotting trunk. At no time were two birds seen to take an interest in this nest. At the beginning, the single attendant threw many billfuls of debris from the bottom of the hole. While incubating, the bird carried in for the nest's lining a number of

billfuls of large brown scales, apparently the ramentum of tree ferns. It was not seen to take any other kind of nest material into the cavity.

Incubation began about April 18. The parent bird's sessions, short in the early morning, lengthened until they exceeded an hour and a half in the late forenoon. The bird covered the eggs for about 4 hours of a 6-hour observation period.

The adult fed the nestlings, of unknown number, with larval and mature insects and carried out droppings. Young were in the nest for the surprisingly long period of 29 days or more. In the absence of its parent, one fledgling flew forth spontaneously just at sunrise and promptly vanished in the tops of vine-laden trees at the forest's edge.

RED-FACED SPINETAIL

Cranioleuca erythroptus

The Red-faced Spinetail is a slender, wren-like ovenbird nearly six inches in length. In adults of both sexes, the forehead, crown, and entire cheeks to the ear-coverts are bright cinnamon-rufous. The tail and much of the wings are also cinnamon-rufous; the remaining dorsal plumage, from the nape to the upper tail-coverts, is olive-brown. The ventral plumage is largely grayish olive, paling to whitish on the throat. The under wing-coverts are deep ochraceous-buff. The short, sharp, laterally compressed bill is blackish on the upper mandible and lighter on the lower mandible; the feet are blackish. The feathers of the relatively long, graduated



Fig. 17. Apex of shoot of a young guarumo tree (*Cecropia sp.*), showing the white protein corpuscles dotting the brown, hairy cushion at the base of each stout petiole. These corpuscles are the food of the Azteca ants that inhabit the hollow stems, and they are also eaten by Red-faced Spinetails, Bananaquits, wintering wood warblers, and other small birds.

tail have acuminate tips, but the shafts do not, as in some other ovenbirds, project beyond the vanes. Immature birds resemble the adults, but the head is almost concolor with the back instead of rufescent, and there are rather prominent, light superciliary stripes.

This northernmost representative of a South American genus ranges from Ecuador to Costa Rica. In western Panamá, it has been recorded at altitudes from 4000 to 10,300 feet above sea level (Ridgway, 1911:186). In Costa Rica, according to Carriker (1910:637), the Red-faced Spinetail is most abundant in the humid forests of the Dota Mountains and on the upper Caribbean slope at about 3000 to 4000 feet, but it occasionally straggles down to 2000 or even 1000 feet above sea level on the Caribbean slope. On the Pacific side of the country it remains at higher elevations, and in years of birdwatching between 2000 and 3000 feet I have never once seen it. In 1937 and 1938, I found this the most common ovenbird around 5500 feet in the heavy, humid forests at Vara Blanca on the northern side of the Cordillera Central. Here, from the dispersion of the family groups in July and August until the following March, it was always alone, although it sometimes joined mixed flocks of other small birds.

The Red-faced Spinetail finds most of its food in the thick coating of moss and lichens on the limbs of the trees in the wet highland forest where it dwells. It also forages in curled dead leaves caught up in the vine tangles. The spinetail is a very active little bird, seldom delaying long in one spot, and it clings to twigs in all attitudes, upside down as readily as upright. It is fond of the little, white protein bodies of the guarumo or cecropia tree, which it avidly plucks from the brown, hairy cushions at the bases of the long, stout petioles of the great palmate leaves. A number of wood warblers, honeycreepers, and other small birds share these dainty tidbits with it. The birds find them chiefly on trees where they accumulate in the absence of the *Azteca* ants which usually inhabit the hollow stems of this swiftly growing tree and subsist on these little pearily outgrowths.

The spinetail's call or song is most peculiar and distinctive. It is a rapid series of sharp notes, delivered in an indescribable tone that seems forced and artificial. It begins at a fairly high pitch and ascends to notes so thin and sharp that they seem to be at the upper limit of human audition.

SLEEPING

In the Cañas Gordas district where Costa Rica borders Panamá on the Pacific slope, I found Red-faced Spinetails sparingly present between 3500 and 4000 feet. Here, at the end of May, 1964, I discovered one of these birds using as a dormitory a nest of the type described in more detail in the following section. The large globular structure, which appeared to be a foot or more in diameter and was composed on the outside largely of green moss, hung 29 feet above the ground at the end of a slender, drooping, leafy branch, where it was quite inaccessible to me. The tree that supported this nest had grown up in a tract of primary forest which had been thinned and cleared of undergrowth in order to plant coffee, which the remaining large trees now shaded. Close by was an area of heavy, scarcely disturbed forest. As the day ended, the solitary spinetail that slept in this nest would arrive silently and unobtrusively through the treetops and dart into the little round doorway in the side, near the bottom. It entered so swiftly that, unless I kept a sharp watch, I would

miss it. In late May and June, the bird retired at times ranging from 5:40 to 5:50 p.m., or earlier on a dark, cloudy evening. On the morning of June 1, it darted suddenly and silently from the nest at 4:52 a.m., while the light beneath the trees was still very dim, although the sky above was brightening with the light of the approaching sun. A number of the birds of the clearings had begun to call and sing 10 or 15 minutes earlier.

I do not know whether this nest had been built specially for a dormitory, or had been used for breeding or intended for that use. However, while the solitary spinetail continued to lodge here from late May until late June, I never found one of these birds near it in the daytime. In this interval, it evidently served solely as a dormitory.

NESTING

When I found my first Red-faced Spinetail's nest on April 9, 1938, I surmised that it belonged to a becard, for in size, form, and situation it resembled a nest of the Rose-throated Becard. I was greatly surprised when continued watching disclosed that the nest had been built by an even smaller bird. Although the ovenbirds as a family are among the most versatile of avian architects, building cabins of adobe and great castles of sticks, I did not know that they also make pensile structures like this. The newly found nest was built around the leafy end of a slender, hanging branch of a tree that grew beside a small, swampy opening in the woods. It swung, at a height of about 20 feet, above this open space. In form, the great, bulky structure was roughly globular, inclining toward ovoid, for it was somewhat broader near the lower end than it was at the upper extremity. Its diameter was at least a foot and probably more. Composed largely of living moss, the nest was green like the broad leaves of the supporting bough that clustered around it. A number of long, thin pieces of dry herbaceous vines had been used to bind together the moss, and the ends of some of them dangled loosely below the nest.

I could not discover how this mossy globe was entered until I saw a spinetail fly out of the surrounding woods with a tuft of moss in its bill and dart into an inconspicuous opening near the bottom. Continued watching revealed that two birds were adding to the structure. Several times they arrived together, usually with moss, which they took inside. But occasionally one flew up with a long piece of fine dead vine or other fibrous material and gave it a turn or two around the supporting twig. While one spinetail was in the nest in the absence of its mate, it repeated several times the rapid, ascending sequence of fine, sharp notes of which I have already written. At the end of May, I watched another pair work at a similar nest, which was attached to the end of a slender, drooping branch of a scrambling composite of the genus *Eupatorium*, projecting from the general mass of vines and creepers that burdened a cecropia tree at the forest's edge. Here, too, both sexes brought material, but since they were alike in appearance, I could not learn whether the male or his mate took the leading part.

The inaccessibility of the spinetails' nests, the prevailing badness of the weather, and the many other birds that I was then studying prevented my learning as much as I wished about their domestic arrangements. Moreover, the spinetails darted in and out of their hanging homes so suddenly that even with the strictest attention one was likely to lose the sequence of their movements, especially in the mist and rain so frequent in these mountain forests. One morning, when incubation was evi-

dently in progress, a spinetail stayed in its nest for 63 minutes continuously. After its departure, I waited for 20 minutes without seeing a bird enter the nest. Since the rain then falling made observation exceedingly difficult, I watched no longer.

By May 13, my first nest held nestlings which required much brooding. At dawn one of the parents flew out, and a minute later its mate arrived from the opposite direction and entered the nest, where it remained for 9 minutes. Thus both parents were brooding the nestlings as well as feeding them, but the suddenness and swiftness of their entry into the nest made it difficult to see what kinds of food they brought. I recognized only a green larva. A week later, the young in this nest called in high, sharp notes whenever a meal was brought to them. By the end of May, they had flown. At my second nest, the parents were still feeding nestlings as late as July 5.

SUMMARY

The Red-faced Spinetail inhabits humid, moss-burdened mountain forests. Through most of the nonbreeding season it lives singly, but it sometimes associates with birds of other kinds.

Its food consists chiefly of insects and other small invertebrates which it finds in the covering of moss and lichens on the limbs of trees, to which it clings in the most diverse positions. It also eats the protein corpuscles of cecropia trees.

It sleeps singly in nests which closely resemble those used for breeding.

Its call or song is a rapid, ascending series of thin, sharp notes of most peculiar tone.

In the Costa Rican mountains, the spinetail's breeding season extends from March or April into July. The nest, a very bulky, roughly globular structure, composed of green moss bound together by thin, dry herbaceous vines, hangs from the end of a drooping branch well above the ground. The inconspicuous doorway is near the bottom. Both sexes build the nest, brood the nestlings, and feed them.

PALE-BREASTED CASTLEBUILDER

Synallaxis albescens

The Pale-breasted Castlebuilder is a slender, wren-like bird about five and a quarter inches long. In both sexes, the forehead is gray, the crown and hindhead cinnamon-rufous, and the remaining upper parts, including the tail and the remiges, plain grayish brown, with a conspicuous patch of cinnamon-rufous on the wing coverts. The sides of the head and most of the under parts are gray of varying shades, which pales to white on the throat and abdomen and is streaked with white on the chest. In some individuals, the bill is wholly black; in others, apparently adult, the upper mandible is black and the lower gray with a darker tip. The eyes are yellowish brown. The legs and toes are pale flesh-color or grayish flesh-color.

This ovenbird, widespread in South America from central Argentina and Bolivia to the Caribbean coast, enters Central America only as far as the middle of the Térraba Valley in southern Costa Rica. Until recently, its extension up the valley from the "savannas" around Buenos Aires de Osa, where it has long been known, was probably prevented by the great stretches of heavy, scarcely broken forest which intervened between this region and the settlements in the basin of El General at the head of the Térraba drainage. With the virtual destruction of this magnificent forest within the last three decades, the spread of the Pale-breasted Castlebuilder up the valley is to be expected. In Costa Rica, the species ranges from the lowlands up to at least 4000 feet in the Cañas Gordas-San Vito region. In Venezuela, it lives as high as 5500 feet (Phelps and Phelps, Jr., 1963:52).

In Costa Rica, the Pale-breasted Castlebuilder inhabits bushy neglected pastures, "savannas" with coarse grass interspersed with scattered low trees and clumps of shrubs, fields covered with low weedy growth, and similar areas. It avoids the higher, denser, vine-entangled second-growth thickets which the Slaty Castlebuilder prefers, but the habitats of these related species overlap and I have found both together. The Pale-breasted Castlebuilder forages on or near the ground, hopping through tangled growth and beneath grass tussocks, where it is difficult to see what it captures; probably, like other species of *Synallaxis*, it is exclusively insectivorous. It exposes itself more often than the Slaty Castlebuilder, not hesitating to fly 50 or even 100 feet across a clear space, which its relative would do only in very exceptional circumstances. Once I watched a Pale-breasted Castlebuilder scratch its head by raising its foot outside its folded wing rather than inside and over the dropped wing, as passerines usually do.

VOICE

The most common call of the Pale-breasted Castlebuilder is a sharp, emphatic *bet chú*, uttered in a dry, rather harsh voice. When I first heard this call it reminded me strongly of that of the Rufous-breasted Castlebuilder of northern Central America. The latter, however, frequently delivers a longer phrase—as, for example, *bet bet bet bet chu*—whereas the Pale-breasted Castlebuilder seems invariably to limit itself to two notes. Its disyllabic phrase, however, may be repeated incessantly for many minutes together. I timed one bird which called tirelessly, at the rate of 36 to 41 *bet chú*'s per minute, for 35 successive minutes, during which it delivered

about 1300 of these phrases. Not infrequently this castlebuilder rises to a fairly high, exposed branch to deliver its notes. I watched one which called for a long time while perching conspicuously from 20 to 30 feet up in the open crown of a roadside tree. With each repetition of the *bet chú*, the feathers of the caller's throat stand out



Fig. 18. Looking into the doorway of nest of Pale-breasted Castlebuilder. Near San Vito de Java, Costa Rica, 4000 feet, May 1964.

momentarily, revealing their dusky bases and making a fugitive dark patch where at other times none is seen, or sometimes one that is much fainter.

Another utterance is a low rattle or *churr* which may be long drawn out, and is easily distinguished from the shorter, harder rattle of the Slaty Castlebuilder. There is also a series of sharp, emphatic notes—*bip bip bip bip*—which sometimes precedes the prolonged rattle. Once I heard a castlebuilder use all three of its notes together, first a loud *bip bip bip a bip bip*, then a very prolonged rattle, and finally *bet chú* several times repeated. The *bip* and the rattle seem to be associated largely with nesting activities. Altogether, the Pale-breasted Castlebuilder is a noisier, less retiring bird than the Slaty Castlebuilder.

THE NEST

On December 25, 1937, I found a nest under construction in the neighborhood of Buenos Aires de Osa, at an altitude of 1200 feet. Near San Vito de Java, in early May of 1964, I repeatedly saw a full-grown bird in juvenal plumage which had evidently hatched earlier in the same year, and in the same neighborhood a pair were then building a nest, at an altitude of 4000 feet. A few miles away at Cañas Gordas, a newly completed nest received its first egg on June 1. It is evident that, at the northwestern extremity of its vast range, the Pale-breasted Castlebuilder has a long breeding season, as has also been reported from South America.

The nest at Buenos Aires was 3 feet up in a tall tussock of coarse grass in a bushy pasture. That near San Vito was 5 feet up in a tangle of calinguero grass (*Melinis minutiflora*) growing over a thorny *Solanum* bush in a neglected pasture. The nest near Cañas Gordas was 27 inches above the ground in a small bush overgrown with calinguero grass and vines, in a narrow strip of bushy roadside growth, between two open pastures.

At two of these nests, I saw both sexes building. Like other species of *Synallaxis*, the Pale-breasted Castlebuilders are indeterminate builders, continuing to add to their nest until the eggs hatch. The structure, composed chiefly of straws, fine sticks, and the like, consists of two parts, the nest proper, which has the form of a squat tower, and the entrance tube, which projects horizontally from the rounded chamber that occupies the lower part of the tower. In a nest from which the eggs or nestlings had vanished, the upright part was 7 inches high by about 6 inches in diameter. This contained the nearly spherical nest chamber, which was about 4 inches in diameter, and was covered above by a thatch about 1 inch thick. The straight, horizontal entrance tube that led into the side of this chamber was about 6 inches long, so that the whole structure was about 12 inches in horizontal length, 7 inches in height, and 6 inches in greatest width. The dry straws and pieces of slender weed stems of which the nest was chiefly made were mostly under 5 inches in length. Very few were as much as 6 inches long, although here and there was one that measured 7 inches in length, but hardly $\frac{1}{16}$ inch in thickness. These pieces had been carefully interlaced to form a firm, cohesive fabric, through which little light passed.

The thatch over the chamber of this nest consisted of coarse grass blades and straws, some with roots attached. The round opening at the outer end of the entrance tube was surrounded by the bases of grass plants with roots attached, forming a bristly collar. The bottom of the chamber was lined with fine, irregular fragments of downy leaves, the stellate pubescence of which clearly indicated that they had come from the same species of *Solanum* that supported the nest, if not from the supporting bush itself. When I carefully sorted over the materials of this abandoned nest, I found two of the large ventral scales of a snake and another small fragment of snakeskin.

Such was the rather elaborate structure of this nest when I found it deserted, three weeks after the eggs were laid. At the time of laying, however, it lacked some of the refinements just described. There was no bed of downy leaves, so that the newly laid eggs rested on the unlined floor of the chamber. There was scarcely any thatch above the chamber, to shed the hard rains of this season, and the entrance tube still lacked the bristly collar.

Another nest was 12 inches high, 11½ inches long, and 6 inches wide at the chamber. It contained fewer straws but more fine, dry weed stems and woody

twiglets, some of which the builders broke directly from shrubs, although other materials were gathered from the ground. The entrance tube, instead of being straight as in the first nest, was at its end bent strongly to the right (of an observer looking into it), a curvature that was caused by an obstruction in the line of the tube's axis. The opening was surrounded by the bases of small herbaceous plants with many short, stiff roots attached, forming a tangled, flexible mass which, without permanently altering its shape, I could bend far enough to the left to look down the tube and see the contents of the chamber. I do not know the function of this bristly collar, which I found on both nests, unless it be to discourage the entrance of certain small predators. At this nest, as in the first, the lining of downy leaves and the thatch above the chamber were not added until after the eggs were laid. A few scraps of snakeskin and a piece of colorless cellophane were tucked into the outside of the entrance tube. The shed skins of snakes and lizards are prominent in nests of the Rufous-breasted Castlebuilder and, to a lesser degree, in those of the Slaty Castlebuilder.

I am uncertain whether the makers of the nests just described deserve the name "castlebuilder" that I first applied to the Rufous-breasted and the Slaty species, which construct decidedly more massive nests, composed of coarser twigs and, at least in the case of the Rufous-breasted Castlebuilder, more elaborate in form. In other parts of its extensive range, however, the Pale-breasted Castlebuilder may build nests considerably bulkier, and apparently also of stronger texture, than the few which I have seen in Costa Rica. In the Orinoco region of Venezuela, Cherrie (1916:258-259) found nests of this species that were 16 to 20 inches in length, and composed of dry, thorny twigs, up to 5 inches long, which had been interlaced into a fabric that was hard to tear apart.

THE EGGS

In nests of the Rufous-breasted and Slaty castlebuilders, I could never see the eggs without making a small opening in the side of the chamber, which I closed as well as I could, and which afterward the birds sealed more perfectly. At two nests of the Pale-breasted Castlebuilder, however, I could view the eggs by pushing a small mirror, attached to a slender stick, down the entrance tube and applying one eye to the opening. Accordingly, I could learn with far less disturbance of the nest when the eggs were laid.

In the first of the nests described above, I was surprised to find an egg at 7:40 a.m. on May 11, when the structure seemed far from finished. The second egg was laid between 5:00 p.m. on May 12 and 6:30 next morning. This egg, which completed the set, was evidently laid early in the morning, two days after the first.

At the second nest, the first egg was present at 7:10 a.m. on June 1, having been deposited since the preceding evening. No egg was laid on June 2. Since no bird emerged when I gently shook the nest at 5:40 a.m. on June 3, I concluded that no bird was within and proceeded to examine the interior. But as I pushed my mirror down the tube, a castlebuilder rushed out, brushing my face as it flew off. Apparently this was the female, about to lay her second egg, early in the morning two days after the first was laid, and the fright I then gave her caused her to drop it elsewhere. For at least five days, this egg remained alone, incubated sporadically by the parents, who also continued to build up their nest. Then, between June 8 and 17, two more eggs were laid, making a total of three, which at the latter date the

parents were incubating with full constancy. Doubtless, but for my unfortunate disturbance, the set in this nest would have consisted of two eggs, as at the first nest. Probably this should not be considered a case of indeterminate laying, but of laying another set in a nest in which one egg of the previous set remained.

In these two nests, the eggs were pure white, without markings. In Venezuela, the Pale-breasted Castlebuilder lays 3 eggs that are uniform pale greenish in color (Cherrie, 1916:258). In Trinidad, the species lays 2 or 3 eggs which are dull greenish white (Belcher and Smooker, 1936:801). These authors state that the castlebuilder is parasitized by the Striped Cuckoo.

INCUBATION

At the first nest, the first egg was incubated little during the two days before the second appeared, and even as late as the third day after the completion of the set, the parents were most neglectful—on this day they were absent continuously from 5:15 to 7:15 a.m. At other times, however, I could tell that one was in the nest by the call of *bet chí* that issued persistently from it.

While the second nest contained only one egg, the parents were exceedingly voluble. It was at this time that I heard one of them call *bet chí* for 35 minutes with hardly a break. Part of this series of about 1300 calls was delivered while the caller was inside the nest. From time to time, this bird's mate answered the *bet chí*'s with the long rattle. On other occasions, I heard the long rattle issuing from the nest. But the castlebuilders spent little time with the egg—only 32 minutes between 7:15 and 9:40 on June 8, for example. At intervals one of them went over the outside of the nest, devoting a minute or two to pulling up falling pieces and putting the structure in order. From time to time, they brought additional materials to the nest, including many pieces for the thatch above the chamber, the thickness of which was increased by 3 inches in the interval between the laying of the first egg and my discovery that three eggs were present. Among the materials added to the thatch were flattish scraps of wood and bits of bark, as well as twigs thicker than those in the walls. The castlebuilders also found fragments of snakeskin to stuff into crevices about the nest.

One morning while I watched, a Southern House Wren approached stealthily through the surrounding herbage, examined the exterior of the nest, filled its bill with bits of snakeskin that had been tucked into the outside of the tunnel, entered the nest with its plunder, then promptly emerged to fly away with the snakeskin, uttering a little *churr* as it went. As far as I could see in my mirror, the wren did not harm the egg.

On June 18 and 19, I spent over 12 hours, covering all parts of the day, watching this pair incubate. The male and female regularly alternated in the nest, but I could not always distinguish the sexes. Ten completed sessions of both of them ranged from 29 to 102 minutes, totalled 592 minutes, and averaged 59.2 minutes in length. The eggs were unattended for only three intervals, lasting 27, 18, and 29 minutes and totalling 74 minutes. One or the other member of the pair was in the nest, presumably incubating the eggs, for 89 per cent of the 11 hours made up of sessions and intervals that I timed in full, which alone are used in these calculations.

Usually, the partner arriving to take its turn at incubation flew up and entered the nest in silence, and then a castlebuilder (presumably the other partner) promptly left. Rarely the new arrival would spend a minute or less going over the outside of

the nest and putting it in order before entering, and sometimes the bird just relieved would devote a minute or less to the same task before it left. After it had flown across the road, it might deliver the long rattle, or sometimes the sharp *bip bip bip bip*, but the silence of the birds at this time contrasted strongly with their volubility before they began to incubate in earnest. While I made the record given above, I saw them bring only three pieces of material as they came to incubate; the only piece that I could identify was a green leaf. Once one of the partners carried a piece of snakeskin from the nest when it ended its turn on the eggs. After they started to incubate, these birds gave far less attention to tidying their nest, bringing new materials, and shifting around those already present, than do related species with larger and more elaborate nests, such as the Rufous-breasted and Slaty castlebuilders.

This nest was above a low bank beside an unpaved road used by jeeps and heavy trucks, but the incubating castlebuilders were not disturbed by the noisy passage of these vehicles, sometimes with loudly clanking tire chains, only 4 yards from where they sat in their snug chamber. My sojourn in this region ended before they hatched their eggs.

SUMMARY

The Pale-breasted Castlebuilder lives near the ground in weedy fields, bushy pastures, and similar areas of low, tangled vegetation. In Costa Rica, at the northwestern extremity of its vast range, it occurs upward to about 4000 feet above sea level.

It is a noisy bird, with a variety of dry, rather harsh notes which at times it repeats with amazing persistence. Its repertoire includes a low rattle or *churr* which may be prolonged.

In Costa Rica, the breeding season extends from late December to at least July. The nest is built by both sexes in a tussock of coarse grass or in a shrub overgrown with tangled grass or vines, from two to five feet above the ground. The structure, composed chiefly of straws, fine twigs, and the like, is simpler than that of some other castlebuilders. It consists of a closed chamber and a long, horizontal entrance tube. Above the chamber is a thick thatch of coarse material that sheds the rain. The floor is lined with fragments of downy leaves that are brought chiefly after the eggs have been laid. Usually a few bits of cast snakeskin are present in the structure. These birds are indeterminate builders and continue to improve their nest during the period of incubation.

Two pure white eggs are laid, early in the morning on alternate days. One female, interrupted when about to lay her second egg, after an interval of some days laid another set of two in the nest which still contained her first egg. All three eggs were incubated together.

Both sexes incubate. During 11 hours, ten sessions by both members of a pair ranged from 29 to 102 minutes. There were only three intervals of neglect, and the eggs were covered for 89 per cent of the time. While incubating, these castlebuilders became far more silent than they had been, and they devoted much less attention to tidying their nest and bringing new material than do castlebuilders with more elaborate structures.

SLATY CASTLEBUILDER

Synallaxis brachyura

The Slaty Castlebuilder is a slender bird about six inches in length. Its plumage is predominantly slaty and deep olive, more brownish on the back than on the under parts. There is a patch of bright rufous-chestnut on the crown and hindhead, and another area of the same color covers much of each wing. The deep gray throat is streaked with white, and a darker patch separates it from the chest. The rather long brown tail is nearly always frayed and worn, with the shafts conspicuous because the vanes are so thin and tattered, a consequence of the bird's constant passage through dense vegetation. The eyes are dull red. The short, slender bill is black. The legs and toes appear jet black in some lights and blue-gray in others, a color change which results from their high gloss. The sexes are alike in appearance.

In Central America, this is the most widespread member of its genus, and it ranges from northern Honduras (where I once saw a single individual near Tela) southward through Nicaragua, Costa Rica, and Panamá, and through Colombia to western Ecuador. It is abundant in the wet Caribbean lowlands and foothills of Costa Rica and Panamá. On the Pacific side of Costa Rica, it seems not to occur in Guanacaste, where the dry season is long and severe, but in the rainier region south of the Gulf of Nicoya. It is very abundant in the Térraba Valley. It extends upward to at least 3000 feet above sea level on the Caribbean slope and to nearly 5000 feet on the Pacific slope of southern Costa Rica. Apparently it breeds wherever it is found.

The Slaty Castlebuilder is most at home in vegetation that is low but dense. It becomes abundant in grain fields that have rested a year or two and are encumbered with bushes and vines that form a head-high tangle, through which a man can hardly force his way. As the second-growth develops a higher and denser canopy of foliage, resulting in a sparser stand of herbage on the more deeply shaded ground, the castlebuilders desert it in favor of newer and lower growth. They frequent neglected pasture lands where the grass and weeds are dense and high, but they are absent from clean, close-cropped pastures, whether these are shady or open to the sunlight. In more intensively cultivated districts, they are confined to bushy hedgerows and riverside thickets. They never enter the forest.

The Slaty Castlebuilders are paired throughout the year. So closely do the birds keep themselves concealed in the low, dense vegetation that it is most difficult for the birdwatcher to convince himself of this fact through visual evidence alone, but I have heard the answering calls of mates out of sight of each other too often to doubt that they stay together at all seasons. In January 1936, a pair roosted in the tall molasses grass (*Melinis minutiflora*) and pokeberry bushes (*Phytolacca rivinoides*) which densely covered over an old maize field in a forest clearing. While studying birds in this clearing, I often heard the castlebuilders as they awoke at dawn. The first to wake up called with a throaty rattle and was promptly answered by the mate, which, to judge by the sound, roosted a short distance away. In the evening, I sometimes heard the pair communicating as they went to rest. I searched in vain for a dormitory nest, and I believe that this species, like the Rufous-breasted Castlebuilder, fails to make use of its elaborate nest for sleeping but rather hides in dense stands of grass, or in bushes.

On the hilltop behind our house one morning in July, I heard the harsh rattle of some Slaty Castlebuilders. Presently one perched in the midst of a small orange tree, with its head bent down and inward until its bill almost touched its breast, and the feathers of its head and neck all standing out. This bird's mate then came and perched beside it to nibble at the outfluffed plumage of the head and neck. After performing this service for a while, the second bird picked up a stick from a small accumulation of them in a crotch of the tree close by the point at which this episode occurred. The first bird continued for a while to hold its head down and its feathers erected, as though it desired more of the same attention, but its mate preferred to move the sticks.

This is the only instance of allopreening that I have witnessed in the ovenbird family, but the apparent rarity of this behavior may be due simply to the difficulty of surprising these elusive birds while they are engaged in their less common activities.

FOOD

The castlebuilders' diet consists largely, if not wholly, of insects, spiders, and other small creatures. The birds forage low in dense vegetation and it is extremely difficult to watch them, except at times toward the end of a severe dry season, when many of the leaves have fallen and the thickets are more open. Then they may be seen for brief intervals as they hop over the ground and through the lower branches of bushes and examine the curled dead leaves, which they sometimes pick up to extract anything edible that lurks within.

Once, while I sat in a blind before a nest of the Orange-billed Nightingale-Thrush, I watched a castlebuilder foraging through the thicket. Reaching the nest while the thrush was absent, the castlebuilder pecked at the mossy side of the open cup; then it stood on the rim and looked down for a moment at the two brown-flecked, blue eggs. Then, of a sudden, it drew back its head and brought down its sharp bill hard against one egg, piercing the shell. The damage done, it at once continued on its way through the thicket. On returning to her nest, the nightingale-thrush immediately noticed the perforation in the shell, and appeared to sample the contents of the broken egg, for she moved her bill mincingly, as though drinking. She sat for nearly 20 minutes on the damaged egg along with the whole one, then rose up, carried the former away, and in a few minutes returned to resume incubation of the single remaining egg.

Why did the castlebuilder pierce the thrush's egg? It was obviously not for the purpose of devouring the contents, for the bird went away as soon as the injury had been inflicted. I do not believe that simple destruction was the motive, for then it is probable that the castlebuilder would have broken both eggs. If, as I believe, this was the same individual that later came very close to the blind, it was a young bird, which possibly had never before seen an egg. Attracted by the shiny blue objects in the nest, it was perhaps moved to investigate them.

VOICE

Although a melodious song has been ascribed to the Slaty Castlebuilder, this observation was almost certainly erroneous. The common call is a throaty, rattling *churr*, uttered by both sexes and used by the mated pair to keep in touch as they forage through dense vegetation where they are mutually invisible. Castlebuilders

also have a sharp, chipping note of peculiar intonation, somewhat sharper than that of the Mourning Warbler, which during the northern winter is abundant in the castlebuilders' habitat. At times this short monosyllable is repeated rapidly many times over.

NEST BUILDING

In El General the Slaty Castlebuilder has a long breeding season. Some begin to build before the middle of January, and some still have eggs in October. Their bulky nest needs a broad foundation and is placed in a bush or small tree with close-set branches or in one overgrown with a tangle of vines that provide additional support. At times, the flat top of a low stump is selected, because of the firm foundation that it offers, but to be acceptable the stump must be surrounded by water sprouts or else overgrown by bushes and vines. The nest site is usually in such low, dense vegetation as these birds frequent, but often it is beside a path or a small opening in the midst of the thicket, or at its edge, or in a bushy hedgerow between open fields. Sometimes it is in a tree with dense foliage standing in a clear space, some yards from the dense vegetation that the castlebuilders prefer. The nests that I have seen ranged in height from 1½ to 15 feet above the ground.

Although somewhat less complex in form than the nest of the Rufous-breasted Castlebuilder of northern Central America and southern México, that of the Slaty Castlebuilder is almost as bulky, and its construction is a great undertaking for a pair of birds hardly larger than house wrens. The nest consists of two parts: a roughly globular chamber, completely enclosed by substantial walls of fine sticks and covered by a high, thick roof, the whole often having the form of a low, round tower; and an entrance tube or tunnel that leads into the side of this chamber and is usually more or less horizontal but may be inclined sharply upward, if the supporting bough takes this direction. One nest with an upwardly-directed tunnel had roughly the form of a large coffee-pot with the spout twisted to the left, as though bent by a fall. A typical structure measured 14 inches in height at the end that contained the chamber, which was 9 inches in external diameter. The overall length (from the end of the tunnel to the back of the chamber) was 17 inches. The tunnel extended out from the wall of the chamber for 8 inches, but taking into account the thickness of this wall, the narrow, tubular passageway which the birds traversed when entering or leaving the nest was 13 inches long.

The walls of the chamber and tunnel were constructed wholly of small dead twigs, some of which were thorny. The great majority of these twigs were between 2 and 6 inches in length. Few exceeded 8 inches, although one, which was very light and slender, was exactly a foot long. The thickest twigs were ⅜ inch in diameter. A few of them were branched. These sticks were carefully interlaced to form a fabric which was thick and dense for the walls of the globular nest chamber yet lighter and more open for the tubular entranceway. This nest rested on a branch of a small tree on an islet in a river. It was just beneath the vines that densely canopied the thicket which covered the islet. Some of the thinner vines were built into the walls of the nest, giving it strength and stability. The tunnel, supported entirely by two slender vines, was much curved in both the horizontal and vertical planes. The entrance tubes of some nests, however, are so straight that one may look down their length into the nest chamber. The number of sticks contained in the nest was very

great; there were hundreds if not thousands of them. Immense labor had been expended in seeking them out, carrying them up to the nest, and pushing and pulling them about until they fitted closely together in a coherent whole.

The ceiling of the chamber, like the walls, was made of small sticks fitted closely together. Above this was piled at least a hatful of broad, dry grass blades, with a few lengths of partly decayed grass stems, to form a thick thatch that would shed the rain. Many of the grass blades were from the Job's-tears (*Coix lacryma-Jobi*)



Fig. 19. Nest of Slaty Castlebuilder in an orange tree. The entrance is at the right. The ruler below the nest is one foot long. Near Almirante, western Panamá, May 22, 1929.

that formed tall, dense clumps along the river banks. The depth of material above the chamber, in part the ceiling of sticks but chiefly the thatch of grass blades, was 7 inches, half the total height of the nest.

This relatively enormous edifice of sticks was not so much a nest as a house built to contain a nest. The nest proper was the hemispherical lining of the lower half of the chamber. The diameter of this cup was about $2\frac{1}{2}$ inches. It was composed wholly of downy leaves which had been plucked while green and bitten or torn into fragments. Some of the fragments were very small and most had a jagged, irregular outline. These bits of leaf were joined by a liberal amount of cobweb into a fabric which with care could be lifted entire from the opened chamber of sticks. The long-rayed, stellate pubescence on the fragments of leaf revealed that they had come from the "berenjena" (*Solanum diversifolium*), a white-flowered, thorny

shrub very common in the low thickets where the Slaty Castlebuilders dwelt. Wherever available, the downy leaves of this or a related species of *Solanum* are preferred for the nest's lining. Although the Rufous-breasted Castlebuilder constructs the larger and more elaborate edifice, it devotes less care to the nest proper or lining, merely laying small downy leaves loosely on the bottom of the chamber, not binding them together with cobweb as its southern relative does. Both species of castlebuilders may lay their eggs when the lining of leaves is hardly thick enough to prevent their touching the hard sticks on the bottom of the chamber. Sometimes they even lay their eggs when there is no lining. They continue to bring fresh leaves and build up the downy bed while incubation is in progress.

This nest contained a single fragment of snakeskin, which had been stuffed into the wall at the point where I had earlier opened it to examine the eggs, and in addition there was a shred of lizard skin. Other nests contain far more of these materials, stuck into the walls or at times lying in the chamber beside the eggs. The Slaty Castlebuilder does not search for the exuviae of reptiles nearly as assiduously as does its rufous-breasted cousin in the north, nor does it carpet the floor of the entrance tunnel with them.

A most unusual nest of the Slaty Castlebuilder, found at the end of August of 1944, was provided with two entrances, leading out from opposite sides of the same central chamber. Each was the usual long, tubular hallway. From end to end, this nest measured 22 inches, and its height was 12 inches. It was unlined when I first saw it, and apparently it never contained eggs. Nests built late in the year are often smaller and have thinner walls, shorter entrance tubes, and, despite the heavy rains at this season, less thatch than those made for first broods.

At an early stage of construction, the castlebuilders' nest is an open cup of small sticks, such as, when lined, would satisfy most birds as a receptacle for their eggs and young. On April 14, 1957, I found a nest at this stage and followed its progress. By April 19, the walls of sticks had been built upward and inward, with an outward extension at one side, the first indication of the future tunnel. By April 21, it had been lightly covered over, converting it into a roofed chamber, and a few sticks had been laid over the lengthening extension that was to form the tunnel. By April 24, both the chamber and the tunnel were well covered with sticks, but there was still no thatch. By April 26, some coarse thatching had been placed above the chamber. Two days later, there was more coarse material on the roof. Between May 2 and 4, an egg was laid in the chamber, which was still without a single piece of green leaf. Some fragments of snakeskin lay on the bare sticks beside the egg, and other shreds were stuck into the outside of the nest. On the afternoon of May 5, I found at least two small pieces of green leaf in the chamber with the single egg, and the thatch had been made a little thicker. The following afternoon, two eggs rested on a few green leaves. In the succeeding days, while the eggs were being incubated, there was an increase in the accumulation of leaves on which they rested and in the number of fragments of reptile skin stuck into various parts of the nest. From my discovery of the nest in the cup stage to the laying of the first egg, 20 days had elapsed, but the nest had been started some days before I found it, and it was by no means finished when laying began.

As in the Rufous-breasted Castlebuilder, the male and female Slaty Castlebuilders construct the nest together. Although, in my experience, they are somewhat less confiding than their northern relatives, they will often proceed fearlessly with their

building while a man stands or sits unconcealed only 2 or 3 yards away. The twigs which the castlebuilders use are generally found on or near the ground some distance from the nest, and considerable skill is displayed in maneuvering these stiff pieces, often longer than the bird itself, upward through close-set, obstructing stems and vines. On reaching the nest, much labor is expended in pushing and pulling each piece into place, so that it interlocks with the other sticks to form a compact fabric. While toiling at their nest, the castlebuilders call back and forth with a rattling *churr*. In $2\frac{1}{4}$ hours, the members of one pair made 30 visits to the nest, each time bringing a single twig. A few days later, when they were building more actively, they brought 12 contributions in 30 minutes.

I once found a nest under construction at the beginning of October, at the height of the rainy season, but as far as I could learn, the birds did not incubate in this nest.

THE EGGS

I have found far more nests of the Slaty Castlebuilder than I have opened to examine the contents, and I have peeped into the chamber through a small aperture in the wall more often than I have made a larger gap to remove the eggs for measurement. Each time that I examined the interior of a nest, I closed up the hole I had made as well as I could with small sticks, and after I went away, the birds returned and by working in more twigs quite obliterated the opening. But with birds of all kinds, unmolested nests appear to fare best; hence I have not investigated the contents of a large number of nests of the castlebuilder.

Each of 23 nests contained two pure white eggs. The second egg is laid before 7:30 a.m., two days after the laying of the first egg. The measurements of six eggs average 21.5 by 17.0 mm. Those showing the four extremes measured 22.2 by 17.1, and 21.0 by 16.7 mm. Carriker (1910:636) stated that "from two to three eggs are laid," and he gave measurements very much the same as the foregoing.

In 24 nests in the valley of El General, 2000 to 3000 feet above sea level, eggs were laid as follows: January, 1; February, 4; April, 3; May, 4; June, 3; July, 3; August, 4; September, 2. The absence of records for March seems significant and is probably caused by the growing scarcity of insects as the dry season progresses.

INCUBATION

In 1936, I watched a pair of castlebuilders at an early nest, the two eggs of which were being incubated when I first saw them on February 7. This was the nest, already mentioned, situated on an islet in the Río Buena Vista. Although I was only about 12 feet from the nest and made no attempt to conceal myself, the castlebuilders went about their activities without appearing to notice my presence.

Since the male and female were alike in appearance, my first effort was to place a distinguishing mark on one or both of them. I wrapped a small tuft of cotton about the end of a twig, saturated the cotton with white paint, and stuck the twig into the loose sticks surrounding the mouth of the entrance tunnel, so that the paint-soaked cotton projected into the passageway. Several times the birds brushed past it as they entered or left the nest, but they acquired only faint white spots, difficult to detect as they flitted through the bushes. Annoyed by the presence of the "paint-brush" in their doorway, the castlebuilders tugged at it whenever they encountered it on entering or leaving, until finally one of them managed to pull it loose and

flew away with it. Twice I placed "paintbrushes" in the mouth of the tunnel, and twice the castlebuilders carried them away.

Since this stratagem for marking the birds did not prove satisfactory, I varied my procedure. Cutting a slender stick about 7 feet in length, I converted its thinner end into a "paintbrush" in the manner already described. Then I quietly approached the nest and held the paint-soaked end of the wand in the entrance tunnel. Next I shook the branch that supported the nest, to make the bird come out and, I hoped, bump into the paint in passing. But it managed to slip by the obstacle without acquiring any noticeable stain. Instead of flying away, as a more timid bird would have done, the castlebuilder hopped and flitted around the nest, close to the white end of the wand which I still held up, uttering a short note of irritation, and approaching to within 2 or 3 inches of the intruding object, in a manner that seemed half inquisitive, half belligerent. Indeed, several times it came so close to the tuft of cotton that I attempted, by means of a short and rapid movement, to touch it with the end of the stick and so place the desired mark, but it always flitted aside just in time to avoid contact.

One member of the pair, however, had acquired a white mark at the base of its bill, over its nostrils. I dubbed this bird "Spot," and since this was the one that incubated by night, it was probably the female. The other, whose tail was exceedingly ragged and frayed, I called "Tattertail."

Morning and afternoon, I devoted ten hours to watching "Spot" and "Tattertail" attend their nest. "Tattertail," the supposed male, took nine sessions on the eggs, ranging from 4 to 44 minutes in length and averaging 27.7 minutes. "Spot" sat in the nest eight times, for periods varying from 18 to 44 minutes and averaging 31.1 minutes. The total time spent in the nest by each partner in the 10 hours was exactly the same, 249 minutes, but since "Spot's" sessions averaged slightly longer than her mate's, if I had timed an equal number of turns on the nest by each, the result would have come out in her favor. Further, she took the long night session. The nest was left unoccupied for five periods, ranging from 2 to 27 minutes and totalling 50 minutes. The two parents together kept the eggs covered for 90.9 per cent of the 10 hours.

Often the castlebuilder arriving to take its turn at incubation hopped over the outside of the nest, sometimes making its circuit again and again, and crawling through the narrow passageway formed by some twigs that projected from the wall of the chamber and touched the top of the tunnel. Then it entered the tunnel, and a few seconds later the mate which had been sitting would emerge. At other times, the bird coming to take its turn at incubation entered the tunnel directly, without a preliminary inspection of the outside of the nest. The changeover was usually accomplished in silence, more rarely with the utterance of the rattling *churr*.

Like the Rufous-breasted Castlebuilders, these birds continued throughout the period of incubation to devote considerable time to the physical structure of their nest. However, they did not give as much attention to their nest as do members of the northern species. Nearly always, when arriving to incubate, the Slaty Castlebuilder brought either a piece of downy green leaf for the lining, or a web of cobweb for binding these leaves together. Special trips were made to fetch dry grass blades for the thatch and sticks for the structure in general; these were rarely brought when the bird came to replace its mate on the eggs. The castlebuilders worked fresh twiglets into the wall at the point where I had separated the sticks for the purpose

of looking inside, continuing for days to be preoccupied with the site of this breach, although to my eyes it had long ago been perfectly mended. Some tufts of spider's cocoon were tucked into the wall at this point and also occasionally elsewhere, but most of this material was taken inside. Later, when they found a large fragment of cast snakeskin, the castlebuilders stuffed this, too, into the outer wall at the point where I had opened it.

Compared with Rufous-breasted Castlebuilders, these birds took little interest in reptiles' exuviae, but devoted more attention to hunting spiders' cocoons, a material which the northern species appears not to use in its nest. Not only did these Slaty Castlebuilders take many things into the nest, but occasionally, at the end of a period of incubation, one emerged with a twig or a shred of withered leaf in its bill, and deposited it on the outside before it flew away.

This pair of Slaty Castlebuilders did most of their repair work and routine inspection in the late afternoon. In 5 hours of the morning, they kept their eggs constantly attended, except for one period of 2 minutes when both were absent. But in 5 hours of the afternoon the eggs were left uncovered for four periods which totalled 48 minutes, during most of which time both parents attended to the nest itself. Sticks from the walls and tunnel and blades of grass from the thatch were constantly slipping down and had to be pulled up and tucked into place. New materials were brought for both roof and walls. On two evenings, the castlebuilders engaged most actively in tidying and repairing their nest after sunset, when the Gray-capped and Vermilion-crowned flycatchers which roosted on the islet had already congregated in the tops of low trees. The castlebuilders continued to be very busy with their housekeeping, going over and over the nest, pushing in a stick here and there, now and again flying off to bring a fresh bit of material, until the light became so dim that I could hardly follow their movements. At last, when it was nearly dark, "Spot" retired into the nest to warm the eggs, while "Tattertail" flew away, doubtless to roost in a bush.

On another day, I found "Spot" busily engaged in putting the materials of the nest in order in the middle of the afternoon. When relieved of incubation by "Tattertail" at 5:23 p.m., she devoted 9 minutes more to arranging things. Her chief concern now was pulling up on the roof and tucking into place the dry grass blades that were constantly slipping down. On this afternoon, the castlebuilders did not use the last light of day for tidying their nest, probably because they had attended to this business at an earlier hour. Yet on arriving in the dusk to begin her long night session on the eggs, "Spot" brought a dry blade of grass and added it to the thatch before she went in.

On yet another afternoon, the castlebuilders' activity took the form of ridding their nest of ants. After bringing a piece of material to the structure and going over it thoroughly to tuck loose sticks into their places, "Spot" began to pick small objects from the outside of the nest and the supporting branch. Approaching closer, I saw that a multitude of minute brown ants were swarming up and down this branch. For 10 minutes, the castlebuilder continued intermittently to pick them off in rapid succession with the tip of her slender black bill; whether she swallowed them or threw them aside I could not learn. Later, after the eggs hatched, I watched "Tattertail" pluck minute objects, apparently more of the same ants, from the nest in much the same manner. The vigorous sideward jerk he gave his head after seizing each ant in his bill indicated that he threw it aside rather than swallowed it.

In the tropics as well as at higher latitudes, many nestlings are destroyed by ants, but only rarely have the parent birds been seen attempting to rid their nests of these invaders. Mickey (1943:204) watched a female McCown Longspur picking ants from the young and nest. Warham (1954:138) saw Splendid Blue Wrens spend about half an hour plucking off small red ants that were swarming up through the vegetation toward their nest and nestlings. I once watched a Gray-capped Flycatcher remove ants from the doorway of her nest. In Ecuador, a pair of Lafresnaye Piculets busily picked termites from around the entrance of their nest cavity in a dead trunk. But ants sometimes swarm over a nest in such myriads that the utmost efforts of the parent birds could hardly save the nestlings from them.

More than 21 years later, in early May of 1957, I again watched a pair of incubating castlebuilders at a nest that was more favorably situated for observation than most, because the small, vine-draped tree which supported it stood almost alone in a fairly clear space in dense second growth. By putting a little improvised paintbrush in the entranceway, I gave one of these birds a white streak on its slaty breast. Since this bird occupied the nest by night, I called it the female. In over 17½ hours of watching, covering all parts of the day, I timed 28 completed sessions by both sexes. These ranged from 2 to 120 minutes in length and averaged 25.2 minutes. The eggs were unattended for 12 periods, ranging from 1 to 48 minutes and averaging 13.0 minutes. Only one of these periods of neglect was longer than 22 minutes, and most were considerably shorter than this. During the active period when changeovers occurred, the eggs were incubated 81.9 per cent of the time. But these castlebuilders ended their day very early, and at 4:11 on a rainy afternoon the female began her long nocturnal session, which continued until 5:34 next morning. This whole interval of 13 hours and 23 minutes was excluded from the record used for computing the percentage of constancy. After being relieved by his mate at 4:11 p.m., the male disappeared for the remainder of the day.

Because of poor light on a cloudy afternoon, I sometimes failed to distinguish the sex of the castlebuilder which entered or left the nest. To compare the parts taken in diurnal incubation by the male and female, 5½ hours of the above record must be excluded, and only 12 hours are available. In these 12 hours, the male took 12 sessions, ranging from 2 to 120 minutes in length and averaging 33.8 minutes. The female took nine sessions, ranging from 9 to 42 minutes in length and averaging 22.6 minutes. The male took two sessions of over an hour and four which continued more than 50 minutes, whereas the female's longest diurnal session lasted only 42 minutes. But to compensate for her mate's greater assiduity in sitting in the morning and early afternoon, she began the night session at least 2 hours before most of the surrounding diurnal birds became inactive in the evening. In this respect, these castlebuilders nesting in the rainy month of May differed strikingly from the earlier pair, which nested in the dry month of February. The latter, it will be recalled, sometimes continued to put their nest in order in the waning light of evening, and the female did not retire until it was growing dark.

The castlebuilders observed in May incubated most constantly in cool and cloudy or rainy weather. When it was bright and warm they sat for shorter intervals and devoted more time to bringing materials and tidying their nest. Yet just after mid-day they incubated for rather long periods and gave relatively little attention to the nest itself, despite the sultry heat produced by the sun shining through a thin canopy of clouds. In sitting more constantly in cool weather and in adding to their

nest when it was bright and warm, the castlebuilders resembled the Black-eared Bush-tits that I studied in the Guatemalan highlands, where daily extremes of temperature were far greater than here at only 2500 feet above sea level.

In 15 hours of active attendance at their nest, this pair of castlebuilders brought green leaves for the lining 16 times, coarse material for their thatch four times, snakeskin twice, one stick, and unidentified objects six times, making 29 additions. This does not include the fallen materials which they retrieved from the tangle of vines directly beneath the structure (never from the ground) and carried back to it. Moreover, they devoted much attention to tucking in pieces that were slipping from the nest and to tidying their elaborate edifice. This work was usually done by the bird which had just been relieved from a spell of incubation by the arrival of its mate, but sometimes the incubating bird would emerge without waiting for relief and turn its attention to the nest. Rarely both partners were so occupied simultaneously. Very often, however, one remained inside until its mate had entered; low rattles emanated from the nest, and then the other partner emerged. Sometimes the castlebuilder in the nest would rattle loudly in response to its mate foraging out of sight.

At one nest, both eggs hatched 18 days after the last was laid. At the earliest nest that I have ever seen, one egg was present on January 11, 1969, and the second was laid before 7:30 a.m. on January 13. One nestling hatched between 5:10 p.m. on January 31 and 7:15 a.m. on February 1. The second nestling hatched between 7:15 a.m. and 1:30 p.m. on February 1, after an incubation period between 19 and 19¼ days.

THE NESTLINGS

Newly hatched castlebuilders have tightly closed eyes and pink skin with sparse gray down. A pair with newly hatched nestlings fed them six times in 2 hours, on each occasion bringing a single small insect in the tip of the bill. They also brought a ventral scale of a snake and some fibrous material for the nest. They brooded the nestlings almost continuously, once for 37 minutes without interruption.

At the nest which I watched during incubation in 1957, both eggs hatched between May 16 and 18. On May 20, I watched the nest from 7:20 to 11:20 a.m. Both parents fed the nestlings, but the white mark that I had placed on one of the adults two weeks earlier had grown so faint that I could no longer tell them apart. Together they brought food 20 times in the 4 hours, or at the rate of 2.5 feedings per nestling per hour. On each visit the parent came with a single article held conspicuously in its sharp, black bill. I recognized small insects, larvae, and spiders. I saw no droppings carried out, yet the nest was kept perfectly clean, whence I inferred that they were swallowed by the parents.

When a parent arrived with food while its mate was brooding, it always entered the nest before the other emerged. Assuming that the new arrival consistently stayed to cover the nestlings while the other left, the young were brooded 14 times, for periods ranging from 2 to 24 and averaging 11.4 minutes. The total time devoted to brooding was 126 minutes, and the nestlings were alone for 114 minutes.

Even with nestlings to care for, these parents did not relax their attention to the nest itself. At least three times in the 4 hours, they brought something to add to the nest: once a large fragment of reptile skin, once a piece of leaf for the thatch, and once an unrecognized object. They also spent much time patrolling the outside

of their edifice and tucking in loose pieces, or just idly hopping over it and resting on or near it. Once one of them, after brooding for 2 minutes, tidied the nest for 16 minutes, then entered to brood for 9 minutes more, until its mate came with food. On another occasion, one patrolled the nest for 17 minutes, and again one devoted 6 minutes to arranging the materials on the outside of the structure.

Just as I was ending my watch, a parent emerged from the nest and flew to the ground, where it began to utter very sharp monosyllables, similar to the usual call note but stronger and more insistent. The mate promptly came and called in the same manner. Soon I noticed a slender green snake, possibly 2 feet long, stretched out on a tangle of green vines near the ground. The snake slid deeper into the massed herbage, and the castlebuilders, still scolding sharply, hopped back and forth through the tangle where it lurked, coming very close, if not actually touching it. I could not see whether they pecked the snake. These green serpents are great nest robbers, and to save the nestling castlebuilders I removed it. Almost at once the castlebuilders resumed feeding their young.

The behavior of the castlebuilders toward the snake was different from that toward a gray, crested lizard, nearly a foot in length including its long tail, which for well over an hour clung motionless to an upright twig less than a yard from the nest. The castlebuilders gave no evidence of having noticed the lizard, although it is inconceivable that it escaped their sharp eyes. I inferred from their behavior that they regarded the lizard as harmless, but I chased it away for greater safety. Likewise, the birds paid no attention to the shiny little lizards called "lúcias," even when they crawled over the nest.

When I returned 10 days later, hoping to watch these castlebuilders attend their feathered young, I found their nest empty, and they were already building a new structure about 40 feet away. Whatever took the nestlings made no gap in the wall of the chamber; hence it must have entered through the tunnel. A number of other despoiled nests were likewise intact, but in other instances there was a larger or smaller gap, usually round, in the wall. From this, we may infer that the nests are pillaged by two types of predators, one of which uses the same entrance as the castlebuilders themselves, while the other tears open the side of the nest. The former are probably snakes, the latter, mammals of varying size. If the predator begins to make a gap in the wall, the parent has plenty of time to escape down the tunnel, but if the predator creeps stealthily into the passageway, the parent may be trapped in its solidly built castle. A nest with two entrance tubes, such as I once found, might be preferable, for if a predator entered one tube the bird could escape by the other. It is not probable that the presence of a second opening would increase the nest's vulnerability to predation, for a small animal looking for an entrance would find its way into the nest almost as soon if there were only one entrance as if there were two, and the advantage of the second entrance to the birds is obvious.

One wonders whether parent castlebuilders are often trapped in their laboriously built structures. Yet it seems certain that this cannot happen frequently, for it would so penalize this type of construction that selection would eliminate it. At the same time, one wonders what advantage these bulky nests can have, what enemies they hold aloof from the eggs, the nestlings, or the brooding parents. In all closed nests, the parents appear to run the risk of being cornered, but most such nests are either high and relatively inaccessible, such as the holes of woodpeckers, or in vertical banks difficult to scale, like the burrows of kingfishers. The castlebuilders'

stronghold is just as accessible as any open nest placed in bushes and thickets; it is far more conspicuous, by no means immune to predation, and impedes escape by the parents whenever the predator enters by the birds' own passageway. It is difficult to see what advantages may counterbalance these obvious disadvantages.

My efforts to learn the true length of the nestling period have been frustrated not only by the frequency of predation but by the habits of the young castle-builders themselves. In 1936, I had a nest in which both eggs hatched between June 6 and 8. When I opened the side of the chamber to look in on June 21, one of the young birds retreated down the entrance tunnel. Although feathered, it could not fly well, but it fluttered to the ground and tried to hop away through the sheltering weeds. Catching it without much difficulty, I replaced it in the chamber beside its nest mate. By the afternoon of the following day, both fledglings had left, when 14 or 15 days of age.

On May 18, 1947, I found a nest with one egg and one nestling so recently hatched that its down was still plastered to its skin. I made few visits to this nest because I wanted to disturb it as little as possible. On the afternoon of June 3, an inspection of the chamber seemed necessary, and before making a little opening in the side, I blocked the entrance tube with my handkerchief. Before I could look inside, both young birds retreated down the passageway but were held by my blockade. After closing the chamber, I gently prodded the outermost nestling with a fine twig, to make it return to its nest, but it refused to budge, possibly because the other blocked its way. Despite all my care, the nestling in front darted forth as soon as I removed my handkerchief. It flew about 20 feet without losing altitude and came to rest in a bush. As I approached, it retreated farther into the thicket. The other young bird remained looking out from the entrance of the tunnel until a parent arrived with a large insect, when it hopped out and fluttered to the ground. Without my interference, these young castlebuilders would almost certainly have stayed in the nest until at least the following day, so that we may place their nestling period conservatively at 17 days.

A month later I met, in the thicket near this nest, two young castlebuilders which were evidently the former tenants. The young birds were accompanied by at least one parent. They were confiding and permitted me to follow them closely along narrow cowpaths that wound through the low, dense growth. Now, at the age of about 46 days, the young birds hunted assiduously for themselves but still received an occasional meal from a parent. All foraged through the bushes and vine tangles, up to ten feet above the ground, and investigated curled dead leaves. The young castlebuilders answered the rattle of the parent with a similar but weaker call, and the parent frequently repeated the sharp monosyllable that reminded me of the Mourning Warbler's note but was higher in pitch.

These young spinetails seemed not to have begun the postjuvinal molt and in coloration they resembled feathered nestlings. They lacked the rufous-chestnut patch on the crown, and the rufous area on each wing was paler and slightly less extensive than in the adults. The plumage of the body was much paler than that of the parents, being generally olive above and grayish olive below, instead of slate-color. The young birds likewise lacked the dark, white-streaked throat of the adult. Their eyes were dark, not red as in the adults. I once saw a bird in this juvinal plumage in mid-February.

A breeding season, which, in El General, begins in January and extends to September or even October, provides time for rearing several broods, but just how many any pair produces in a year is unknown.

SUMMARY

The Slaty Castlebuilder inhabits low, dense, secondary vegetation in humid regions from sea level up to about 5000 feet. It lives in pairs throughout the year. Allopeening occurs.

It appears to subsist wholly on insects and other small invertebrates, which it finds while hopping over the ground or amid low vegetation, especially in curled dead leaves.

Both sexes utter a throaty, rattling *churr*, which helps them to keep in contact while they forage in dense vegetation where visibility is narrowly restricted. They also voice a sharp *chip*, which becomes loud and insistent when they are annoyed.

In El General, the long breeding season extends from January to September and sometimes October. The bulky nest is placed in a bush or small, vine-draped tree, from 1½ to 15 feet up. Constructed by both sexes of small, closely interlaced twigs, it consists of a globular chamber entered through a long, tubular, lateral passageway. Above the chamber is a thick thatch of coarse materials, which sheds the rain. The bottom of the chamber is lined with a pad consisting of large and small fragments of downy leaves, usually of *Solanum*, bound together with cobweb. This is added largely or wholly after the eggs are laid. Scraps of cast reptile skin are stuck at various points around the edifice. Nest building may begin three weeks before the first egg is laid; the structure may be still unfinished at that time. Rarely a nest is provided with two entrance tunnels.

Two or, rarely, three white eggs are laid, with an interval of at least two days separating the deposition of the first and second eggs.

Incubation is performed by both sexes, whose daytime sessions rarely exceed an hour and average about 25 to 30 minutes. At one nest, the parents covered the eggs for 91 per cent of 10 hours; at another, they attended the eggs for 82 per cent of 15 hours. Throughout the incubation period, both sexes bring many pieces of green leaf for the lining; spider web to bind them together; coarse material for the thatch; sticks; and bits of reptile skin. They spend much time tidying their nest and retrieving fallen pieces, and they may remove ants from it.

At one nest, the incubation period was 18 days; at another it was between 19 and 19¼ days.

The young are hatched with sparse gray down on pink skin, and they are sightless. Both parents brood them and nourish them with insects and spiders, which are brought, one at a time, in the tip of the bill. Even while attending nestlings, the parents find time to carry a few pieces of material to the nest and to keep it in good repair. Parents protested loudly when they saw a snake near their nest, but they were indifferent to a large lizard very close to it.

Some predators make a hole in the side of the nest, whereas others enter through the tunnel. The former are probably mammals and the latter snakes.

The young remain in the nest at least 17 days and can fly fairly well when they leave. Thirty days after their departure, they forage for themselves but receive an occasional meal from their parents. The juvenal plumage is far less intensely colored than that of the adults.

RUFOUS-BREASTED CASTLEBUILDER

Synallaxis erythrothorax

The Rufous-breasted Castlebuilder is a slender, wren-like bird nearly six inches in length. In both sexes, the upper parts are dull brown, inclining toward gray on the top of the head. The long, slender tail is chestnut-brown. The wings are largely chestnut, which becomes more brownish toward the ends of the remiges. The sides of the head and neck are grayish brown. The white chin and throat are covered with fine, close-set, blackish streaks. A broad blackish band separates the streaked throat from the warm chestnut-rufous of the breast, which color extends to the sides and the under wing-coverts. The abdomen and under tail-coverts are grayish. The eyes are red; the short bill is black; and the legs and toes are grayish.

The Rufous-breasted Castlebuilder inhabits the lowlands of southern México, Guatemala, Honduras, and El Salvador. On both sides of Central America, it ranges upward to about 3500 feet above sea level, in the more humid regions where neglected clearings are overgrown with dense, lush vegetation. Although the castlebuilder is not especially wary of man, the impenetrability of the thickets in which it passes most of its life makes the bird difficult to observe. One cannot follow it into the low, tangled second growth where it lurks without making sufficient disturbance to frighten away the boldest of birds. The castlebuilder's unmistakable notes issue from many a streamside vine tangle in the cleared regions of the Caribbean lowlands of Guatemala and Honduras, but one does not often catch a glimpse of it. Yet on the rare occasions when it forages at the thicket's edge, it often permits the watcher to approach close enough to distinguish its red eyes and the fine dark streaks on its white throat and to notice that the chestnut-brown feathers of its tail are frayed and worn. Although these feathers have earned the designation "spinetail" for this species and its relatives, they are not spinous-tipped like those of woodcreepers and certain other ovenbirds. Sharp-pointed rectrices would be of little use to castlebuilders, which do not climb up the trunks of trees. But often these feathers are so worn and frayed by the birds' constant passage through dense vegetation that the shafts, nearly denuded of their vanes toward the end, appear to terminate in spines.

Castlebuilders subsist on caterpillars, mature insects, and spiders, which they pluck from the foliage in the manner of a wren or sometimes gather from the ground. They vary their diet with small berries.

VOICE

The most frequent utterance of the Rufous-breasted Castlebuilder sounds like *pet chu, pet pet pet pét chu*, delivered with rising inflection and the emphasis on the last *pet*. The final *chu* is shorter and softer. More rarely the bird delivers a rolling *uddle uddle uddle uddle*. A longer utterance, which I sometimes heard from castlebuilders attending nests, sounds like *krr-r krrr-r krr kr kr; wita wita wita wita wita wita wit*. The first phrase was given slowly and deliberately, the second with increasing rapidity. This call, of which I noticed a number of variations, lacked melody, yet was pleasant to hear. At times, especially when their fledglings appear to be in peril, the castlebuilders make a low rattling or knocking sound.

NEST BUILDING

Although I arrived at Alsacia Plantation, in the middle Motagua Valley of Guatemala, in mid-February of 1932 and at once began to search for birds' nests of all kinds, I found none of the conspicuous structures of the abundant Rufous-breasted Castlebuilders until the beginning of April. Then, in the course of three days, I discovered five nests, all recently begun. Some had apparently been started before the end of March. Two years earlier, on the northern coast of Honduras, I had found these birds busy with their nests in May.

The site of the castlebuilders' bulky and elaborate structure is usually a vine-draped bush or small tree. A nearly horizontal limb with numerous lateral twigs is necessary for its firm support, and two or more horizontal branches that are parallel and close together provide an even more satisfactory foundation. Rarely the nest is built in a network of interlacing vines. Most of the 21 nests that I recorded were between 6 and 12 feet above the ground, but two were only 5 feet up, and one was about 20 feet high. Usually the nest was near a stream or at least a trickle of water, but once I found a pair of castlebuilders building in a lime tree near the top of a dry, grassy ridge. When nearly finished, this structure was abandoned, apparently because the birds had found that the locality failed to satisfy their requirements.

The male and female castlebuilders cooperate closely in the construction of their nest. To their chosen site they carry sticks to make a slight platform, to which they gradually add a flaring rim, until the structure becomes an open cup. At this stage, it resembles the completed but still unlined nest of many other birds, but it would be far too wide for the castlebuilders, if they intended to use it in this form.

As the pair of castlebuilders continue to add to their cup, hopping and flitting laboriously upward from branch to branch carrying sticks longer than themselves, they sometimes deposit their burden just a little short of the rim. In this manner they lengthen the rim, on the side from which they habitually approach along the horizontal supporting branch, into a lip or spout. Elsewhere they build the walls of the cup upward and finally inward. As the birds add more sticks to the lip, it gradually lengthens and broadens into a runway, along which they hop with the material that they continue to add to their nest. Meanwhile, as the walls of the cup become higher, they are extended along the sides of the runway, until it becomes a long and narrow trough. They begin to cover the structure at the point where the trough joins the cup, and from here they extend the roof in both directions simultaneously. By this procedure, the cup is transformed into a roughly spherical chamber, with a vaulted rather than a flat ceiling, and the trough is gradually converted into a tunnel.

The diminutive birds seek on or near the ground the dead and often thorny twigs which they require for their nest. Those which they select are sometimes twice and rarely three times the castlebuilder's length of nearly 6 inches. The thickest sticks are about $\frac{1}{4}$ inch in diameter. The heavier ones weigh two and rarely as much as three and a half grams. As a castlebuilder begins to fly up to its nest with a heavy stick, grasped near the middle in its slender bill, it is frequently dragged back to earth by the weight of its load, but it persists in its efforts to rise until it gains a low branch in the tangle where its growing structure is located. Then, by a series of hops and short flights from perch to perch, with frequent flitting of wings, it



Fig. 20. Nest of Rufous-breasted Castlebuilder. Near Tela, Honduras, July 31, 1930.

gradually attains its goal, showing considerable skill in guiding its clumsy burden between the close-set branches through which it makes its way. On reaching the nest, the bird deposits the stick and then industriously pushes and tugs at it until it fits securely in the desired position. Often, however, the stick is knocked from the castlebuilder's bill by some obstruction that the bird apparently failed to notice, or it may be dropped because of its weight. Then the tireless bird follows the stick to the ground and begins anew the task of raising it by a circuitous course to the nest. Likewise, the castlebuilder descends to bring back the sticks which fall from the nest while it is arranging them. In this, the castlebuilder differs from its relative the Firewood-gatherer of Argentina, which, according to Hudson (1920, 1:225), rarely descends to recover the sticks that it drops while bringing them to its bulky nest, with the result that enough sticks to fill a wheelbarrow may accumulate beneath the nest tree.

In less than two weeks, the castlebuilders may completely cover the cup or bowl, which they thereby convert into an oven-shaped nest chamber with the entrance at one side, but the elaborate nest is still far from finished. The tunnel is still only about half covered and must be roofed to the end. To leave the distal end of the tunnel open, as does the Slaty Castlebuilder, would afford a method of entry into their castle too direct for the Rufous-breasted Castlebuilders. As a further safeguard, like the winding approach to some old Spanish fortress, they close off the outer end of the tunnel and place their doorway above it. This opening is situated in the center of a circular pile, often a miniature tower, of usually thorny twigs, which are not only shorter but always much finer than the sticks used elsewhere in the structure. The entranceway sometimes reminds one of a squat chimney. This low tower or chimney, and frequently the entire length of the tunnel above whose outer end it stands, is surrounded by a broad platform of coarse sticks, on which the birds can



Fig. 21. Rufous-breasted Castlebuilder about to enter its nest. The bird's bill points to the round doorway in the center of the platform. Near Tela, Honduras, September 4, 1930.

alight and walk around. The orifice that leads into the nest is so inconspicuous that, until I watched a castlebuilder enter, I could not discover how it did so.

The nest chamber, when first covered with thin twigs, still lacks a roof which will shed water. To supply this deficiency, the birds now devote much labor to bringing short, thick sticks, broad pieces of bark, weed stalks, dry petioles of the *cecropia* tree, fragments from the broad leaf bases of shell-flowers and heliconias and similar giant herbs, and other coarse materials, which form a thatch adequate to shed the rain. This thatch is sometimes piled to a height of 8 or 10 inches above the ceiling of the nest chamber.

Almost a month may elapse before the structure appears to be completed, but its energetic builders are not yet satisfied; they continue to give their attention to it until the eggs are laid, which, in the case of nests begun early in the breeding season, may not occur until five or six weeks after the first sticks were laid in place. Even while they attend eggs and nestlings, the castlebuilders continue to bring more materials to their edifice, increasing its bulk without essentially altering its form, until it becomes a monument to the tireless industry of the little builders, all out of proportion to their own size. The nest's final dimensions depend, among other things, on how long it is used and the nature of its site. The bulkiest nests are found where the supporting branches form a broad and strong foundation, which will hold everything that the birds continue to lay upon it. A narrow foundation is eventually loaded until it will bear no more, and a weak one will sink down beneath the increasing weight of sticks. For all these reasons, there is considerable variation in the size of

these nests. A fairly typical structure measured 29 inches in greatest length by 19 inches in height at the large end, where the nest chamber was situated. The interior of this chamber was from 5 to 6 inches in diameter, and the distance from the floor to the ceiling was $4\frac{3}{4}$ inches. Above the chamber, the thatch was piled to a height of 10 inches. The tunnel that led into the chamber was 14 inches long and $1\frac{1}{2}$ inches in internal diameter. The platform of sticks which surrounded it was 18 inches in length by 17 inches in width.

The furnishings of this imposing structure consist of green leaves and fragments of the cast skins of snakes and lizards. The leaves are used to line the bottom of the chamber where the eggs rest, and for this purpose the soft, downy foliage of a species of *Solanum* common in second-growth thickets is usually chosen. The reptilian exuviae are stuffed into the walls at various points, and sometimes they are laid on the floor of the entrance tunnel to form a soft carpet. A few scraps of skin may be mixed with the leaves on which the eggs rest. Both the leaves and the reptile skin are brought chiefly after incubation has begun.

At the end of May, 1930, I gave attention to a pair of castlebuilders which a few days earlier had lost their still incomplete set of newly laid eggs. These birds promptly began a new nest in a small acacia tree close by a river, about 100 feet distant from their earlier structure. The branch of the acacia which they had chosen for their nest's support seemed too strongly inclined, and probably for this reason they soon abandoned this site in favor of a more adequate one in a willow tree 15 feet away. I watched this pair of castlebuilders at work one morning when their latest nest in the willow was at about the same stage as their nest in the acacia. Both partners worked on the new nest, but one of them, from force of habit, sometimes carried a stick to the abandoned foundation in the acacia tree. When this occurred, the bird in the willow called *pet pet pet chu*, as though to guide its partner to the correct location, and then the latter brought the next stick to the willow tree. Usually, however, castlebuilders work in silence. This pair transferred many sticks from their pillaged structure to the replacement nest.

With the Rufous-breasted Castlebuilders, nest building has become an obsession. With the exception of other members of the same family, scarcely any bird which uses its nest for a single season builds a structure larger and heavier relative to its own size and weight. These great, complex edifices of sticks occupy the castlebuilders' attention for five or six months each year. Unlike the majority of nest builders, they continue to work into the waning light of evening, when other diurnal birds are seeking their roosts. Neither incubation nor the care of their young causes them to neglect these cherished structures. So absorbed do they become in the occupation of building a nest, that they continue to carry sticks to it while a man stands in full view hardly more than an arm's length away. With a machete, I have cut my way noisily through the brush tangle in which these castlebuilders lived to within a yard of their nest, without interrupting their building. While practically all other birds clearly make their nests merely as receptacles for their eggs and young, with the castlebuilders the construction of the nest seems to have become an end in itself.

THE EGGS

In the middle Motagua Valley in 1932, laying in the earliest nests that I discovered began around May 7. In this region and on the northern coast of Honduras, I found five sets of three eggs and three sets of four eggs. In at least some instances,

two days elapsed between the deposition of successive eggs. The eggs may be either pure white, or white with a faint tinge of blue, or else a beautiful pale blue, only slightly lighter than that of the American Robin's eggs. I always found all the eggs of a set alike in color, and the blue eggs were somewhat less common than the white ones. The measurements of 19 eggs average 21.1 by 16.7 mm. Those showing the four extremes measured 21.8 by 17.5 and 19.8 by 15.9 mm.

When newly laid, the eggs may rest on the bare sticks of the nest chamber, or perhaps a few small downy leaves and shreds of snakeskin inadequately separate them from this hard floor. Additional leaves are placed beneath them as incubation proceeds. On May 21, 1930, I opened for the first time two nests which I had watched the castlebuilders construct in the Lancetilla Valley of Honduras. Each contained two newly laid eggs. After my examination, I carefully closed each nest, sticking in fine twigs in an attempt to obliterate the gap that I had made in the rear wall as the only means of seeing the contents. When I returned the next day, both nests were empty, and below one of them were fragments of shell. Later, however, I opened other nests before laying began, and although the set of eggs was still incomplete the birds proceeded with their laying and then started to incubate. Probably, by an odd coincidence, the first two castlebuilders' nests that I opened in order to see the eggs were pillaged by predators within the following 24 hours. Despite popular superstition, which as a novice in bird study I inclined to take seriously, and accounts in uncritical writings, birds of all kinds scarcely ever remove or destroy their eggs because their nests have been touched or altered by a human visitor. Although there are a few reliably reported instances of this (see Armstrong, 1947:35), it has never, to my knowledge, happened at any of the nests that I have studied. Abandonment, rather than ejection of the eggs, is the usual reaction of birds to excessive interference with their nests.

INCUBATION

Both sexes incubate. At two nests, one in Honduras and the other in Guatemala, I marked the attendants by putting a small paintbrush in their doorway, in such a fashion that they rubbed against it and acquired white spots as they passed in or out. After marking the parents at a nest beside the Tela River in Honduras, I watched them incubate from 7:50 to 10:45 a.m. and from 2:20 to 4:40 p.m. on September 2, 1930. In the approximately 5 hours of observation, the partner which I called the female, because it occupied the nest by night, took six sessions, ranging from 6 to 40 minutes and averaging 24.8 minutes. This bird's mate, apparently the male, incubated only three times, for 14, 14, and 18 minutes. The eggs were left alone for five periods, ranging from 3 to 36 minutes and averaging 18.6 minutes. Excluding sessions and recesses that were not completed, in 288 minutes the female covered the eggs for 149 minutes, the male for 46 minutes, and they were unattended for 93 minutes. The eggs were incubated for 67.7 per cent of the time.

The nest in the Motagua Valley was watched from 6:30 to 11:30 a.m. on May 27, 1932, but part of this period is excluded from the following record, because the birds were disturbed while I placed my paintbrush so that they would mark themselves. One partner, whose sex I do not know, took five sessions, ranging from 11 to 43 minutes and averaging 30 minutes. The other partner took four sessions, ranging from 4 to 22 minutes and averaging 13.3 minutes. The eggs were neglected for four periods, ranging from 3 to 20 minutes and averaging 11.5 minutes. In 249 minutes,

one parent covered the eggs for 150 minutes, the other parent for 53 minutes, and they were unattended for 46 minutes. The eggs were incubated for 81.5 per cent of the time. I watched both nests while seated two or three yards away, without any concealment, since the castlebuilders seemed to ignore my presence.

From these watches and other shorter ones, it appears that in fair weather, when the castlebuilders are active, they rarely sit for more than 45 minutes at a stretch. If relief does not arrive at the end of this interval, the sitting bird leaves the eggs unattended while it goes off to forage. Frequently, however, one of the parents returns to take charge of the eggs after its mate has sat for only 10 or 20 minutes. When this occurs, the incubating bird often remains within the nest until its mate has entered, but sometimes, on hearing the other approach, it emerges and the two meet on the outside of the nest. At times, the incubating castlebuilder calls loudly while in the chamber, in response to the notes of its mate out of sight in the vine tangles.

To preserve in good order a nest as large and complex as the castlebuilders' requires unremitting attention, and these birds do not stint the time they devote to it. Before entering or after leaving the tunnel, they usually find time for a round of inspection, and they almost always notice something that needs adjustment. A broad piece of bark has fallen from the roof to the entrance platform, and it must be replaced in the thatch where it belongs; sticks which are slipping down must be pulled up into secure positions. Some pairs of castlebuilders like to keep a free passage around the base of their entrance chimney, and they walk around and around it, pushing to the outside any larger sticks which impede their progress. Fresh leaves are brought daily to the nest and added to those beneath the eggs. This mat continues to increase in thickness, since the old, withered leaves are not removed.

It has already been mentioned that castlebuilders continually bring new sticks to their nest during incubation and they even bring a few while they feed their nestlings. But their unending search for the cast skins of snakes and lizards seems to occupy most of the time left after they incubate their eggs and feed themselves. They seem never to have enough of these cast skins. If the bird flying up to take its turn on the eggs does not carry a stick or a green leaf, it will very probably bear a fragment of reptile skin in its bill. This pale material is either stuffed into crevices about the exterior of the nest or taken inside. Some is carried into the nest chamber, but far more is used to cover the bottom of the tunnel. One pair, whose nest I pulled apart after they had finished with it, had completely lined the floor of their entrance in this manner, from the doorway right up to the nest itself.

The castlebuilders never seem satisfied to let these precious exuviae rest long in one spot. They frequently shift them from one place to another on the outside of the nest, or they carry a piece from the exterior to the interior, or they bring out a fragment which has hitherto reposed inside. When its turn at incubation is over, a castlebuilder often emerges from the entrance chimney with a bit of skin in its bill and deposits the fragment somewhere on the outside of the nest before it flies off to forage. This habit of bringing cast snake skins to the nest is shared by the Slaty Castlebuilder, by flycatchers of the genus *Myiarchus*, by house wrens, and by other birds which nest in enclosed spaces. Few birds, however, search for this material with as much zeal as do the Rufous-breasted Castlebuilders. Although the partner which is off duty is chiefly concerned with the care of the nest and the search for

reptile skin, frequently the pair will leave the eggs unwarmed for many minutes while they engage in this occupation.

When the thatch was piled above the chamber of the nest beside the Tela River, the tunnel held it away from the platform at one side, with the result that there was formed a little nook or niche, large enough for the castlebuilders to turn around in it. This cranny held an irresistible attraction for them; on arriving or before leaving the nest, and often during their rounds of inspection, they disappeared into it for a few seconds. Here they deposited, temporarily or permanently, some of the leaves and bits of reptile skin that they brought to the nest. I could not discover that this niche had any special significance in the nest's economy, and in other structures I failed to find a corresponding nook.

The amount of energy which the castlebuilders devote to bringing contributions to their already completed nest will be more vividly conveyed to the reader by means of a few numerical examples. In the approximately 5 hours which I devoted to watching the pair beside the Tela River, the incubation record of which has already been given, the partner, probably the female, which performed the larger share of incubation brought green leaves nine times and one stick. The other partner compensated for his smaller part in incubation by bringing far more material: snake skin, seven times; sticks, five times; green leaves, twice; pieces for thatch, twice—total, 16 contributions. This bird evidently found a treasure-trove of snake skin, for in the middle of the morning he came to the nest four times in quick succession, each time bringing a large, limp shred.

At the nest in the Motagua Valley, however, the partner which devoted more time to incubation likewise brought more material during its recesses. In 5 hours, it took to the nest three billfuls of reptile exuviae, two green leaves, two sticks, and one unidentified object—total, eight contributions. The other partner brought only four billfuls of reptile skin. At both nests, the castlebuilders, in addition to bringing these new materials, shifted a number of pieces already present in the nest.

At one nest, the period of incubation was 17 or 18 days.

THE NESTLINGS

The newly hatched castlebuilder has pink skin, with sparse, dark gray down on the top of the head, the back, and the wings. Its eyes are tightly closed, and the interior of its mouth is yellow. As the nestlings grow older, they call for food with low trilling chirps. Both parents feed them with caterpillars, small winged insects, and spiders. The adults continue calmly to attend their young while a man stands watching a few feet away. When the nestlings are removed from the nest in their presence, the parents make neither vocal protest nor demonstrations of any kind, but seem to be indifferent to what is happening. In this respect they resemble a number of other birds which rear their young in holes or other enclosed spaces.

Hawks, herons, and several other kinds of birds are said to repair their old nests at the outset of a new nesting season, in order to use them again, but this renovation consists principally in building a new nest on the remains of an old one, rather than in mending a particular defect. Thus these nests grow from year to year and sometimes attain enormous size, as is often true of the Bald Eagle, whose nest after decades of occupancy may weigh a ton or two. The majority of birds cease to give attention to the structure of the nest after they have begun to incubate. I have seen the nests and young of hummingbirds, oropendolas, orioles, and finches come to

grief (or be saved from disaster only by my timely intervention), in consequence of defects which might have been remedied by procedures that the birds had already used in the nests' construction, but which they seemed unable to undertake now that this phase of the breeding cycle had passed. Of all the birds that I have studied intimately, only castlebuilders and some related species consistently and efficiently repair definite injuries to their nests.

The only way to learn exactly what a nest contains is to separate the sticks at the back or side of the chamber far enough to push in a hand and feel or, better yet, to insert a small electric bulb and mirror—a method of examination which did not occur to me while I studied the Rufous-breasted Castlebuilder many years ago. In order to follow the course of incubation and the development of the young, it is necessary to open the same nest repeatedly in this manner. After each examination, I pressed together the sticks that I had parted and stuck additional pieces into the small gap which nearly always remained, but I never seemed able completely to obliterate the evidence of my intrusion. The castlebuilders, on returning to their nest, would promptly notice the place where I had opened the wall and bring fine twigs to stuff into the chinks, until one could not tell that the structure had been opened. The point where the breach had been made would occupy the attention of the birds for several days; the break seemed to worry them even after it had been perfectly mended. They stuffed green leaves and fragments of reptile skin, both of which are ordinarily placed elsewhere in the structure, between the twigs in the position of the break.

One day, after my routine examination of a nest which sheltered two nestlings, I left a fair-sized gap in the side wall. The moment I left, one of the parents, which had been fidgeting around a little way off, flew up with a stick which it thrust into the breach. Then it continued with great industry to bring twig after twig to the gap, flying down again and again to carry up those twigs which had fallen beneath the nest, instead of hunting for them at a distance. Meanwhile, the other parent brought an insect to the hungry nestlings. The domestic organization of this pair was perfect; neither bird was in the least flustered nor uttered a sound. Each of them seemed to know exactly what the unusual situation demanded. When dusk was deepening into night, I returned to the nest and found one of the castlebuilders still working little twigs into the nearly obliterated gap, while its mate busied itself with arranging the sticks on the platform.

I surmised that the parent castlebuilders might use their elaborate nest as a dormitory. Without crowding the nestlings, they could find, in the chamber, in the entrance tunnel, or in various protected nooks about the exterior of the great mass, retreats which seemed safer and snugger than any which the surrounding thickets provided. But after the nestlings became feathered and no longer required nocturnal brooding, both parents slept at a distance from the nest. When I discovered how often these nests are pillaged, the advantage of this arrangement became apparent to me. The early separation of young and parents, during the night when the latter could do nothing to protect their offspring, decreases the probability that a predator will destroy the whole family at once. If, as frequently happens, the nestlings are eaten, the parents may survive to rear another brood. Only nests far more immune to predation than the castlebuilders', such as those of certain woodpeckers, toucans, barbets, and swallows, are used as dormitories by the parents while the young are growing up in them.

Let a bird place her eggs where she will, in a woven pouch swinging from the tip of a slender twig 100 feet in the air, in a hole in the solid trunk of a tree, deep in the ground, or, as in the castlebuilders, in an elaborate stronghold of sticks entered by a long and narrow passage, she is never able to elude all the mouths that hunger for them. The castlebuilders are not exempt from the heavy toll levied upon eggs and nestlings of all kinds, and their nests are despoiled with surprising frequency by small creatures, snakes or perhaps mammals, which are slender enough to enter through the tunnel and remove the eggs or young without making a gap in the wall. As with other kinds of nests, any interference by man seems to increase their liability to destruction; of the many that I watched, only in a single instance did the parents succeed in bringing forth a fledgling. By refraining from touching this nest for two weeks after the eggs hatched, I probably contributed to its success. When finally I separated the sticks at the back of the chamber, one of the parents hopped very near me and made a little rattling noise in its throat. As I pushed in my hand to feel for the nestling, it apparently escaped through the tunnel and fluttered to a little clump of spiny bushes across a cowpath from the nest, for I saw both parents attending it there.

One of the parents now attempted to take a dropping from the young bird, as though it were still in the nest, but the fledgling seemed to resent this attention. It turned its open bill toward the parent, in a manner that suggested a threat rather than an appeal for food. Next it tried to escape from the parents by hopping to another twig, then to the ground, where it rapidly made its way toward me until it was almost at my feet. The parents followed until they were nearly within arm's length of me and they made more low, rattling sounds. When I stooped to pick up the fledgling, it fled back into the thicket. When finally I drove it into the open, it moved so rapidly over the ground and through the low grass that my pursuit might have been fruitless had it not fallen into a slough that stopped its retreat after it had gone about 20 feet. Its alacrity in hopping over the ground and through the herbage suggested that the young castlebuilder, like the young ani, may frequently employ this means to escape its enemies.

When at last I held the young bird in my hand, I found it well feathered. Its forehead and crown were slaty; the back and rump were brownish olive; the wing-coverts were largely rufous; the remiges were rufous on the basal half, dusky toward the ends; the short rectrices were rusty brown; the throat was spotted with lighter and darker shades of gray; the breast, sides, and flanks were tawny; the abdomen was grizzled; the under tail-coverts were olive. The bill was yellow, with blackish tip and culmen; the eyes were deep brown; and the legs and toes were flesh-color. From the adults it differed most conspicuously in its tawny instead of chestnut-rufous breast, its brown rather than red eyes, and its largely yellow instead of black bill.

While I held the young bird in my hand, the parents made no demonstration and uttered no note of protest or alarm. After I released it in the thicket, one of them offered it a small black berry, which it disdained. The parent then swallowed the berry. Doubtless, if undisturbed, this fledgling would have remained in the nest several days more than the 14 or 15 days that it was actually there.

While the young bird was growing up in the nest, the downy leaves that had been taken in during the period of incubation had broken into small fragments. These particles were bound into a somewhat coherent mass by an abundance of fine

threads, which appeared to have been spun by an insect larva or a spider. The fragmented downy leaves formed a soft, dry lining on which the nestling had reposed. They had the pleasant fragrance of freshly dried hay.

A LATE NESTING

In the second half of August, 1930, I found a very large nest, only 5 feet above the ground, in a low, vine-draped acacia tree that stood with a few others of its kind on the edge of a wide, boulder-strewn flood plain of the Tela River. When I made a small opening in the side of this structure, a musty odor emanated from the interior, and I found brown decaying leaves covering the bottom of the chamber. I took this as evidence that this nest had held eggs earlier in the season, and probably a brood had already been reared in it. Watching at intervals in the following days, I saw the castlebuilders bring sticks and a fragment of snakeskin to the pile. Later, fresh downy leaves and some bits of reptile skin were placed above the old, moldering leaves, and by August 29 three white eggs had been laid on them.

After incubation began in this late nest, I marked the attendants with paint and made the record of sessions and absences that has already been given. As I continued to watch in the late afternoon, which was dark and rainy, I found that the white marks on the birds were becoming less distinct, and in the poor light I could not always distinguish them. Accordingly, I decided to mark one member of the pair in a manner which would be both conspicuous and fairly permanent. If one approaches in a casual and incautious manner a castlebuilders' nest in which incubation is in progress, the rustling of the shrubbery and the crackling of dead sticks underfoot warn the sitting bird, which flies out while the intruder is still several feet away. But by advancing stealthily, I succeeded in placing a hand over the entrance, without frightening out the male, which was then warming the eggs. Then I gently shook the little tree, and he emerged right into my fingers, where he struggled weakly to escape but uttered no sound. A companion applied white enamel without stint to the feathers of his crown. He was molting freely; many tiny feathers stuck to the paintbrush and my hand. After a minute we released him, a strangely transfigured castlebuilder.

Early the next morning I returned to the nest, expecting to follow the order of sessions on the eggs with less difficulty than on the preceding day. The female was in attendance; she brought sticks, green leaves, and scraps of snakeskin, and covered the eggs most of the time. But the hours sped by, and still "Whitewall" failed to appear. At last he flew up with empty bill, but instead of proceeding to the doorway, he alighted on the far side of the chamber, where I had opened it and the wall was thin. He wore a conspicuous white crest, because the feathers, stiffened with the dried enamel, refused to lie flat. I realized immediately that we had overdone his transformation. Clinging to the side of the nest, for a minute he communicated with his mate through the wall. I inferred from what followed that he was not welcomed; he promptly disappeared, and I did not glimpse him for the remainder of the day, although I frequently heard a castlebuilder's voice, probably his, issuing from the neighboring thicket.

When finally the female left the nest, she uttered a call that was new to me: *krr-r krrr-r krr kr kr; wita wita wita wita wita wita wit*. The first phrase was delivered slowly, the second with increasing rapidity. Later I heard the same utterance, with slight variations, from her and other castlebuilders.

Two days later, I made another long watch at this nest and was rewarded by seeing "Whitecrown" fly up to it with a piece of reptile skin, which he took to the far side of the structure. Here he encountered his mate, busy arranging sticks. Both were hidden from me, but I heard the same low notes as on his former brief visit; their purport was doubtless the same, for he promptly flew off again, and I did not see him for many days. His mate was trying to incubate her eggs alone. From 8:34 to 10:38 a.m. on September 5, she took three sessions lasting 43, 46, and 4 minutes, separated by recesses of 29 and 2 minutes. Alone, she seemed to be keeping the eggs covered about as constantly as she and her mate had formerly done together. Perhaps she would before long have found another partner, for sometimes a strange castlebuilder appeared near her nest, and on leaving it she often called and was answered from the depth of the thicket. But she was destined never to reap the reward of her patience. Two days later, I failed to see her at the nest, and on opening it I learned that the eggs had vanished.

Why did "Whitecrown" leave the nest after we had marked him? I believe that he tried to resume his attendance of the nest and eggs, but his mate apparently refused to accept him because of his altered appearance. Probably she now regarded him as a stranger, for birds quickly detect changes in their companions' guise, and the feathers of the head play a most important role in the recognition of individuals (Nice, 1943:204-205). Many species which inhabit the same region but remain distinct differ from each other less than the transformed "Whitecrown" differed from a normal Rufous-breasted Castlebuilder. His returns to the nest, once with a piece of reptile skin, revealed his readiness to attend it as formerly, but each time that he came he was rebuffed by his mate, and so at last he stayed away. One might argue that he feared to re-enter the nest in which he had been caught, but those who have captured birds for banding know that they may return again and again to the same trap, where each time they are taken in hand before they are released. Moreover, the female's continued presence in the nest should have helped to restore "Whitecrown's" confidence.

While I watched, on the afternoon of September 2, the nest of "Whitecrown" and his mate, the latter returned to it followed by a strange bird which uttered a harsh *churr*. The male Rufous-breasted Castlebuilder emerged from the nest, where he had been incubating, and joined his mate in driving away the intruder. An hour and a half later, the stranger silently returned and shifted two sticks on top of the nest. The female, which was then inside, did not emerge, having evidently mistaken the trespasser, which she could not see but whose movements she probably heard, for her own mate. After 2 minutes, the stranger spontaneously departed. From the description which I then wrote, I identified the trespasser as a Slaty Castlebuilder, a bird with which I later became familiar in Costa Rica. This was the only Slaty Castlebuilder that I saw in seven months in the vicinity of Tela. The incident illustrates castlebuilders' great preoccupation with nests of their own or of related species.

After the castlebuilders have abandoned their nests, they are frequently occupied by large, black ants, which swarm out when the supporting branch is shaken. Sometimes, indeed, the ants take possession of nests while the birds are still using them, for I once found a pair of castlebuilders carrying sticks to a structure that they had begun about a month earlier, and when I examined it I was stung by the ants that rushed out. If the nests escape ants, termites invade them and build a network

of tunnels over their surface. Even if a nest happens to escape all insect invaders, during the long wet season it is so weakened by decay that it is unfit for use in the following year. The industrious castlebuilders must begin their nests anew each spring.

SUMMARY

The Rufous-breasted Castlebuilder inhabits low, dense second-growth from sea level up to about 3500 feet. Its tail feathers are worn thin by its constant passage through the thickets. It subsists on caterpillars, mature insects, spiders, and the like, which it plucks from foliage or gathers from the ground. Berries are sometimes eaten.

The castlebuilder's most common utterance sounds like *pet chu, pet pet pet pét chu*, delivered with rising inflection and the emphasis on the last *pet*. This phrase is pleasant but not musical.

In the middle Motagua Valley of Guatemala in 1932, nest building started about the end of March. The large and elaborate nest requires a broad and firm foundation, and it is usually placed on a horizontal branch with lateral twigs, or on two parallel branches, in a shrub or small tree that is often draped with vines. More rarely it is situated in a dense tangle of the vines themselves. Nests were found from 5 to 20 feet up, but few were above 12 feet.

Both sexes build the nest, sometimes devoting as much as six weeks to it, before the eggs are laid. The complex structure, composed chiefly of fine, firmly interlaced twigs, consists of a rounded chamber that is reached through a long, horizontal tunnel or tube. This tube itself is entered through a low tower of finer twigs placed above it. The entrance tunnel is surrounded by a broad platform of coarser sticks. Above the chamber, coarse material, such as pieces of bark and petioles, is piled to a height of 8 or 10 inches, forming a thatch that sheds rain. A large nest may be about 30 inches long and 20 inches in greatest height.

The bottom of the nest chamber is lined with downy green leaves, usually of a shrubby *Solanum*, which are carried in chiefly after laying has started. Fresh leaves are brought daily and placed above the withering old ones until the eggs hatch. During the course of incubation, the castlebuilders seem to spend most of their spare time searching for cast skins of snakes and lizards, which they stuff into crannies in their nest and may lay down as a carpet along the entrance tunnel. They are constantly shifting these cherished exuviae, as well as other components of the nest, from place to place in the structure. As long as a nest is in use, the castlebuilders devote much attention to keeping it tidy by replacing falling pieces. They carefully repair a gap in the chamber's wall, even while the nest contains nestlings.

In the Motagua Valley in 1932, the first eggs were found in early May. Sets of three eggs were slightly more frequent than sets of four. The eggs were of three kinds: pure white, white tinged with blue, and pale blue. All the eggs in a set were found to be of the same color, and sets of pure white eggs were somewhat more common than sets of blue eggs.

Both parents incubate, taking sessions which usually last from 10 to 30 minutes and rarely exceed 45 minutes in good weather. The incubating partner does not always await the arrival of its mate, and both may neglect the eggs while they attend to the nest. In about five hours of observation, the eggs were incubated 67.7 per cent of the time at one nest and 81.5 per cent of the time at another nest.

At one nest, the period of incubation was 17 or 18 days.

Newly hatched nestlings have pink skin with sparse, dark gray down, closed eyes, and yellow mouth cavities. Both parents nourish the young with caterpillars, small winged insects, spiders, and an occasional berry. They make no demonstration of any kind when the young are removed from the nest in their presence. After they cease to brood the nestlings, neither parent sleeps in the nest.

A nestling which was frightened from the nest at the age of 14 or 15 days was well feathered and hopped away over the ground with alacrity, without attempting to fly.

A late set of eggs, probably representing a second brood, was laid in an old nest at the end of August. Breeding apparently continues through September in the Caribbean lowlands of Honduras and Guatemala. The elaborate nests deteriorate so much during the rainy months that they must be built anew at the beginning of each breeding season.

GENERAL SUMMARY OF INFORMATION ON THE FURNARIIDAE

The ovenbirds, castlebuilders, firewood-gatherers, spinetails, and their allies are small or middle-sized passerines which are united in a family of about 210 species and restricted to Middle and South America. The family is best represented in South America, particularly in its more southerly portions; many species occur in the South Temperate regions of Argentina, Chile, and Brazil, but relatively few are found north of the Isthmus of Panamá, and none reaches the United States. Of all the avian families of the Western Hemisphere, this is the most heterogeneous in external form, habits, and nidification, if not also in anatomical structure. Perhaps the greatest uniformity among the many species is in plumage, brown of many shades being the prevalent color. But even in this there is considerable diversity. Some species, especially of *Synallaxis* and related genera, are chiefly gray or slate-color, with areas of warm rufous-chestnut on the crown, wings, breast, or tail. Other members of the family have conspicuously streaked or spotted plumage. Ornamental plumes are rare in the family, but in Des Mur's Spinetail of Chile the two central rectrices are twice as long as the body and have poorly developed vanes; the next pair of tail feathers are only half as long as the central pair; and the outer rectrices are greatly reduced. In the family as a whole, the sexes are nearly always alike.

In form and habitat, the diversity exhibited by this family is immense. Some ovenbirds are stout, long-legged, and ambulatory, resembling the more terrestrial members of the Icteridae; some suggest marsh wrens and live in rush-covered swamps; others have been compared to titmice because of their manner of foraging among the terminal twigs of trees; a number of species creep up and down over the thicker limbs of trees much as nuthatches do; yet others ascend the trunks in an upright posture and greatly resemble woodcreepers in form, coloration, and mode of foraging, including their habit of propping themselves with a spine-tipped tail. The presence of so great a diversity of forms in this family implies a corresponding variety of habitats. Ovenbirds dwell in the tropical forests; in low, dense thickets; in marshes and swamps; on open plains with sparse vegetation; among the rocks and tussock grass of the bleak, frigid Andean heights; and many are at home in the mountains of southern Central America, where a number of kinds specialize in hunting over the moss-covered boughs of the trees in cool, wet forests.

Scarcely ever gregarious, ovenbirds live in pairs or family groups or at times alone. Among those which remain paired throughout the year are the Red Ovenbird, Firewood-gatherer, and Laughing Cachalote (Hudson, 1920, 1:198, 224, 234), and in Central America the Slaty Castlebuilder, Ruddy Treerunner, and apparently also the Buff-throated Automolus. Among species which are found singly after the close of the breeding season are the Buff-fronted Foliage-gleaner, the Streaked-breasted Tree-hunter, and the Red-faced Spinetail, all birds of the humid highland forests. Most members of this family are nonmigratory, but the Rush-loving Spinetail of Argentina performs long migrations (Hudson, 1920, 1:205), and other species that breed in the South Temperate Zone apparently migrate to a certain extent.

The food of the ovenbirds consists chiefly of insects, spiders, and other small invertebrates, which are gleaned from the most diverse sources. The leaf-tossers (*Sclerurus*) hunt on the floor of lowland forests, where with their bills they tirelessly toss the dead leaves and other litter right and left. The automoluses ransack curled

dead leaves, usually in the lower strata of the forest. With its peculiar, narrow, upwardly tilted bill, the xenops pecks into slender decaying twigs and vines to extract the larvae which lurk in the pith. In its manner of foraging the xenops reminds one of a piculet. At higher altitudes, the tree-hunters (*Thripadectes*) tear apart the bases of tank-bromeliads to disclose the creatures that hide in the imbricated leaves. These stout ovenbirds include many frogs, salamanders, and lizards in their diet. Lizards are also eaten by the Buff-throated Automolus, and probably many of the larger ovenbirds vary their diet with cold-blooded invertebrates.

In voice, the ovenbirds are less diversified than in form and habits. As in other tracheophones, their vocal powers are limited and their longer performances consist chiefly in the reiteration of a single note or at best a few different notes. Many of these birds appear to possess no utterance more complex than a rattle, either low and weak or loud and harsh. The far-carrying, long-continued rattle of the Buff-throated Automolus is one of the distinctive dawn sounds of the lowland forests of Central America. In other members of the family, the notes are soft and clear. The Plain Xenops utters a clear, sharp, little trill, much like that of the Olivaceous Piculet, which this diminutive ovenbird closely resembles in several other respects. Despite their simplicity in composition, the songs of some kinds of ovenbirds are of great beauty; of all that I have heard, the pure, ringing notes of the Scaly-throated Leaf-tosser are the most pleasing. A number of those species which remain mated at all seasons sing responsively or in unison, and Hudson (1920, 1:199) has vividly described the rhythmical duet sung by a pair of Red Ovenbirds while the male and female face each other. He mentions also (*op. cit.*:205) that the Brown Cinclodes darts up vertically into the air to pour out "with great energy a confused torrent of unmusical sounds," but singing in flight seems to be unusual in the family.

In western Ecuador, I saw a Pale-legged Ovenbird feed its mate, but I have no other record of nuptial feeding in the family.

The nests of ovenbirds display a diversity in both form and situation far surpassing that of any other family of birds in the Western Hemisphere, not excepting even the Tyrannidae and the Icteridae. The family takes its name from the domed structures of hardened mud with a round doorway in the side, miniatures of the clay baking ovens widely used in Latin America, which are built by species of *Furnarius* on a stout branch of a tree or on a fence post. Each nest is entered through an antechamber made by overlapping the outer wall, somewhat as at the mouth of a helical snail shell; in some nests the entrance is to the left and in others it is to the right. Nests of both types may be found in the same locality.

Nests of clay are far less widespread in the family than elaborate closed structures of twigs which, because of the quantity of sticks they contain, earn for the builders the name "firewood-gatherers," and the extraordinary complexity of which wins for other species the name "castlebuilders." The nest of the Rufous-breasted Castle-builder is an edifice 2 feet or more in length by about 1½ feet in height. It consists of a rounded chamber entered through a long, narrow, horizontal passageway, which in turn is entered through a low tower or chimney of finer and often thorny twigs piled above its outer end. Above the chamber is a thick pile of coarser materials, including stout petioles and pieces of bark, which form a thatch to shed the rain. The bottom of the chamber, where the eggs rest, is lined with downy green leaves that are added daily as long as incubation lasts. The floor of the entrance tunnel

may be lined with many fragments of the cast skin of snakes and lizards. Other pieces of reptile skin are stuck into crevices in various parts of the structure, and they are continually shifted from place to place by the restless birds. The nest of the Slaty Castlebuilder is somewhat smaller and simpler in form than that of the more northern species; the entrance tunnel opens directly at its outer end, with no pile of finer twigs to make the opening more difficult to find. The lining of the chamber is, however, more elaborate, consisting of downy leaves broken into small pieces and felted together with cobweb.

The nest of the Laughing Cachalote of Patagonia is described by Hudson (1920, 1:234) as a spherical structure 4 or 5 feet in diameter. A narrow arched gallery, neatly made of slender sticks, leads into the side of the nest, near the top, and the chamber is unusually spacious. This edifice of sticks is so strongly made that it supports the weight of a man. Although in the warm lowlands castlebuilders line only the bottom of the chamber where the eggs rest, the Black-winged Spinetail, which builds great nests of closely interwoven sticks among the sword-like leaves of *Puya* on the frigid heights of the Peruvian Andes, thickly lines the chamber and entrance tunnel all around, using for this purpose wool, horsehair, seed down, and other soft materials (Dorst, 1957:597).

Very different from these solid castles of sticks is the pendulous nest of the Red-faced Spinetail of the Costa Rican mountains. Attached to the end of a slender, drooping, leafy twig or vine well above the ground, the bulky globular or ovoid structure, a foot or more in diameter, is composed largely of green moss and long pieces of dry vines. It is entered through a narrow and inconspicuous round aperture in one side, near the bottom. In size, shape, and site it much resembles a nest of the Rose-throated Becard. Hudson (1920, 1:207) described the nest of the Rush-loving Spinetail as a domed, oval-shaped structure, about 9 inches deep, with a small circular aperture close to the top and protected by a visor-like projection. It apparently resembles rather closely a marsh wren's nest and is built in similar situations.

A unique type of nest is constructed by the Spotted Barbtail, which attaches a bulky mass of green moss to the face of a vertical cliff or the side of a mossy log bridging a woodland stream. This mass is penetrated from the bottom by an upwardly directed tube that leads to a chamber in the top of the nest, where the eggs rest in a shallow depression in the moss (Skutch, 1967).

Although many of the ovenbirds fashion nests of marvelous complexity—many types of which we lack space to describe—a large proportion of the species breed in cavities in trees, burrows in banks, or in the closed structures which other birds have built and abandoned. The Plain Xenops excavates in soft, decaying wood a small cavity with a neatly rounded doorway, or it takes possession of a similar hole made by the Olivaceous Piculet. In either case, the xenops lines the bottom of the hole with shredded bast fibers. The beautiful Buffy Tuftedcheek nests in a cavity in a decaying trunk, which it lines chiefly with the chestnut-colored scales from the fronds of tree ferns. The automoluses and leaftossers nest in burrows, which they often dig for themselves; at the dilated inner end of the tunnel they build a shallow nest of the petioles or rachises of compound leaves. The Streaked-breasted Tree-hunter uses rootlets for its nest in a burrow. The kind of nest least often favored by ovenbirds is the conventional open structure built by the majority of passerines, but a few members of the family are content with these simple constructions. According to

Hudson (1920, 1:216, 223), the Striped Spinetail and the Wren-like Spinetail fashion open nests of grasses, softly lined with feathers.

Of special interest are the nests with several chambers built by a few species of this family. Those of the Rufous-fronted Thornbird of northern South America are attached near the ends of slender branches of trees or to vines, where they often hang vertically. Composed of rather coarse sticks, they may attain a height of 7 feet and contain eight or nine rounded rooms, which are usually superposed but occasionally situated side by side. Each of the chambers has its own opening to the outside and there is normally no internal communication between them. The chambers are lined on the bottom with the most diverse materials, including vegetable fibers, flakes of bark, rachises of compound leaves, feathers, scraps of paper, pieces of cellophane, tinfoil, and other trash. Three or four individuals, evidently parents and their full-grown young, may join in building one of these amazing structures, but no more than one pair was found breeding even in a large nest. The smallest nests used for reproduction contained two chambers. Nearly always the eggs are laid in the lowest and oldest chamber, which is the one least accessible to a climbing or creeping predator approaching along the supporting branch' (Skutch, MS).

Such snug and substantial nests as thornbirds and many other ovenbirds build are naturally coveted by birds of other families which use enclosed nesting cavities. In Venezuela, the nests of the Rufous-fronted Thornbird are the preferred site of the Troupial, which also uses them as dormitories, sometimes destroying the eggs or nestlings of the evicted builders. At least five other species breed occasionally in nests of the thornbird. Hudson (*op. cit.*) gives numerous examples of the occupancy of nests of the Furnariidae by other kinds of birds in Argentina.

Nests of the Pale-breasted Castlebuilder and the Yellow-throated Spinetail are parasitized by the Striped Cuckoo (Belcher and Smooker, 1936:801-802). These authors suggested that the cuckoo, which is a much larger bird and would have difficulty in entering these nests through the narrow passage used by the builders, makes an opening in the side in order to slip in and lay her eggs. Castlebuilders and spinetails readily repair such gaps in the nest walls.

The nest is built by both sexes in species of *Synallaxis*, *Furnarius*, *Cranioleuca*, *Xenops*, *Phacellodomus*, and probably many other genera. As far as I could learn, a female Buffy Tuftedcheek built alone. Weeks or even months are devoted to the construction of some of the more elaborate of the nests made by members of this family. The Red Ovenbird may begin in the autumn to build its clay nest and work throughout the winter whenever there is a period of mild, wet weather (Hudson, 1920, 1:200). In Paraguay, the Red Thornbird may likewise work at its great nest of sticks all winter, spending months on a single one (*op. cit.*:231). Rufous-breasted Castlebuilders may work at nests begun early in the season for five or six weeks before they start to lay.

The eggs of ovenbirds may be pure white; tinted with green or blue; less often blue; and rarely, as in the Hudson Spinetail, pale buff. The Rufous-breasted Castlebuilder may lay either white or light blue eggs, but those in the same set appear always to be uniform in color. As far as I know, the eggs of ovenbirds are always unmarked. The Central American members of this family lay sets of two, three, or sometimes four eggs. In the South Temperate Zone, the sets are larger, ranging from three to six or, as in the Pale-breasted Castlebuilder, nine eggs, which may,

however, have been the product of more than one female. Sets of four or five eggs appear to be most common in this region (Hudson, 1920, 1:195-235).

Incubation is performed by both sexes in the Red Ovenbird (*op. cit.*:201), Rufous-breasted Castlebuilder, Slaty Castlebuilder, Plain Xenops, Buff-throated Automolus, Spotted Barbtail, Rufous-fronted Thornbird, and Scaly-throated Leaf-tosser. As far as I could learn by long and careful watching at a single nest of the Buffy Tufted-cheek, only one adult took an interest in it at any stage. The Scaly-throated Leaf-tossers took sessions of about an hour's duration. Those of the Plain Xenops ranged from 12 minutes to nearly 2 hours. The periods on the eggs of the Buff-throated Automolus varied from 1 to more than 3 hours. The castlebuilders, which spend much time keeping their elaborate household in order, take shorter turns on the eggs, lasting from a few minutes to about three quarters of an hour, rarely longer. Despite the fact that both sexes incubate and that in some species the sessions are quite long, ovenbirds fail by a good deal to keep their eggs constantly covered. There is often a considerable period of neglect between the departure from the nest of one parent and the arrival of the other.

The castlebuilders devote much of the time that they steal from incubation to seeking new materials for their complex nest and to rearranging those already present. The other species, too, continue until the eggs hatch to bring occasional billfuls of material to the nest, even when it is a very simple structure in a hole or burrow, but the amount brought to these less elaborate nests is so slight that it can hardly account for the long neglect of the eggs by both members of the pair. Hudson (1920, 1:201) described the songs in which the male and female Red Ovenbirds join as one replaces the other on the eggs, but I have noticed no ceremony attending the change-over in the Central American species of ovenbirds that I have studied. Indeed, one member of the pair so often leaves before the other arrives that often the latter comes to take charge of an unattended nest.

Incubation periods are long in the Furnariidae, lasting about 16 days in the Tussac Bird (Cawkell and Hamilton, 1961:22), between 15 and 17 days in *Xenops*, 16 or 17 days in *Phacellodomus*, 17 to 19 days in *Synallaxis*, 20 to 22 days in *Automolus*, and at least 21 days in *Sclerurus*.

The nestlings are hatched with tightly closed eyes and the sparse down typical of passerines. Except in the Buffy Tuftedcheek, both parents brood and feed them, at least in the species for which information is available. The food given to nestling ovenbirds usually consists of adult and larval insects, spiders, and other small invertebrates. To this the Buff-throated Automolus adds an occasional lizard, and the Streaked-breasted Tree-hunter adds small lizards and amphibians. The parent usually comes to the nest with a single article carried prominently in its bill. The pieces brought to the nest are usually substantial and the rate of feeding is slow; even for older nestlings it rarely exceeds 2.5 times per nestling per hour. Droppings are carried away by the parent birds, and the nest is kept perfectly clean. As young ovenbirds become feathered they are likely to be noisy, especially when they are given food, which they receive with a chorus of chiming notes. Hudson (1920, 2:72-73) wrote that the loquacity of the nestlings of the spinetail that bears his name guides the Chimango or Common Carrion Hawk to their domed nest, well concealed beneath a cardoon bush, and so leads to their destruction.

I have never known any ovenbird to simulate injury, although Miller (1955:500) has seen the Pale-breasted Castlebuilder do so in Colombia. Dorst (1957:598),

however, described a different sort of display which parent Black-winged Spinetails give when a man approaches their nest. This display attracts neighboring individuals of the same kind, until as many as 15 may be present, all skipping rapidly among the leaves of the *Puya* plant where the nest is placed, moving their tails up and down, and calling together in an attempt to distract the trespasser's attention from the nest. In the usual absence of a distraction display, ovenbirds are similar to many other birds that breed in burrows, holes, and well-enclosed nests. Apparently distraction displays save the occupants of open nests more often than those of closed ones, whose safety depends upon inaccessibility to predators rather than upon luring them away.

The few nestling periods that I have succeeded in learning range from 13 or 14 days in the Plain Xenops and 15 in the Scaly-throated Leaf-tosser to at least 17 in the Slaty Castlebuilder, 18 in the Buff-throated Automolus, 21 or 22 in the Rufous-fronted Thornbird, about 25 in the Tussac Bird (Cawkell and Hamilton, 1961:22), and at least 29 in the Buffy Tuftedcheek. The height of the latter's nest in a dead trunk apparently accounts for the unusually long nestling period. If the nest of the castlebuilder is disturbed when the young birds are about two weeks old and covered with plumage but scarcely able to fly, the nestlings escape down the nest's long tunnel, flutter to the ground, and hop rapidly away. If undisturbed, they stay in the nest for several days more and can fly fairly well when they depart spontaneously.

In a family of generally subdued coloration and without sexual dimorphism in plumage, the young as a rule differ little in appearance from the adults. In the Rufous-breasted Castlebuilder, the fledglings lack chestnut-rufous on the breast but already display a large expanse of rufous on their wings. In the Slaty Castlebuilder, the young are without the rufous-chestnut crown of their parents, and the rufous area on each wing is smaller and paler than in the adults. In the Red-faced Spinetail, the juvenal plumage lacks the bright rufous that is so conspicuous on the crown and face of mature birds. In these and other species, the full breeding plumage is apparently soon acquired, for I have not known a member of this family to breed in immature or transitional plumage.

The Plain Xenops roosts singly in old woodpeckers' holes or other cavities well above the ground in decaying trunks. The Red-faced Spinetail sleeps alone in a bulky hanging nest such as it uses for breeding. Spotted Barbtails lodge singly in inverted pockets of moss attached to the face of a cliff, similar to, but not so well made as, the breeding nests (Skutch, 1967). In the Firewood-gatherer of Argentina, the young sometimes remain with their parents for three or four months after they are fledged, all the family going about and feeding in company, and all sleeping at night in the old nest (Hudson, 1920, 1:224). In the Rufous-fronted Thornbird of Venezuela, newly fledged young are led by their parents to sleep in the many-chambered nest. They may continue to lodge with their parents until the following breeding season, when they have long been self-supporting, and they sometimes help their parents to build. A nest with eggs and nestlings was occupied nightly by six grown birds, including the parents and four others that were evidently offspring from two broods of the preceding year. After the latest brood of two fledged, this two-chambered structure was entered at nightfall by eight lodgers. Thornbirds that have lost their nests sometimes seek those of other families, forcing their way in against strong opposition when it is nearly dark (Skutch, MS).

FAMILY DENDROCOLAPTIDAE

STREAKED-HEADED WOODCREEPER

Lepidocolaptes souleyetii

The woodcreepers or woodhewers are slender birds of predominantly brownish coloration which creep up the trunks of trees searching for food. Although the family displays considerable range in size, color pattern, and shape of bill, the general similarity of many species, including those in diverse genera, makes field identification, except for a few well-marked forms, a matter of great difficulty until one becomes familiar with the voices and peculiarities of habit of each species.

The Streaked-headed Woodcreeper is a slender, long-tailed, prominently streaked, brownish bird, about seven and a half inches in length. In both sexes, the top of the head, the hindneck, and the upper back are brown, thickly streaked with buff. The rump, the upper tail-coverts, the tail, and the wings are cinnamon-brown or cinnamon-rufous, without stripes. The sides of the head and neck are streaked with deep brown and brownish buff. The chin and throat are pale buff, and the remaining under parts are pale grayish brown, each feather with a central stripe of pale buff margined laterally by a narrow line of black. The eyes are brown. The fairly long and slender, slightly curved bill is horn color, darker on the culmen. The legs and toes are dark gray.

The species ranges from southern México to Perú, northern Brazil, and Trinidad. In Central America, it is more common on the Pacific side, especially in the north, than in the Caribbean drainage. It occurs from sea level up to about 3000 feet on the Pacific slope of Guatemala and to 4000 feet on the same slope of southern Costa Rica, whereas in western Panamá it has been recorded as high as 4500 feet (Ridgway, 1911:266). It is found in heavy rain forest, especially near the margin, but it is perhaps even more common in lighter types of woodland, among the shade trees of coffee plantations and in dooryards and pastures with scattered trees. Although usually it forages well up in the trees, I once saw one of these woodcreepers hunting among the spiny prop-roots of a chonta palm, almost within arm's length of me. The Streaked-headed Woodcreeper lives in pairs throughout the year, and it rarely joins mixed flocks of small birds.

Like other woodcreepers, this species climbs trunks in an upright position, although as it works outward along the branches its body may become horizontal or even downwardly inclined. It grasps the bark with three toes directed forward and slightly diverging and the fourth toe pointed backward. The incurved, projecting ends of the shafts of all the stiff tail feathers engage rough bark and provide additional support. The Streaked-headed Woodcreeper climbs upright trunks as easily as does a woodpecker, and in much the same manner. Its flight is swift and direct but rarely long continued. Once I watched a pair of these birds whose nest was in a great fig tree growing in an open pasture. Much of the food which they took to their nestlings was found among the trees beside a river, 500 or 600 feet from the nest. To reach the fig tree from the stream without making a detour, they had to cross a low, open ridge. In making this journey, they would climb far up the trunk of a tall tree that stood in the pasture near the river. From that point they flew in a

descending course to the trunk of another tree, up which they crept to recover the altitude they had lost. From this point they proceeded to a third tree along their route, climbed this to gain height for their flight to the fourth, and from this tree, which stood on the back of the ridge, they flew down to the fig tree that held their nest. Thus, despite their weak flight, they covered a long distance.

FOOD

As far as I have seen, the Streaked-headed Woodcreeper subsists wholly on insects, spiders, and other invertebrates, which it finds while creeping up the trunks of living and dead trees and outward along their branches. When the woodcreeper has reached the upper limit of profitable foraging, it does not reverse its course and work down another side of the same trunk, as a nuthatch might do, but it flies to a point low on a neighboring trunk, up which it then creeps. When it captures a large insect, it may beat the prey against a branch until it becomes quiescent, before swallowing it. Often with its slender bill it pries off flakes of loose bark, or lifts tufts of moss, to see what may be beneath them. Once I watched a woodcreeper hunting up a tall dead tree beside a road, breaking off loose pieces of bark in its usual manner. As it lifted up one such piece, a swarm of small insects, apparently bees or wasps, darted out. The bird hastily retreated to another branch.

One afternoon, in a coffee plantation, I watched a Streaked-headed Woodcreeper digging into the rotten top of a broken-off trunk of an *Inga* tree. With its sharp bill, the bird pecked vigorously at the soft wood, delivering blows almost like a woodpecker. The sound of the taps reached me 50 feet away. From time to time, the woodcreeper broke away small pieces of wood and dropped them to the ground. After a while, a large blackish object, probably a beetle, fell from the hole and the bird dived downward in pursuit, apparently catching it in the air, although I did not see this clearly. Then it resumed its pecking in the same place. For at least 5 minutes after I found it at work, the woodcreeper continued this activity, for which its slender, delicate bill seemed poorly fitted. This was the only occasion when I ever saw a member of the Dendrocolaptidae acting in the manner implied by this name and its English equivalent "woodhewer."

SLEEPING

At all seasons, except while brooding nestlings, Streaked-headed Woodcreepers sleep alone in a cavity in a trunk or branch, usually well above the ground. They prefer a cavity resulting from decay to one made by a woodpecker, possibly because such crannies are less conspicuous and are therefore less likely to be investigated by nocturnal prowlers. The hollow chosen as a dormitory may be in the end of a broken-off, upright trunk or branch, so that the opening faces upward and permits rain to enter. I have known woodcreepers to sleep in such poorly sheltered places even in the wettest weather, despite the apparent availability of roofed lodgings in the same grove. From this we may infer that concealment is more important to them than dryness.

Woodcreepers of this and other species are among the last of the diurnal birds to seek their roosts, which they enter long after woodpeckers and most other birds that sleep in dormitories have gone to rest. The brown woodcreepers are not easy to follow with the eye as, in the waning light, they creep up the dark trunks to their

hiding places. Likewise, they become active very early in the morning, while woodpeckers remain snugly ensconced in their well-carved chambers. Once I found a Streaked-headed Woodcreeper roosting in a crevice in the top of a thin stub standing in a new clearing in the forest. Its dormitory was not far above a large hole, which each night was occupied by a pair of Fiery-billed Araçaris, whose huge beaks are feared by most smaller birds. But since the woodcreeper entered its hole after its larger neighbors had retired for the night, and left long before they became active in the morning, it might not have been aware how close to them it slept.

In March, many years ago, I found a Streaked-headed Woodcreeper sleeping in a natural cavity, which it entered through a long, narrow fissure. The cavity was in the base of one of the lower limbs of a great dead tree standing in a recently burned clearing, close by the forest. In the late twilight, after practically all other birds had fallen silent and the finer details of the vegetation had fused into vague, dark masses, the woodcreeper would fly into the clearing, voicing its clear trill, and alight on the trunk of the big tree, where its slim, dark figure fused indistinguishably with the dark expanse of charred bark. I watched on several evenings before I discovered just where, among the many remaining branches of the tree, this bird went.

As this woodcreeper went to rest, a second individual, doubtless its mate, answered its trills with similar notes from somewhere on the edge of the clearing. One evening, a second woodcreeper followed the first into its narrow crevice, but immediately both flew out, one apparently pursuing the other. I thought that I saw one of the woodcreepers return to the cavity, but the light was now so dim, and all small objects so indistinct, that I might have been deceived. I have witnessed similar episodes in the evening twilight with the Plain Xenops, the Rufous-browed Wren, and other species the adults of which commonly sleep alone.

VOICE

The most common utterance of the Streaked-headed Woodcreeper is a long-drawn, melodious trill, all on the same key, delightfully soft and clear. At all seasons, the constantly mated male and female keep in contact by exchanging these trills, and I have then noticed no difference between their voices. Possibly this utterance, for all its sweetness, should be regarded as a call rather than as a song. In the tracheophone families, which include the woodcreepers, the distinction between song and call notes is by no means so clear as in finches and other songbirds with far more versatile vocal organs.

This basic utterance of the Streaked-headed Woodcreeper is modified in several ways to serve special purposes. As the nesting season approaches, the woodcreeper delivers a trill conspicuously shorter and higher than the ordinary trill. It is a fine, delicate song, with an ethereal quality like that of the Wedge-billed Woodcreeper's trill. While I had under observation a pair of which the male was distinguishable by an abnormality in his plumage, I heard him give this higher, softer trill in response to his mate's usual call; he also delivered some trills intermediate in character between the special trill and the ordinary one. I did not see the female in the act of giving this high trill. I have heard this special courtship song chiefly from mid-January into March, and also in late April, when a female which lost her mate was joined by a newcomer.

When the woodcreepers are angry or annoyed, their trill becomes shorter and sharper, more like a churr, and the birds' anxiety is further expressed by twitching

wings. In addition to these longer utterances, the woodcreepers at times call to each other with a mournful single note.

ANTING

On the morning of May 13, 1962, a Streaked-headed Woodcreeper clung near the ground in a dracaena shrub in our dooryard. It plucked something small from the cut-off end of a branch, rubbed the object beneath the remiges of a partly extended wing, then appeared to swallow it. After repeating this performance once or twice, the bird flew away. The end of this branch was hollow and contained some small black ants.

NEST BUILDING

In El General, the Streaked-headed Woodcreepers prospect for nest cavities in late February. In these preliminary explorations, they often back into the hole tail first, a cautious mode of ingress also used by woodpeckers and other birds when entering a cavity which might have other occupants. Both sexes investigate prospective nest sites, and by the first of March I have seen them carry in a few flakes of bark, although I have watched no sustained nest building so early in the season. At this stage, one male retreated from his mate as though afraid of her.

Although I have twice known these woodcreepers to breed in holes made and abandoned by woodpeckers of medium size, more often they select a natural cavity in a dead or even in a living tree. The narrower the orifice, the better they seem to like it. The highest nest that I have found was about 80 feet up, in a natural cavity in a badly decayed upright branch of a dead tree standing beside a road. The tree was separated from the forest by a low, dense thicket. An unusually low nest of these woodcreepers was in a cavity formed by the partial concrecence of two ridges projecting from the huge, irregular trunk of a giant living fig tree that grew in an open pasture. Access to this snug hollow was through a narrow, vertical slit, about 20 feet above the ground, but the nest itself may have been far below the doorway. The entrance to the lowest nest that I have seen actually attended by the woodcreepers was 15 feet up in a natural cavity in a dying *Inga* tree.

A pair of woodcreepers built a nest and laid eggs in the hollow stub of a large stilt-palm standing in a new clearing, about 100 feet from the forest's edge. The columnar palm trunk was broken off about 15 feet above the ground, and the upwardly directed aperture gave access to a long, tubular space enclosed by a thin but very hard shell. When the woodcreepers began to carry in material, the bottom of the cavity was about 9 feet vertically below the orifice, or only about 6 feet above the ground. Before the eggs were laid, they and a Tawny-winged Dendrocincla, which contested this cavity with them, had raised the level some 19 inches. The lone female dendrocincla wrested this cavity from the two woodcreepers, which retreated when she flew at them, and she incubated their eggs and reared a single young woodcreeper. A more detailed account of this is to be found in the section on the Tawny-winged Dendrocincla (p. 409).

In addition to these varied sites, I have twice watched woodcreepers carry much material into the space between a large sheet of bark and the trunk from which it was becoming detached, but I have not found them incubating or feeding nestlings in such an open situation. Although these woodcreepers forage in the forest, I have not found them nesting there. All breeding activities that I have watched took

place in new clearings or in coffee plantations, within 1000 feet or less of the forest.

On May 11, 1936, I saw a pair of Streaked-headed Woodcreepers carrying material into the space between the trunk of a dead tree and a sheet of bark which was breaking loose from it. This dead tree was in a clearing high above the Río Buena Vista, in the basin of El General. For the next 25 days, these birds continued to take material into this cranny, which was evidently quite capacious. Although sometimes they brought a few pieces in the forenoon, I was most successful in finding them at work late in the afternoon. From about 3:00 to 4:00 p.m. on May 16, a single woodcreeper, whose sex I could not learn, worked most assiduously, carrying many flakes of bark into the nest space. This material was pulled from the trunk and branches of the tree in which the woodcreeper was building, and from neighboring fire-killed trees. Sometimes, when a flake was difficult to detach, the woodcreeper grasped the free end in its bill and tugged, pulling now to the right and now to the left, at times even pivoting around to the lower side of a slender branch in its spirited determination to gain possession of the prize. But often the scale of bark proved to be too firmly united to the tree, and the bird was at last obliged to relinquish it. If the woodcreeper obtained a piece of bark from a branch high above the nest cavity, it dropped down like a falling brown leaf, to alight on the trunk below the cavity and climb up and in.

At about 4:00, when the toiling bird was inside the cavity, the trill of its mate sounded from the neighboring forest, and an answering trill came low and subdued from the narrow aperture. The approaching bird flew up and entered the cavity. Soon one of the woodcreepers left and returned promptly with a piece of bark for the nest. Thenceforth, for many trips, there was always one bird in the nest, and since I could not distinguish the two, I was uncertain whether the same individual stayed constantly within. I surmised that the woodcreeper which had worked so hard for the last hour was now resting, while the newcomer carried on the task. After 15 minutes, both woodcreepers emerged from the cavity and began to bring material to it. While a single bird was in sight, it worked in perfect silence, but when the two worked together, they called to each other with melodious trills.

At several other nests, I have seen both sexes working together, trilling back and forth as they broke pieces of bark from the trees and carried them into the nest space. The pair which built in the hollow palm trunk descended the long, tubular cavity in an upright position, tail first, rather than head foremost in the manner of the Tawny-winged Dendrocincla which built in the same hollow. The tree with the loose sheet of bark fell about a month after I first noticed the woodcreepers building within it, and I was able to examine the materials which they had deposited there. Their accumulation consisted of many pieces of bark, ranging in size from small fragments to flakes nearly 5 inches long. The birds had chosen almost exclusively stiff or corky outer bark rather than flexible, fibrous inner bark. I could find no trace of eggshell, nor had I noticed that the woodcreepers had begun to incubate there. In the hollow palm trunk where both the woodcreepers and the dendrocincla had built, I found, after the nestling's departure, pieces of hard bark up to $3\frac{1}{4}$ inches in length by 1 inch in width by $\frac{3}{32}$ inch in thickness, although most of the fragments were considerably smaller than this. These flakes of bark were taken in by the woodcreepers rather than by the dendrocincla, which chooses different kinds of materials. As far as I have seen, the Streaked-headed Woodcreeper's nest is composed wholly of flakes of hard bark, as is the nest of the Spotted-crowned Wood-

creeper. Even while they incubate, woodcreepers of both sexes continue to bring many pieces of such bark to their nest.

THE EGGS

My only accessible nest of the Streaked-headed Woodcreeper was that in the palm trunk which the Tawny-winged *Dendrocincla* also claimed. Here, by inserting a small mirror, along with a lighted bulb, through a narrow fissure in the side of the trunk, I could see, far below, two pure white eggs. Since a woodcreeper emerged from the only egg which hatched, they were evidently eggs of this species, although the *dendrocincla* incubated them and reared the nestling. In this, the latest nest of the Streaked-headed Woodcreeper that I have found in El General, the eggs were laid in mid-June. In another nest, the eggs, as calculated from the date when the parents began to carry in food for nestlings, were laid late in March. In this region, April appears to be the month when most of the woodcreepers incubate.

Belcher and Smooker (1936:799) recorded two nests of this species in Trinidad. Each of these nests contained two, pure white, glossy eggs in April and May. The only nest which these authors describe was "in a knot-hole of an immortelle tree about ten feet up: it was made of green weed-stems and plant-down, fairly well put together." This material is so different from any that I have seen Streaked-headed Woodcreepers take into five nests that I have closely watched, that I suspect some irregularity here. Possibly the woodcreepers had taken possession of a nest built by some other bird.

INCUBATION

Both sexes incubate. In April of 1956, I found a nest in a small coffee grove near our house. One of the attendants had a patch of whitish feathers on its hindhead and nape. Since the normally colored mate of this bird occupied the nest by night and was evidently the female, this woodcreeper with a touch of albinism was doubtless a male. The nesting of this pair in 1956 was successful, and during the next two years I saw this white-naped bird from time to time in the trees about the house or in the neighboring forest. In 1957, there was no woodcreeper's nest in this little plantation, but in 1958, the white-naped woodcreeper nested, possibly with the same partner, in another hole made by the Golden-naped Woodpecker, in an *Inga* tree near his nest site of two years earlier. During this nesting the male disappeared, and soon afterward the nestlings, although faithfully attended by the female, which seemed to have acquired a new mate, were somehow destroyed. For two seasons, this peculiarly marked woodcreeper provided a unique opportunity to learn how the sexes share the duties of the nest. Information of this kind is exceedingly difficult to obtain for members of this family, because the male and female are nearly always similar not only in plumage but also in voice.

In 1956, my longer watches at the white-naped woodcreeper's nest during incubation totalled approximately 15 hours. In this time, the woodcreeper with normal plumage, which slept in the nest and was evidently the female, took 13 sessions on the eggs, ranging from 7 to more than 72 minutes and averaging 37.5 minutes. The longest session was taken as a storm was gathering, and I did not wait for its termination, because the rain drove me to shelter. The white-naped woodcreeper was much less attentive, taking only three sessions, which ranged from 15 to 42 minutes and averaged 28.3 minutes. Since the bird in charge of the eggs often

flew away before its relief arrived, the eggs were left unattended for 14 periods, ranging from 2 to 41 minutes and averaging 21.2 minutes. Considering only that part of my record made after the woodcreeper's first morning departure from the nest and before her final retirement for the night, the female was in the nest for a total of 488 minutes, the male for a total of 85 minutes, and the eggs were neglected for 297 minutes. The eggs were attended for only 65.9 per cent of the daytime.

In 1958, I watched the nest of the white-naped bird and his mate from 12:00 noon to 6:00 p.m. on April 4, and from 5:30 a.m. to noon on April 5. Assuming that these strictly diurnal birds passed an uneventful night, this gave me a complete record of activities at the nest over a period of 24 hours. The female entered the hole at 5:57 p.m. on the showery evening of April 4 and first emerged at 5:51 a.m. next morning. In the active period of 12 hours and 6 minutes, the female took 11 completed sessions, ranging from 5 to 57 minutes and averaging 26.9 minutes. The white-naped male was much more attentive than he had been two years earlier and he took eight sessions, which ranged from 6 to 37 minutes and averaged 16.4 minutes. The nest was unoccupied for 17 periods, ranging from 4 to 41 minutes and averaging 16.9 minutes. The female was in the nest for a total of 300 minutes, the male for a total of 138 minutes, and the eggs were neglected for 288 minutes. Despite the white-naped bird's increased participation, the nest was attended for only 60.4 per cent of the day, which was slightly less than at the earlier nest.

Even when a woodcreeper was in the hole, the bird did not incubate constantly but spent considerable time looking through the doorway. Each of the partners did this once for about 10 minutes and for many shorter periods. Sometimes, especially in 1956, the female came out and clung to the side of the stub by the doorway in order to stretch her wings, preen, and scratch her head, which she did while hanging to the bark by one foot and raising the other above her slightly relaxed wing, between it and her body. In order not to make the record too complicated, I did not take into account all these short interruptions to incubation, but considered each session to extend from the bird's arrival at the hole to its flying away. Often the incubating bird did not stay until its partner arrived; when it did wait for relief, it left the hole before the other entered, so that both were never inside together. After emerging from the cavity, often by passing sideways through the orifice, the departing woodcreeper usually climbed up the trunk for some distance before it took wing, but at times it appeared to fly right out through the narrow doorway.

When a Squirrel Cuckoo alighted near the nest, the white-naped woodcreeper, instead of staying inside beyond the larger bird's reach, hastily fled. Yet I have never seen a Squirrel Cuckoo harm any bird or its nest.

When it arrived to take a turn on the eggs, the woodcreeper often took in a flake of bark, and sometimes it emerged with a piece in its bill and carried it away. On one occasion, the female left with a flake of bark as her mate arrived with another flake. Thus the materials of the nest were constantly changing, but since more pieces were brought to the nest than were removed from it, the accumulation of bark flakes continued to grow throughout the course of incubation. In 15 hours of observation in 1956, the female took in seven pieces of bark and removed four pieces; the male took in five pieces and removed none. In 12 hours in 1958, the female brought six pieces and removed three; the male took in five pieces and carried away one.

In the nest in the palm stub, one egg was present on June 15, and the following day there were two. They were incubated by the Tawny-winged Dendrocincla, and one hatched on July 1. As the nestling grew older, its plumage and voice left no doubt that it was a woodcreeper rather than a dendrocincla. Thus the period of incubation of the Streaked-headed Woodcreeper's egg was about 15 days.

THE NESTLINGS

In 1956, I saw the white-naped woodcreeper enter the nest with a flake of bark on the afternoon of April 13, and early in the morning of April 16 the parents were carrying food into the hole. Evidently the eggs hatched in this interval. Later, when the nestlings were feathered, I sometimes saw two heads in the doorway simultaneously. Thus, it is improbable that the brood was larger than this, for woodcreepers seem usually to lay two eggs.

On April 16, when the nestlings were probably not over two days old, I watched their nest for the first 5 hours of the morning. Between 5:34 a.m., when the female ended her night session, and my departure at 10:36 a.m., the female brooded for seven periods, ranging from 4 to 43 minutes and totalling 131 minutes. The male brooded for five periods, ranging from 3 to 16 minutes and totalling 43 minutes. The nestlings were alone for nine periods, ranging from 2 to 33 minutes and totalling 128 minutes. In brooding, as in incubating, the female was the more attentive parent, but the disparity in their participation was now not so great as it had been while they incubated. In feeding the nestlings, the two parents took nearly equal shares, the female bringing food nine times and the male seven times. As far as I could see, they brought only small insects to the nest. To deliver these to the nestlings, each clung in the cavity with its head downward and the end of its long, chestnut tail visible in the round doorway. I did not see either parent remove a dropping. Some of the nestlings' food was evidently brought from a long distance, for on the preceding day I had seen the white-naped parent foraging in the forest, possibly 1000 feet from the nest.

On April 23, when the nestlings were about eight days old, I watched this nest from 7:00 to 11:00 a.m. Now the female alone brooded, for periods of 11, 2, and then 2 minutes. Later in the morning, she lingered in the nest for 7 minutes, with her head in the doorway and her bill open, panting. The male always left promptly after delivering food. He fed the nestlings 10 times, and the female fed them 11 times, making 21 meals for the two nestlings in 4 hours. Now, while the parents offered a meal to the nestlings with head downward, their chestnut tails projected about 2 inches from the doorway; a week earlier the end of the tail was barely visible inside the orifice. After delivering a meal, the parent turned around inside the hole and emerged headfirst. Once, however, the male managed to pass his morsel to a nestling while only halfway in the hole, and then he backed out. When he brought an unusually large insect which the unseen nestlings apparently had difficulty in swallowing, he trilled softly inside the hole. Later, I heard similar trills issuing from the cavity while the female was delivering food. Both parents now carried away droppings in their bills.

On April 30, from 7:00 to 11:00 a.m., the two nestlings, now about 15 days old, were fed 16 times by each parent, or a total of 32 meals in 4 hours. On each visit the parent brought a single insect, whose brown color suggested that it had been plucked from bark rather than from foliage. Frequently the insect brought had very long

antennae. The nestlings, now well feathered, came to the doorway for their meals, which were passed in to them while the parent clung in front. Having no longer any occasion to enter the cavity for the purpose of delivering food or brooding, the parents remained constantly outside. They no longer removed droppings, as they had done a week earlier, whence I inferred that the bottom of the nest was becoming foul. The young birds probably passed all their time clinging upright to the walls of the deep chamber and were not troubled by this growing accumulation of waste matter. They now uttered, chiefly at mealtime but sometimes while waiting for their parents to bring food, a trill which resembled that of the adults, but it was weaker, and less mellow and melodious. At times I saw two streaked, brown heads in the doorway together.

When a Turkey Buzzard perched in the top of the nest tree, the parent woodcreepers became greatly excited. They uttered over and over a short, sharp trill that suggested tenseness and anxiety, and at the same time they twitched their folded wings with little jerky movements. The sharp notes and wing-twitching continued for many minutes after I chased the vulture away.

On the evening of April 30, neither parent entered the hole to spend the night with the young. On the afternoon of May 3, at least one nestling remained in the hole, but early next morning the nest was empty. From the time that I first saw a parent carry in food on April 16, the young were in the nest at least 18 days, and possibly they were 19 days old at the time of their departure. After their exit, the hole was abandoned, and no member of the family returned to roost in it. I could not learn whether the parents led their offspring to some other snug hole at nightfall or left them clinging to a trunk in the open, while they themselves took shelter in cavities. A nest which I had watched some years earlier was likewise not used for roosting after the young emerged.

A month after the young woodcreepers left their nest, I saw the white-naped parent foraging over the trunks of the *Inga* trees, which shaded the coffee grove, in company with two young birds which closely resembled him in size and plumage. One pursued him as though for food, but it received nothing while it was in view.

In 1958, I last saw the white-naped woodcreeper take bark into the nest on April 10. The following day, he and his mate were bringing insects for newly hatched young. On April 21, I failed to see the white-naped bird at the nest. Two days later I heard, for the first time in weeks, the high, delicate courtship trill of the Streaked-headed Woodcreeper. On April 25, I watched the nest from 5:30 to 9:30 a.m., again without seeing the white-naped parent. A second adult was present, but he was a bird with normal plumage and was indistinguishable from the female. Doubtless it was he that gave the courtship trill when one woodcreeper passed the other on the branch above the nest. He also went without food to look into the nest, and he pecked or hammered at the doorway. I could not quite convince myself that he was bringing food; yet 21 meals in 4 hours, which compared favorably with the rate of feeding by both parents at the earlier nest, suggested that there were two attendants, as did two feedings close together early in the morning. Two days later, before I could settle this question, the doorway had been enlarged by some predator which tore away the surrounding wood, and the nestlings had vanished. At a height of 25 feet, this ill-fated nest was about 15 feet lower than the successful nest in the neighboring tree two years earlier.

The nestling Streaked-headed Woodcreeper in the palm trunk was reared by its

foster parent, the Tawny-winged *Dendrocincla*, on food different from that provided by woodcreeper parents. I saw it receive a number of small lizards, and green insects entered prominently into its diet. The woodcreepers that I watched brought mostly brown insects to their nest and no lizards. Despite this unusual regimen, the nestling woodcreeper thrived under the *dendrocincla*'s care, and it left the palm trunk when 19 days old.

SUMMARY

The Streaked-headed Woodcreeper inhabits woodland and clearings with scattered trees in regions of heavy and moderate rainfall. On the Pacific side of Central America, it occurs from sea level up to 4000 feet. It lives in pairs throughout the year.

Its flight is rarely long sustained, and it makes extended journeys by flying downward from a point high on one tree trunk to a point near the base of another trunk, climbing up this, taking a downwardly inclined course to a third, and so on, until it reaches its destination.

The woodcreeper subsists on insects, spiders, and other invertebrates, which it finds while creeping up the trunks of trees and outward along their branches, probing into crevices in the bark, prying off loose flakes to expose small animals hiding beneath them, and lifting tufts of moss. It rarely works downward, but after climbing high on one trunk, it flies to the lower part of another, which it then ascends.

Streaked-headed Woodcreepers roost singly in crannies and hollows in trees, usually well above the ground. Often the birds choose a cavity whose upwardly directed opening permits rain to enter, which suggests that concealment is more important to them than dryness. In the evening they retire after the light has grown very dim, and at dawn they are among the first birds to become active. When one woodcreeper attempted to join another, probably its mate, in its lodging, both flew out of the cavity in the dusk.

The common utterance of this woodcreeper is a long-drawn, soft, melodious trill, all on the same key. At all seasons, the mated male and female call back and forth with this same trill. As the nesting season approaches, a shorter, higher, more delicate trill is uttered, apparently by the male alone. Annoyance or alarm is expressed by a sharper trill, which sometimes becomes almost a *churr* and is delivered with twitching wings. At times the woodcreeper calls with a mournful single note.

In El General, Streaked-headed Woodcreepers begin prospecting for nest cavities in late February. For the nest site, a natural hollow in a dead or living tree is preferred to a woodpecker's hole, although the latter is sometimes used. The entrances to breeding nests ranged from 15 to about 80 feet above the ground, but the nests themselves were often situated well below their doorways. Nests were found in dead trees standing in new clearings near the forest and in shade trees of pastures and plantations; no nests were found in forest trees.

The nest itself is composed wholly of loose flakes of hard or corky bark, up to three and rarely five inches in length, which the woodcreepers pluck from trees, often tugging vigorously to detach them. Male and female share the task of building. When working alone, the birds are silent; when both work at the same time, they call back and forth with their usual trills. Once a pair spent much time carrying

flakes of bark into the space between a large, loose sheet of bark and the trunk from which it was breaking away, but breeding in such situations was not observed.

The set seems usually to consist of two white eggs, but few nests have been accessible for examination.

Incubation is performed by both sexes. A pair of which the supposed male was easily recognized by an abnormal patch of white on his nape was studied in two years. The partner in normal plumage, believed to be the female because it regularly occupied the nest by night, performed by far the greater part of the diurnal incubation at the first nest of this pair, but two years later the white-naped bird spent nearly half as much time on the eggs by day as she did. Sessions of incubation by either partner were rarely as long as an hour in fair weather. The eggs were frequently neglected by both parents, for intervals ranging from 2 to 41 minutes. At the first nest, the eggs were attended for 66 per cent of the 15 hours devoted to observation; at the second nest, they were attended for only 60 per cent of 12 hours.

Throughout the period of incubation, both partners frequently brought a flake of bark when coming to take a turn on the eggs, and less often they carried a piece of bark from the nest as they left.

A pair of Streaked-headed Woodcreepers and a Tawny-winged Dendrocincla carried nest material alternately into the same hollow palm trunk. Two eggs were laid by the female woodcreeper, but they were incubated by the dendrocincla. These eggs hatched in about 15 days.

The young are fed by both parents, chiefly with brownish insects, brought singly. Feeding rates ranged from 1.6 times per nestling per hour when the nestlings were a day or two old to 4 times per nestling per hour when they were about 15 days old. Both parents brooded, but the female did so for longer periods, and, as the nestlings grew older, she continued to brood after the male had ceased.

Droppings were, at first, apparently swallowed by the parents. Later, they were carried out of the nest in the bills of the parents. Finally, when the nestlings took their meals through the doorway and the parents no longer had occasion to enter the hole, the sanitation of the nest was neglected.

As they grew older, the nestlings uttered a weak version of the adults' trill. Two nestlings left their high hole at the age of 18 or 19 days. A single nestling reared by a Tawny-winged Dendrocincla, which gave it small lizards and other food of kinds not brought to their nests by parent woodcreepers, left the nest when it was 19 days old. After the departure of the young, neither the fledglings nor the adult woodcreepers returned to sleep in the nest cavity.

SPOTTED-CROWNED WOODCREEPER¹

Lepidocolaptes affinis

The Spotted-crowned or Allied Woodcreeper is the highland counterpart of the Streaked-headed Woodcreeper, from which it differs chiefly in its slightly larger size. It has spots rather than streaks of buff on its brown head and hindneck and few or no streaks on its back. It ranges through the mountains from eastern and southern México to western Panamá. In Guatemala it occurs from about 5000 to 10,000 feet above sea level, where it is fairly abundant in the mixed forests of pine, oak, alder, arbutus, and other broad-leaved trees that cover much of the more elevated portions of the country. It is not rare even in the nearly pure stands of cypress (*Cupressus Benthamii*) on the mountain tops between 9000 and 10,000 feet. An anomaly in a heat-loving family, the Spotted-crowned Woodcreeper lives at heights where severe nocturnal frosts are frequent in the winter months. In Costa Rica and adjacent parts of Panamá, its altitudinal range is similar. Here it dwells in mossy, epiphyte-burdened forests composed of a great variety of broad-leaved trees, including many oaks and alders. From the woodlands it enters adjoining clearings with scattered trees to forage and to nest.

In the Guatemalan highlands above 7000 feet, I found Spotted-crowned Woodcreepers in pairs throughout the year. When not breeding, they wandered through the woods in company with other small birds, both residents and winter visitants. There was hardly ever more than one pair of woodcreepers in a single mixed flock, a situation which suggested that they defended a territory even in winter.

FOOD

In its mode of foraging, this woodcreeper differs little from its lowland congener. Nearly all its hunting is done as it climbs up vertical trunks and creeps outward along lateral branches, much in the manner of the smaller Brown Creeper which, in the Guatemalan highlands, sometimes forages in the same tree. Rarely the woodcreeper reverses its course and for a short distance descends a trunk with its head downward. It appears to subsist wholly on the insects, spiders, and other invertebrates which its slender bill extracts from chinks and crevices in the bark or from among the moss and lichens that cover the trunks and limbs in the cloud-bathed highland forests. I never saw this woodcreeper eat fruit.

VOICE

The song of the Spotted-crowned Woodcreeper is a rapid sequence of weak, melancholy notes, quite different from the beautiful, soft, clear trill of its lowland relative, the Streaked-headed Woodcreeper. The striking difference in voice is the best means of distinguishing these two closely similar species. The call of the Spotted-crowned Woodcreeper is a plaintive note, between a whistle and a squeak.

SLEEPING

Like other members of its family, the Spotted-crowned Woodcreeper sleeps singly in cavities in trees. It retires late, when the light has grown so dim that its

¹ This life history is an abridgement of Skutch, 1945a, with the addition of later observations.

brown form fuses with the dusky boles up which it creeps, so that it would be most difficult to follow to its dormitory if it did not use its voice freely as it goes to rest. Likewise, it darts forth from its sleeping chamber in the dim light of early dawn, long before woodpeckers and toucans emerge from their holes. From July until the following March, a solitary woodcreeper lodged in a narrow natural cavity near the top of a low, barkless stub, standing in a pasture near the forest's edge in the Costa Rican mountains. On the evening of July 27, it carried a fragment of bark as it entered its hole for the night, although the nesting season was long past. Another woodcreeper roosted for a while in a neighboring pasture, in a thick, hollow stump that was entered through a gap about 2 feet long and 6 inches in width. Apparently, the bird lodged in this exposed cavity only until it could find a snug crevice with a narrow opening, for by the end of the month it no longer slept here.

NEST AND EGGS

On the Sierra de Tecpán in the Guatemalan highlands, I found a single nest at an altitude of about 8500 feet. It was at the edge of a tract of woods, in an oak tree which had apparently been cut down many years earlier. The upright shoots which had sprung from the living stump had thickened to form massive upright branches that pressed close together, leaving narrow crevices between them. The woodcreepers had built their nest in a cranny in the midst of the branches, reached through a gap between two of them. The opening was only 5 feet above the ground and was so narrow that I could not insert my flattened hand. At the end of April, the shrill cries of nestlings emerged through the cleft between the branches, but it was impossible to see them even with a light and mirror.

At Vara Blanca, between 5000 and 6000 feet above sea level in the Costa Rican mountains, I found three occupied nests in April, May, and June. All were in decaying trunks standing in clearings, not far from the forest. The narrow, inconspicuous doorways of these nests were at heights of 18, 23, and 26 feet above the ground. The lowest cavity, in a massive trunk that had been nearly consumed by fire and rot, extended about 11 inches below the entrance. From front to back it measured 6 inches and from side to side about 9 inches, but because of its irregularity these figures are only approximate. In inserting a ruler to measure this chamber, I inadvertently knocked several small chunks from its excessively decayed sides. In the rear wall were chinks through which light entered the chamber. Its front wall consisted of only a thin layer of hard, resistant bark. The bottom was covered with small, thin flakes of stiff bark, upon which, with no softer lining, the eggs rested. Although this nest chamber was far more spacious than necessary, the gap in the covering of bark through which the woodcreepers entered, $2\frac{1}{8}$ inches in height by a scant inch in width, was barely wide enough for them to squeeze through by turning sideways, with their wings toward the ends of the elongated crevice.

The second nest was in an old hole made by the Prong-billed Barbet. A small, fat bracket fungus, overgrown with moss that hung in loose strands around its edges, grew immediately above the narrow, round doorway and, bulging out below, constricted this orifice, making it difficult to detect from the ground and entirely shielding it from above. The floor of the deep, regular chamber was likewise covered with flakes of hard bark which the woodcreepers had carried in. The third nest, in a natural fissure in a badly decayed trunk, was entered through a narrow, vertical cleft about as long as the woodcreepers themselves. I did not examine its interior.



Fig. 22. Subtropical forest on the Barba massif, Cordillera Central of Costa Rica, at about 7500 feet above sea level. Spotted-crowned Woodcreepers and Hairy Woodpeckers lived in this woodland and adjoining pastures.

All three nests were so cunningly concealed that they were discovered only by seeing the owners enter or leave.

The first Costa Rican nest contained two eggs when found on April 19. The following day they hatched. The second nest held two eggs when first examined on May 10; the third held an unknown number of young on June 16.

Years later, nearly 7000 feet up on the Cordillera Central of Costa Rica, I found a nest in a very different situation. It was in a cavity at the base of the irregular trunk of a large cypress, one of a row of such trees that had been planted between two pastures far from forest. The entrance, an irregular vertical slit too narrow to admit my hand, was only 2 feet above the ground. In March, I watched a pair of woodcreepers examining this cavity, but thereafter it remained untenanted for so long that I lost interest in it. However, on April 21 there was an egg in it, lying on some pieces of bark, and on the following day the second egg was laid. The eggs of this species, apparently always two in a set, are pure white and equally blunt at the ends.

INCUBATION

The pair nesting in the old barbet hole were so indifferent to my presence that I watched them while sitting on a log, without concealment of any kind. Both sexes incubated, as was evident from the numerous changeovers which I witnessed. In 6

hours of the morning, they took 10 sessions that ranged from 6 to 47 minutes and averaged 26.7 minutes. Usually each member of the pair remained with the eggs until its mate came to replace it, but sometimes, for unknown reasons, it flew off after sitting for only a short while and left the nest unattended. There were only four such periods of neglect, ranging from 3 to 31 minutes and totalling 58 minutes. Together the two birds covered the eggs for 82 per cent of the 6 hours of observation. Once the incubating bird, hearing its mate call in the neighboring forest, answered with its melancholy trill from within the hole, but usually it sat in silence. At night a single woodcreeper, of undetermined sex, slept in the nest.

The changeover was usually effected without vocal sound. The bird in the hole seemed to become aware of its mate's arrival by the slight noise it made as it flew against the trunk, usually at a point several yards below the doorway. This was the signal for the incubating bird to come forth. It could distinguish this sound from that made by other birds alighting on the trunk. A pair of Masked Tityras, building their nest in a hole higher up, frequently landed on the top and sides of the trunk, yet the woodcreeper which was incubating never came out as they did so. Each partner left, headfirst, before the other entered; I did not once see them in the hole together, as happened at another, more spacious nest.

Often the woodcreeper returning to incubate brought a piece or two of bark. Not only did these birds bring material to the nest, but they also threw things out of it. Once a piece of bark an inch long and several times dusty matter, probably debris of decaying wood from the bottom, were ejected through the doorway while the woodcreepers incubated. One afternoon, both members of the pair actively carried in flakes of bark which they broke from neighboring dead trees. They brought such material several times, and one slipped into the nest with its burden while a ladder was being raised against the trunk. The other, more shy, would not enter until my helper and I had retired a short distance. It then entered the cavity, although we stood in plain view. On this date, incubation had been in progress for about ten days. Two days later, I watched for similar activity in the early afternoon, but between 1:00 and 3:00 p.m. the woodcreepers brought material no more often than they had done on the morning of the preceding day. They continued to carry bark into their hole until their eggs hatched. Since both parents added to the nest after the eggs were laid, I inferred that they had built it together, as in the Streaked-headed Woodcreeper.

At times, Spotted-crowned Woodcreepers, when incubating or brooding, sit with such constancy that loud hammering on the trunk will not even bring them to the doorway to look out. Such secretive behavior adds to the difficulty of discovering their well-hidden nests. At other times, however, a parent in the same nest may be brought into the open by slight tapping on the base of the trunk, or it may look out as one walks heavily toward the tree.

The nest in the cypress tree in a pasture was close to an unpaved road. When the incubating bird heard the footsteps of an approaching pedestrian, it clung in the doorway and watched him pass. If I walked over the grass directly toward the nest, the bird would stay in the doorway, head up, and watch me come almost within arm's length. Then it would climb up the trunk and fly away.

At this nest, the second egg was laid on April 22; one egg hatched by daybreak on May 9 and the other before nightfall, after an incubation period of 17 days.

THE NESTLINGS

The newly hatched nestlings had tightly closed eyes, pink skin, and fairly abundant dark gray down. The mouth lining was deep yellow, and the flanges at the corners were whitish. The parents soon removed the empty shells. Feather rudiments began to sprout when the nestlings were about five days old. At the age of eight days, they bristled with long, conspicuous pinfeathers, and the remiges were just beginning to burst from the ends of their sheaths. Now, while waiting for their parents to come with food, the nestlings continually repeated high-pitched cries that were audible at a distance of 200 feet. When two weeks old, the young woodcreepers were well clothed with plumage and, on their upper parts at least, closely resembled their parents, even to their spotted heads. Some days earlier, their high-pitched cries had changed to a weak version of the adult trill, and they repeated this incessantly while waiting for their meals. But they became silent when a squirrel climbed over their rotting trunk, scratching loudly with its claws, and once passing directly over their doorway. When about 16 days old, the nestlings began to receive their food through the doorway, thus sparing the parents the necessity of forcing their way through the narrow aperture. Now from time to time I could see their brown, slender-billed heads as they took brief glimpses of the outside world.

Both parents brooded the young and fed them at a fairly rapid rate. In the first 2½ hours of the morning after they hatched, two nestlings received food 12 times. Aside from a small green larva, the articles given to them could not be identified. In 1½ hours of observation on May 3, the two nestlings, now 13 days old, were given 22 meals, consisting chiefly of insects and insect larvae. They were never given vegetable matter, as far as I could see. The parents removed droppings only as long as they were obliged to enter the chamber to feed the young. When all food was delivered through the doorway, they quite neglected the nest's sanitation, and the flake of bark on the bottom of the cavity soon became covered with droppings. Since the young birds now spent much of the day clinging to the sides of the deep chamber, and since they doubtless slept in this position, the dirtiness of the cavity's floor probably did not bother them. After the young were 12 days old, they passed the night alone; brooding had now come to an end. Their expanding plumage seemed already to afford sufficient protection in the sheltered nest.

At two nests, the parents arriving with food would alight on the trunk some distance below the doorway, then climb up to it. Sometimes one of them continued above the opening, paused to look around, then descended the trunk tail first, with the body upright, until it regained the level of the entrance. Usually the bird sidled somewhat obliquely downward, but once it hitched straight down for about 18 inches, just as a woodpecker would have done in similar circumstances. At the nest in the old barbets' hole, the tails of both parents were badly damaged by squeezing beneath the bracket fungus on their innumerable passages in and out of the narrow doorway. Both birds lost several of their central tail feathers, but even without these longest rectrices, they managed to climb up the trunks with their customary ease, using the lateral tail feathers as props.

The latest of three nests at Vara Blanca was 5 feet directly below a cavity occupied by Blue-and-White Swallows. In mid-June, both pairs of parents were feeding nestlings. At least one of the woodcreepers was greatly interested in the offspring of its neighbors. After feeding its own nestlings, it sometimes climbed up

the trunk and delayed a few minutes beside the entrance of the swallows' nest. The agitated swallows circled in the air, uttering notes of complaint and swooping at their visitor. Sometimes they came so near the woodcreeper that, to avoid them, it would drop down several feet, deftly catching itself in an upright position lower on the trunk. Usually, however, the bird took little notice of the swallows' protests and hostile demonstrations. Once, while a swallow was inside the nest cavity with its nestlings, the woodcreeper several times started to enter but was apparently deterred by the swallow's usual threat—a widely gaping mouth, probably accompanied by a hiss. Finally, becoming bolder, the woodcreeper stuck its head through the doorway, picked up a white dropping along with a straw from the swallow's nest, and flew off with them.

From two nests which I could reach, the nestling woodcreepers flew forth when 19 days old. Neither they nor their parents returned to sleep in the now heavily soiled chambers. I could not learn whether the parents led the fledglings to some other dormitory or left them to roost clinging to trunks in the open until each could find its own shelter. The woodcreeper which in July I found lodging in a hollow trunk with a gaping side may well have been one of the young from a neighboring nest, whose parents had not shown it a more suitable dormitory. Even if the woodcreepers do not, like some wrens and woodpeckers, provide shelter for their fledglings, they continue to feed them for a good while. A month after leaving the nest in the old barbets' hole, one of the young woodcreepers still received food from a parent, easily recognized by its damaged tail. As the same time, the young woodcreeper, now 50 days old, was finding part of its own nourishment.

Apparently the Spotted-crowned Woodcreeper rears a single brood each year.

SUMMARY

The Spotted-crowned Woodcreeper ranges in the mountains from eastern and southern México to western Panamá. In Guatemala, Costa Rica, and adjacent Panamá, it occurs from 5000 to 10,000 feet. It is paired throughout the year.

It forages on trunks and horizontal branches, subsisting wholly on insects, spiders, and other invertebrates which it extracts from bark, moss, and lichens.

This woodcreeper sleeps singly in cavities in trees, retiring late in the day when the light is dim. It arises early at dawn, before most other hole-roosting birds become active.

Its song is a rapid sequence of weak notes, quite different from the soft, clear trill of its lowland congener, the Streaked-headed Woodcreeper. Its call is a plaintive note, between a whistle and a squeak.

Occupied nests of this species are found in April, May, and June. They may be placed in natural cavities or fissures in tree trunks, or in holes made in trunks by other birds. Five nests were placed at heights of 2, 5, 18, 23, and 26 feet. The nest floor is covered with small flakes of hard, thin bark.

The eggs, apparently always two in a set, are pure white and equally blunt at the ends. Both sexes incubate; usually the incubating bird waits for its mate to replace it on the eggs. Sessions of incubation ranged from 6 to 47 minutes and averaged 26.7 minutes. The eggs were covered for 82 per cent of the 6 hours of observation. Often, the birds brought bark to the nest when coming to incubate; they also threw bark and other material from the nest cavity during incubation. The incubation period at one nest was 17 days.

The newly hatched nestlings had tightly closed eyes, pink skin, and fairly abundant dark gray down. When eight days old they bristled with long pin feathers and gave repeated high-pitched cries while waiting for the adults to bring food. At 14 days of age, they were well feathered; between 8 and 14 days of age their cries had changed to weak versions of the adult trill. When about 16 days old, they received their food through the entrance of the cavity.

Both adults brooded the young and fed them, bringing chiefly larval and adult insects; they brought no vegetable material. They removed droppings until they were able to deliver food through the cavity entrance; at this point sanitation was neglected.

From two nests, the young fledged when 19 days old. No member of the family returned to sleep in the nest chamber. One young woodcreeper 50 days old was still being fed by an adult, although it was also obtaining at least part of its own food.

This species apparently raises one brood a year.

WEDGE-BILLED WOODCREEPER

Glyphorhynchus spirurus

One of the smallest of the woodcreepers, this short-billed brown bird is about five and three quarters inches in length. In both sexes, the top of the head is sooty brown. The back is russet-brown, which brightens to cinnamon-rufous on the rump, upper tail-coverts, and tail. A patch of ochraceous-buff, visible chiefly when the bird is in flight, adorns each russet-brown wing. There is a narrow buffy stripe above each eye. The cheeks are dark brown, finely flecked with buff. The feathers of the chin and throat are buff with dusky margins. The remaining ventral plumage is largely tawny-olive, with conspicuous wedge-shaped marks of light buff on the chest. The short, wedge-shaped bill has a blackish upper mandible and a lighter lower mandible. The eyes are brown and the feet are blackish.

The Wedge-billed Woodcreeper ranges from southern México to Bolivia and Brazil. An inhabitant of the more humid forests, in Central America it is found throughout the length of the Caribbean side but on the Pacific side it occurs only to the south of the Gulf of Nicoya. Most abundant in the lowlands, it extends in decreasing numbers far up into the mountains. In Costa Rica, I have found it up to nearly 5000 feet, and on the Volcán Chiriquí in Panamá, where a number of lowland species extend to unusually high elevations, it has been recorded up to 7000 feet (Ridgway, 1911:277). In northern Central America, the species is rare and is confined to the lowlands.

Using the rigid tail feathers as support for its upright body, the Wedge-bill climbs up the trunk of a forest tree, then flies down to repeat the process on a neighboring tree. As it slowly ascends, it incessantly strikes the bark with its short, pointed, dark bill. Its head is almost continuously in such rapid motion that it is difficult to see just what the bird does, but it appears to be plucking numerous minute organisms from the bark. Occasionally, with an upward movement of its bill, it knocks off a small flake of bark. It scarcely ever eats an object large enough to be visible to an observer on the ground. Rarely it reverses its movements and slides downward, tail foremost, for a short distance.

In the vicinity of Puyo in the Province of Napo-Pastaza in Ecuador, at an altitude of about 3000 feet in the eastern foothills of the Andes, this little woodcreeper was the only representative of the family that I found in the forests and clearings in the course of seven weeks. Here it seemed more abundant than I have found it at corresponding altitudes in Central America. In late August, I discovered a Wedge-bill roosting in the top of a low stub of *Heliocarpus* standing in a clearing. The bird was in a cavity resulting from the decay of the very soft wood. Like the larger woodcreepers whose dormitories I have found, it slept alone, and it retired late, after the light had become dim. The Wedge-bill entered its dormitory 40 minutes after the last of the three Lafresnaye Piculets which slept in a hole they had carved low in the same stub.

In the Sarapiquí lowlands of northeastern Costa Rica, the Wedge-bill is most abundant, not only in the heavy forest but in adjoining cacao plantations with scattered shade trees. Here, in 1967, I found one of these woodcreepers roosting in an unusual situation. In front of the house at "La Selva" was an old, decaying

stump of some massive tree with buttresses. In the twilight of several evenings in May, I saw a Wedge-bill emerge from the neighboring forest and fly to this stump. Attempts to see it during the night failed because it slept lightly and flew out as I approached with a flashlight. Evidently it roosted clinging upright in the open furrow between two of the plank buttresses, within a yard of the ground, for I found no cavity which it might have entered.

The Wedge-bill's song is a fine, very rapid trill that tapers off sharply. This slight, appealing song resembles that of one of the weaker-voiced of the wood warblers. In late March, one Wedge-bill repeated his rapid trill again and again as he crept over a great trunk irregularly fluted with ridges and deep furrows, investigating the channels and climbing down into the closed spaces to which they led. He was alone and appeared to be prospecting for a nest site. Late on an afternoon in May, I heard two Wedge-bills singing back and forth as they climbed up neighboring trunks in the forest. Each uttered a rapid trill followed by four stronger notes that were more widely spaced.

The call is a fine, sharp *chip* which may be rapidly repeated a number of times.

NESTING

While I wandered beneath great trees in the valley of El General on June 16, 1939, a small brown bird darted out of a cavity in a badly decayed stump, not far from a small, clear rivulet. Uttering a sharp *chip*, the bird flew off through the undergrowth of tall, slender saplings too rapidly to be identified, nor would it return while I watched from a distance. Accordingly, I left and revisited the stump later in the morning. I happened to come in view of it just as a brown bird alighted beside the cavity's narrow entrance to relieve its mate, which darted out and away. Becoming aware of my approach, the new arrival flitted to a neighboring slender tree, where it clung upright, keeping behind the trunk and peering around at me now on one side, now on the other, and repeating a sharp, nervous *chip*.

Having identified the owners of the newly found nest as Wedge-billed Woodcreepers, I proceeded to examine the cavity with greater care. The massive stump in which it was hidden was far advanced in decay, and it bore on its irregular summit a great-leafed aroid, a species of *Monstera* with perforated leaves. The lower end of the nest's doorway was only 31 inches above the ground. The opening, long and narrow, measured $2\frac{3}{4}$ inches in height and only $1\frac{3}{16}$ inch in width at its widest point. As I later saw, the Wedge-bills were obliged to pass through the opening sideways, with their wings toward the ends of the elongate slit, in the way that Spotted-crowned Woodcreepers and other larger members of the family sometimes enter and leave their nests. This narrow aperture gave access to an irregular, deep chamber, resulting from decay, very spacious for birds so small and slender. On the bottom was a lining of fine, dark, fibrous material, upon which rested two pure white, glossy eggs, slightly ovate in form.

That same afternoon I set my blind before this, my first, Wedge-bill's nest, and all of the following morning I watched it. Both sexes incubated, each remaining in the hole until relieved by the other, so that they kept the eggs constantly covered. Usually the bird which had been in attendance flew out as its mate alighted close by the doorway, and then the newcomer entered. Once, when the new arrival hurried in before the emergence of the other, it promptly came out and clung beside

the orifice until the other left, whereupon it entered for its turn on the eggs. Each partner sometimes brought a billful of fine, fibrous material when it came for its turn at incubation, which suggested that both had built the nest.

Although I could not distinguish the sexes of these birds, their regular alternation in the nest enabled me to keep them distinct, and I called them "A" and "B." A's three completed sessions lasted 18, 86, and 90 minutes. B's two completed sessions lasted 40 and 68 minutes. Five sessions by both sexes averaged 60.4 minutes. Once I heard B utter a fine trill in the nest just before leaving, and later B trilled as it alighted on a neighboring trunk. A was in the habit of voicing a rapid series of fine, sharp notes as it flew away, and sometimes it gave a single one of these *chip*'s as it entered the nest, but I did not hear A sing. Apparently B was the male of this pair.

By June 26 there were two pink-skinned nestlings with long, dark gray down. The interior of their mouths was yellow. My departure from this locality prevented further observations at this nest.

I found no other nest of the Wedge-bill until June 4, 1967, when I discovered one in the Sarapiquí lowlands. This was at the base of the massive trunk of one of the *Pentaclethra macroloba* trees so abundant in the wet forests of that region. It was situated in a cranny among the irregularly projecting buttresses or upward extensions of the roots of the living tree. The lowest part of the vertically elongated entrance was only 14 inches above the ground. The two white eggs, already soiled, rested about 5 inches below this opening, on a pad of dark, fibrous materials. In the middle of the morning, they were illuminated by a bright sunbeam that penetrated the woodland canopy and fell on the nest. By June 9, these eggs had hatched.

From published records, it appears that the Wedge-billed Woodcreeper frequently, and perhaps usually, selects a low cavity for its nest. In British Guiana, Beebe and Beebe (1910) found a nest which was evidently lower than a man's head, and in Nicaragua, Richmond (1893) discovered one the doorway of which was only 10 inches above the ground, while the nest itself was at, or possibly below, ground level. A nest found by Carriker (1910:649), at an altitude of about 2000 feet on the Caribbean slope of Costa Rica on April 17, 1903, contained eggs the incubation of which was already far advanced. Richmond's nest in Nicaragua held eggs on May 26. These two records, taken with mine, indicate that in southern Central America the breeding season extends at least from early April into July. In British Guiana, however, Beebe (1925a:155) found evidence of breeding from June to November. Although only two eggs were found in the Central American nests of this species, Beebe's low nest in British Guiana held three. Carriker gave the measurements of two eggs as 19 by 12 mm.

SUMMARY

The Wedge-billed Woodcreeper inhabits humid woodland from sea level up to 5000 feet and occasionally even to 7000 feet in southern Central America, but it is most common in the lowlands.

As this woodcreeper climbs up tree trunks, it constantly strikes the bark with very rapid motions of its head. Occasionally it knocks off a flake of bark with an upward movement of its bill. It seems to subsist principally on organisms available in large numbers but too small to be seen by an observer on the ground.

A Wedge-bill slept alone in a cavity resulting from decay, located in the top of a stub in a forest clearing. The bird went to rest late in the evening, after the light had become dim.

The song is a fine, rapid trill that seems to taper off to a sharp point. The call is a sharp *chip*, often rapidly repeated.

A nest found in Costa Rica in mid-June was in a fairly spacious cavity in a massive, rotting stump in the forest. The entrance, only 31 inches above the ground, was an elongated slit so narrow that the birds had to turn sideways to pass through. In the bottom of the chamber, two white eggs rested on a bed of dark, fibrous material. The doorway of another nest, in a cranny at the base of a living forest tree, was only 14 inches above the ground. This nest also held two eggs, in early June.

In the course of a morning, the two parents, sitting alternately for periods which ranged from 18 to 90 minutes, kept the eggs constantly covered. Both brought fibers as they came for a turn at incubation. The incubation period is unknown.

The nestlings had pink skin with long, dark gray down, and the interior of their mouths was yellow. The nestling period is unknown.

TAWNY-WINGED DENDROCINCLA

Dendrocincla anabatina

The dendrocinclas are woodcreepers of medium or rather large size, with a straight bill of moderate length and generally brown or rufous plumage without prominent streaks. Although not terrestrial, they stay nearer the ground than most members of this scansorial family. The Tawny-winged *Dendrocincla* is one of the more distinctively colored species in this plainly attired genus. It is about seven and a quarter inches in length. In both sexes, the pileum, hindneck, and back are dark olive-brown. The rump is lighter brown, shading into cinnamon-rufous on the upper tail-coverts and the tail. The wing-coverts are brown like the back, but the remiges are tawny with dusky ends. The sides of the head are brown, with a narrow light streak that begins at the upper edge of the eye and extends above the ear-coverts. The chin and throat are pale buff, and the remaining under parts are light olive-brown, becoming more cinnamonaceous on the abdomen and under tail-coverts. The eyes are yellowish brown, the bill is black, and the feet are blackish. The creamy feathers of the chin are often puffed out prominently, and along with the large tawny patch with a dark border displayed by each spread wing, they provide a good identification mark. But on some individuals or in some aspects, the chin and throat are not conspicuously lighter than the breast.

The species ranges from southern México to western Panamá. From central Costa Rica northward, it is confined to the more humid Caribbean side, but in southern Costa Rica and Panamá, it is found only on the Pacific side, being replaced by the Plain-brown *Dendrocincla* on the eastern side of the Cordillera. In southern Costa Rica, it is fairly abundant from sea level up to 4000 feet, and near the Panamanian border I found it sparingly present at 5000 feet.

The Tawny-winged *Dendrocincla* lives near the ground in the heavy forest and taller second-growth woods, but it sometimes ventures forth into adjacent clearings to take advantage of a favorable nest site. Its flight is swift and slightly undulatory. Its social habits are confusing. I have most often found it following army ants, and in November, December, and January I have sometimes seen two individuals keeping amicable company as though they were mated. Yet when I studied nests of this species, I never received even a suggestion that the female had a partner. Moreover, there is often only a single dendrocincla with a swarm of army ants, and if two are present, they are at times extremely antagonistic toward each other. In the lowland forests near the Golfo Dulce, where this woodcreeper is more abundant than in the elevated basin of El General, a large swarm of army ants was accompanied by four dendrocinclas in December. One frequently flew at another and chased it away. Probably two pairs were present, and one pair was intolerant of the other.

In El General, where I have rarely seen more than two dendrocinclas in a mixed flock of birds that attended army ants, one often chases another. As they fly rapidly from tree trunk to tree trunk, the tawny patches on their wings make a fine display. In early May, I witnessed a fierce encounter between two dendrocinclas that tried to forage with the same swarm of ants. First, they grappled and fell to the ground. When they arose, one fled screaming, with the other in hot pursuit. The fugitive flew to an upright trunk and hung there with the assailant clinging to its back, and

for a while it tried vainly to turn its head and rid itself of its tormentor. This continued for what seemed a good while, although actually it was probably only a few seconds before the two flew off together, and I lost sight of them. Although in the motley crowd of birds which follow the army ants and compete for the insects they stir up, one individual often chases another of its own or a different species, these pursuits are usually mild and rarely result in contact. The encounter between the two Tawny-winged *Dendrocinclas* is the only serious conflict that I can recall having watched in these circumstances. Afterward, only one Tawny-winged *Dendrocincla* and one Ruddy *Dendrocincla* foraged with this swarm of ants. The former often chased the latter, which is the rarer species in El General.

The Tawny-winged *Dendrocincla* is the most unsociable, aggressive small bird that I have studied in tropical America, putting to flight other woodcreepers larger than itself, and even forcibly evicting woodpeckers from their holes. Numerous instances of this bird's pugnacity will appear in the course of this life history.

The available evidence suggests that a male and a female keep company through the early months of the year and until the female begins to incubate, after which they become intolerant of each other. But it would be difficult to prove this of a retiring forest bird the nests of which are seldom found.

FORAGING AND ANTING

The Tawny-winged *Dendrocincla* hunts over the lower parts of the trunks rather than high in the trees like many other woodcreepers. Whenever possible, it seems to take advantage of the army ants to drive from concealment and make readily available the small creatures on which it subsists. In this it resembles the Plain-brown *Dendrocincla*, the Ruddy *Dendrocincla*, and the Barred Woodcreeper. I have often found a Tawny-winged *Dendrocincla* foraging with ants near a Barred Woodcreeper or a Ruddy *Dendrocincla*, and sometimes I have seen these three dendrocolaptine species in the same mixed flock of small birds. All four of these ant-followers pursue the same tactics: they cling upright to a trunk of a large tree or even a sapling, close above the ants that scurry over and through the ground litter, and when they spy a suitable insect or other small animal that the ants have driven into the open, they drop down, seize it in their bill, and return to a tree to devour it. Sometimes they cling to a trunk close beside a column of ants that stream up and down it, catching the small creatures that the hunters drive out of the crevices, or perhaps stealing them from the ants themselves. They do not intentionally eat the ants. In British Honduras, Willis (1960a:158-159) found Tawny-winged *Dendrocinclas*, Ruddy *Dendrocinclas*, and Barred Woodcreepers foraging with army ants, much as they do in Costa Rica.

Of the seven kinds of birds that followed the previously mentioned swarm of army ants in the heavy forest near the Golfo Dulce, the *dendrocinclas* were the most fearless of me, and during the three hours which I spent with this mixed company, they engaged a larger share of my attention. Often I had two or three in sight at one time, and occasionally I saw four of them. Sometimes they clung to upright or leaning trunks only three or four yards from me. One *dendrocincla* flew up and plucked an insect from the surface of a palm frond which I could touch from where I stood. They picked the small fugitives from the bark of trees, the foliage, and the ground. Close beside a small rivulet, one captured a large black spider of

dangerous aspect, and after knocking the victim against a trunk for a while, the captor swallowed it with an effort.

Soon after I fell in with this crowd of birds and ants, a dendrocincla flew to a trunk up which the army ants were swarming, picked up an ant or some other insect, touched or rubbed it rapidly beneath an outstretched wing, then seemed to swallow it. Again and again, this bird plucked an insect from the same trunk, at a point 12 or 15 feet above the ground, then clung to another slender trunk or an ascending branch, where it partly spread its wings and turned its tail forward. Clinging in this strained posture, it placed the captive insect beneath a wing with a very rapid movement, or at times appeared to rub it against the ventral surface of the tail, after which it seemed to swallow the insect.

I saw no more of this odd behavior until nearly three hours later. The *Eciton* ants were again swarming along a slender trunk which bore a number of epiphytes. Of a sudden, a dendrocincla flew up to the trunk, seized an insect, rubbed it against a wing, then ate it. At the same time, another dendrocincla darted up to the same trunk from the other side, picked up a similar object, carried it to a neighboring tree, and rubbed it against the inner surface of its wing as the first had done. Both of these birds repeated this act a number of times. The first was only eight or ten feet from me, and I saw clearly that it swallowed each insect after placing it momentarily beneath a wing. The insects so treated appeared to be ants, but they were much larger than the army ants. Probably they were ants of some other species whose arboreal nest the *Eciton* ants had invaded. At about the same time that the two dendrocinclas anted simultaneously, I saw the army ants carry a number of white objects down the trunk from which these birds picked the insects which they used. The white bodies were apparently the larvae or pupae of the unfortunate larger ants, but they were carried out of sight while my attention was engaged by the dendrocinclas.

On an occasion some years later when a dendrocincla anted on a trunk up which army ants were swarming, the objects which she snatched from among them to rub beneath her wings again seemed larger than the army ants and were apparently some other kind of ant whose nest was being pillaged by the hunting horde.

At nests which I watched, the parents brought, in addition to a variety of large and small insects and some spiders, many small lizards. Whether these reptiles were captured as they fled from army ants or in some other situation, I did not learn. Dendrocinclas are skillful flycatchers, often darting far out from a trunk to catch an insect in the air.

SLEEPING

Throughout the year, Tawny-winged Dendrocinclas roost in cavities in trees, always singly, except when they are brooding nestlings. In mid-August of 1959, I learned that a lone dendrocincla was sleeping in a low, hollow stub in the forest, in which a pair of Black-faced Antthrushes had already raised four broods, two of them earlier in the same year. On August 20, I watched the dendrocincla emerge from this cavity while the dawn light was still very dim. Possibly this bird was preparing to nest here, as on several occasions I found it in the hole after sunrise, and on the antthrushes' nest were a few pieces of material which this intruder might have placed there. However this may be, the dendrocincla slept but never nested in this

cavity, which a few days later contained the third set of eggs that the female ant-thrush laid there in the same year.

In 1960, 1961, and 1962, a dendrocincla nested in holes which woodpeckers had carved in a dying avocado tree in a small coffee grove near our house. During three months after the departure of her nestlings in mid-May of 1960, the parent sometimes slept in the cavity where she had nested, but she apparently had alternative lodgings, for on some evenings she stayed away. Like other woodcreepers, she retired late in the evening, when the light had become very dim, and she flew forth in the first gray light of the new day. Usually she repeated her mournful call many times before she entered her lodging in the dusk.

From August of 1960 until the end of the year, I lost track of this dendrocincla. Returning to the coffee plantation late in January of 1961, she found a male and a female Golden-naped Woodpecker lodging in different holes which they had carved in the old avocado tree, and she proceeded to dispossess them. Woodpeckers retire much earlier than dendrocinclas, and when these Golden-napes came to their holes in the evening, she often rushed at them, repeating her melancholy cries, so fiercely that they fled with excited *churr*'s. Sometimes she grappled with them in the air and feathers fell, probably only from the woodpeckers. Often the persecuted woodpeckers would retire into a hole in a neighboring tree rather than confront this termagant in the avocado, but sometimes they would slip into their places in the avocado while their tormentor was not watching.

After the male woodpecker was installed in his roost, he would repulse the dendrocincla from his doorway with pecks so vigorous that she learned to leave him alone. But it did not fare so well with the young female Golden-nape who lodged nearby. One evening after this woodpecker had retired, the dendrocincla forced her way in and drove her out. The two then clutched in the air, and the Golden-nape cried out. But a little later, while the dendrocincla was absent, the woodpecker re-entered her dormitory. When the dendrocincla returned after the light was dim, she went straight to her own hole without molesting the female woodpecker sleeping so close above her. This dendrocincla's temper seemed to fluctuate from day to day, and on some evenings she did not molest the woodpeckers. As they retire earlier, so woodpeckers arise much later in the morning than dendrocinclas do, and sometimes the dendrocincla would be present in the morning to harry the woodpeckers as they left their dormitories.

In mid-February, when the dendrocincla stayed away from the avocado tree for several nights, a Streaked-headed Woodcreeper lodged in one of the holes, not that which the dendrocincla claimed. Nevertheless, when the latter returned, she drove away the larger woodcreeper as it was about to enter its dormitory. The woodcreeper fled unresistingly. At some periods in her long tenancy of the avocado tree, the dendrocincla lodged in an old and dilapidated cavity, although a sounder one was available in the same tree.

After twice losing eggs from her nest in the avocado in 1961, the dendrocincla laid there the third time and had better luck. When these nestlings no longer required brooding, the female wished to sleep in an old cavity above the nest hole. Meanwhile, the Golden-naped Woodpeckers had moved elsewhere, and a male Red-crowned Woodpecker had taken up lodgings in the hole which the dendrocincla now desired. After giving her nestlings their last meal in the failing light, the dendrocincla climbed up the trunk and easily drove the Red-crown from his dormitory, which

later she entered for the night. All her neighbors of approximately her own size, or smaller, seemed to fear her.

After her young had flown, the dendrocincla continued for months to lodge in the cavity from which she had driven the Red-crowned Woodpecker. One evening in August, she arrived with a piece of bark or something similar in her bill, to find that a male Golden-nape had installed himself in her dormitory. She delayed in a neighboring tree until it was nearly dark, then flew to the doorway and tried to enter. The woodpecker resisted, and for about a minute I heard squeals which seemed to come from him. The dendrocincla flew away, but soon she returned and entered the hole without opposition. I had not seen the woodpecker leave. Did he escape unnoticed by me in the dusk, or did the two birds sleep in the same hole? To settle this question, I watched at daybreak. Only the dendrocincla left the hole.

The dendrocincla continued to pass her nights in this dormitory until, in the following March (1962), she nested in a hole lower in the same dead tree. After the premature loss of this nest, she went elsewhere and successfully reared two fledglings. In mid-May, when these young no longer required her presence at night, she returned to the dead avocado tree, where she continued to lodge in her former dormitory until November, when my record ends. The holes carved by Golden-naped Woodpeckers in this dead tree had provided her with dormitories for more than two and a half years.

Soon after this dendrocincla returned to sleep in the avocado tree in mid-May of 1962, I noticed that, before retiring in the evening, she led two fledglings to holes in neighboring trees, as will be told in more detail beyond. The asocial behavior of the Tawny-winged Dendrocincla was manifested early, for the juveniles slept in different trees, and the female lodged apart from them.

VOICE

Vocally, the Tawny-winged Dendrocincla is less gifted than many other woodcreepers. Its song is a high, sharp trill or rattling *churr*, delivered in varying keys and often continued without a pause for a surprisingly long while. Its call is a high-pitched, unmelodious monosyllable which suggests a complaint. From the dendrocinclas which foraged so close to me in the lowland forest I heard low, soft, "complaining" notes, and at times a peculiar *churr*.

THE NEST

In the valley of El General, the Tawny-winged Dendrocincla may begin to prepare its nest in a hole as early as the last week in February. The first two nests that I found were in hollow stumps of the "chonta" or stilt palm (*Iriartea*) in recently made clearings in the forest. One of these stumps, 5 feet high and 4¾ inches in diameter, stood amid charred remains of the woodland about 75 feet from the edge of intact forest. The central hollow of this stump was about 2½ inches in diameter, and the eggs rested 13½ inches below the skyward-facing opening at the top. The second nest was in a slightly older clearing, already overgrown with bushes and vines, about 100 feet from the edge of standing timber. The columnar palm trunk that held this nest had been broken off about 15 feet above the ground, and the central tubular hollow extended downward a distance of 11 feet, to the point where the trunk tapered off amid the stout, spiny prop roots that upheld it. In this deep well the eggs also lay exposed to the sky, about 7 feet below the opening

at the top. This nest, in which a dendrocincla raised a Streaked-headed Woodcreeper, is described in more detail in the concluding section of this life history.

My second group of nests was about 500 feet from the forest, in a dead avocado tree in a small coffee plantation, in which Golden-naped Woodpeckers had carved a number of holes. This was the tree where the dendrocincla slept for over two and a half years, as already told. Her first nest in this dead tree, occupied in April and early May of 1960, was 20 feet above the ground, in a hole of the usual woodpecker type, with fairly sound walls. Here the two eggs, protected from the elements, rested about 10 inches below the round doorway in the side. Two fledglings were raised, and a second brood was apparently not attempted by this parent. At the end of February of 1961, this dendrocincla began to carry nest material into a similar hole 14 feet up in the same tree. This was below the cavity in which she had been sleeping, and she did not begin to pass the night in the nest hole until a few days before she laid the first egg there. A few days later, the eggs vanished, and then the female lodged in the higher hole until, early in April, she laid again in the hole from which the first set had been lost. This second set of eggs also disappeared before hatching. After their loss, the dendrocincla came at nightfall to the doorway of her nest, repeating plaintive cries, but after hesitating there for a moment, she flew away through the dusk. Yet a few days later she resumed sleeping in the nest hole, where after another week she laid the season's third set of eggs. This time she hatched them, and raised her nestlings until they were feathered, before some predator tore open the doorway. Since I had surrounded the trunk with a sheet of metal to prevent the ascent of climbing mammals and reptiles, the culprit was evidently a bird. However, at least one of the nestlings, driven prematurely into the open, survived this assault.

In early March of 1962, the dendrocincla prepared for the third season to breed in the dead avocado tree, choosing her last year's nest cavity with a widely gaping entrance, in preference to the higher hole with a smaller doorway, and apparently sounder walls, where she had lodged between breeding seasons. Again the eggs vanished before hatching, possibly taken by Fiery-billed Araçaris.

After the loss of these eggs, she moved to a large clump of tall timber bamboos at the end of our garden beside the forest, about 500 feet from the dead avocado tree. Here she built her nest in the broken-off end of a stub 10 feet high, on the side of the clump toward the forest. The opening faced upward, permitting the entry of the torrential downpours of this season, but the bamboo was sufficiently decayed to permit the water to drain past the septum on which the nest rested; otherwise it would have been flooded. In this hollow the dendrocincla successfully reared two nestlings. I was absent from the farm during the nesting season of 1963 and most of that of 1964, but after my return in the latter year, I found the dendrocincla feeding a late brood in another broken-off bamboo of this same clump. This decaying stub was 15 feet high, and here the bird was still attending her young on July 22.

The Tawny-winged Dendrocincla nests, then, in a hole in a tree, or at least in an arborescent growth, which may be either open to the sky or covered, with a doorway in the side, like the woodpeckers' holes it occupied. The amount of nest material which the dendrocincla takes into her nest depends on the depth of the cavity. The nest in the above-mentioned low palm stump consisted of two parts. First, there was a mass about 2 inches thick, plugging the central hollow of the stump, and composed

chiefly of rootlets, mostly fibrous, but a few that were stiff and hard, as of a tree fern. Mixed with these rootlets were a few long, thin strips of fibrous inner bark, short pieces of petioles, and some black fungal rhizomorphs or "vegetable horsehair." Upon this compact mass rested the second part, a handful of loose material, chiefly papery bark, most of which was reddish brown in color and in flakes an inch or less in length, although a few were larger. Among these flakes were a few whitish foliaceous lichens and long, narrow strips of bast.

The high stub of the stilt palm, where a dendrocincla raised a Streaked-headed Woodcreeper, contained a filling of nest materials 19 inches thick, which had been accumulated by the combined efforts of the lone dendrocincla and the pair of woodcreepers. Since this nest is discussed beyond, here we need pay attention only to the dendrocincla's contributions. I attribute to her a layer of green moss, 8 inches thick, which rested upon a 6-inch accumulation of pieces of hard bark that had evidently been carried in by the pair of Streaked-headed Woodcreepers. Although I have never seen a Tawny-winged Dendrocincla take moss to a nest, I once watched a Plain-brown Dendrocincla carry much green moss into a hollow trunk in the forest. Probably when the cavity is very deep this readily acquired filling is used to raise the nest toward the opening, but when the hole is relatively shallow, as in the case of the other Tawny-winged Dendrocinclas' nests that I have seen, moss is omitted. I have watched so much building by two species of *Lepidocolaptes* without ever seeing them gather moss, that I am fairly certain that the Streaked-headed Woodcreepers did not contribute this ingredient to the accumulation of mixed origin. Above the moss were 2½ inches of lichens and strips of inner bark, with an admixture of moss in the lower part of this layer. The intermingling of these two kinds of materials suggested that both had been carried into the cavity by the same agent, doubtless the dendrocincla. Then followed an inch of hard flakes of bark, for which the Streaked-headed Woodcreepers were responsible. Finally, at the very top, was a layer, 1½ inches in thickness, composed of lichens, fibrous bark, and strips of monocotyledonous leaves up to 10 inches in length and ½ inch in width. All of this, I believe, had been carried into the hollow palm stub by the dendrocincla. While she incubated, I saw her bring some of this material.

The woodpeckers' holes in the dead avocado tree in which the dendrocincla nested were not so deep as the hollow centers of the palm stumps and they required little filling. The only fairly active building in which I saw this dendrocincla engage was done in the evening, often in the gathering dusk after the woodpeckers had retired for the night. In 1961, I first noticed the dendrocincla carrying material into the hole 14 feet up on February 26, 15 days before she started to lay in this cavity. In 20 minutes beginning at 5:35 p.m., she took eight large billfuls of material into the hole, often uttering her mournful cry as she worked. The accumulation of material in the cavity grew slowly, and although I watched on numerous other evenings, I saw no comparable building activity until March 11. From 5:40 to 6:10 p.m. the dendrocincla brought nothing. Then, in the failing light, she started to pull lichens from a trunk close beside me and to take them into the nest chamber. Finally, when it was almost too dark to distinguish her from the trunk up which she crept, she entered this hole for the night, the first time I saw her do so. During most of the interval when she was slowly accumulating material in this hole, she had slept in a cavity higher in the same dead tree, as already told.

While building in the twilight, this dendrocincla was always alone. One evening

I saw her trying to pull a piece of bark from a neighboring tree when it was already so dark that I could hardly have seen her if she had not been silhouetted against the sky. These spurts of vespertine nest building may be compared to similar bursts of food bringing in the evening twilight when the dendrocincla has nestlings. In either case, the concentrated activity is unpredictable: on one evening it will occur but on the following evening, with similar weather, it may not.

As in other dendrocolaptine birds, the dendrocincla continues to accumulate loose materials in her nest throughout the period of incubation, until her eggs hatch and she starts to bring food for the nestlings.

THE EGGS

Each of the six sets laid by the Tawny-winged Dendrocincla that I have seen consisted of two eggs. The pure white eggs are ovate, narrower on one end than the other, instead of being equally blunt at both ends, as in some other species of woodcreepers. In one instance, at least two days separated the laying of the first and second eggs. In one case, the second egg of a set was laid between 6:00 and 7:05 a.m.; in another, between 6:00 and 7:30 a.m.

The earliest egg of which I have a record was laid in the avocado tree on March 7 or 8, 1962. In the preceding year, laying began in this tree on March 13 or 14. By March 17, the two newly laid eggs had vanished. On April 5, after an interval of about 19 days, the dendrocincla resumed laying in this same hole, to which she had brought little or no new material since the disappearance of the first set. The second set of eggs also mysteriously vanished, on April 19, but on May 1, I found here the first egg of a new set of two. In this case, the interval between the loss of one set and the resumption of laying was only about 11 days.

The latest nest that I have found in El General held nestlings on July 11 and they were still present on July 22. Here the eggs were laid in June.

INCUBATION

I devoted two mornings to watching nest 1, which was situated in a low palm stub in a new clearing devoid of shade. The dendrocincla became active very early, and although I entered the blind at 5:45 a.m., before I was well settled within it she returned to her two eggs, bringing a piece of bark in her bill. At 6:51, after incubating for 66 minutes, she left the stump and flew into the forest. After an outing of 26 minutes, she returned to her eggs at 7:17. When a cow walked noisily over the logs which cluttered the clearing, 100 feet from the nest, the dendrocincla looked out with her head and shoulders above the irregular rim of the palm stump. Reassured by her survey, she descended to resume incubation. This session lasted until 8:44, or 87 minutes, and was followed by a recess of 39 minutes. Returning at 9:23, the parent sat only 47 minutes, until 10:10. After this departure, no dendrocincla appeared until 11:15, when I left. The eggs had been attended only 60.7 per cent of the 5½ hours that I watched.

Thinking that incubation would become more constant as the time for hatching approached, I waited a week before I again spent a morning at this nest. Meanwhile one egg had vanished. This time the dendrocincla passed a more restless forenoon. She was absent when I entered the blind at 5:50 a.m. Returning to the nest at 6:22, she sat until 6:40, when a Buff-throated Woodcreeper, which had been exploring the stumps in the clearing, finally reached the dendrocincla's palm stub

and peered down into it. The occupant at once sallied forth and chased the larger woodcreeper to the edge of the forest, where the two dodged back and forth among the trunks. At 6:50 the dendrocincla returned to her egg. While she incubated, a Southern House Wren hopped over the top of the palm stump and leaned far over the central cavity to look down into it. The wren repeated this many times, but the dendrocincla did not emerge to chase the far smaller bird. At 7:45, when an airplane passed over the valley, the dendrocincla looked out, then flew to the forest. At 8:12 she returned to the nest and sat until 9:17, when she left spontaneously. After this session of 65 minutes, she took a long recess and had not returned when I ended my watch at 10:17 a.m., an hour after her departure.

Taking the two mornings together, this dendrocincla's sessions, when not interrupted by intruders, ranged from 47 to 87 minutes. Her recesses varied from 26 minutes in the early morning to more than an hour after the sun rose high. Possibly she stayed away from the nest so long because she found it intolerably hot in the confined space in the center of the dark-colored stump on which the sun was beating. At about this time, a brood of Southern House Wrens were found dead in the center of another palm stump like that which the dendrocincla occupied, and I suspected that they had been killed by the excessive heat.

On a cool afternoon, the dendrocincla took a session of 87 minutes, which was followed by a period of neglect of 41 minutes. This absence ended at 6:00 p.m., when the dendrocincla returned to her nest for the night with flakes of bark in her bill. Next morning she left at 5:32, in the dim light of dawn, and was away for 28 minutes.

Often, as she returned to her eggs, the dendrocincla brought a piece of bark or other material from within the neighboring forest. On reaching its edge, she sometimes clung upright to the trunks and repeated a mournful monosyllable as she nervously twitched her wings. At other times, when nothing excited her suspicion, she approached her nest in silence. If she heard a noise while sitting, she would ascend to the top of the hollow stump and look around with only her head and shoulders above the rim. According to the result of her scrutiny, she would either descend to her eggs again or fly away. On leaving the nest, she always flew directly into the forest, never into the clearing.

Looking into the top of the trunk after her departure, I would find the eggs more or less covered with loose pieces of bark and bits of foliaceous lichen. I tried to learn whether this was deliberately done or was the unintended consequence of the movements of the loose pieces at the top of the nest as the dendrocincla rose up to go. In the late forenoon, when the eggs were left alone in the heated center of the palm stump for an hour or more, I usually found them well covered with bark and lichens. One day they were so completely overlaid that I could see nothing of them. On the other hand, after the bird's spontaneous departure in the late afternoon I found the eggs only half covered, and in the dim light of dawn she left them largely exposed. When the dendrocincla flew out hastily because I hammered on a neighboring stump, the eggs were left without any covering, quite exposed to the sky. I concluded that the dendrocincla covered her eggs deliberately.

At the second nest, however, I could discover no constant difference in the thoroughness with which the eggs were covered, whether the dendrocincla left spontaneously or hurried out as I approached noisily. This nest seemed to contain more loose pieces of whitish foliaceous lichens than the first, and possibly they

merely fell over the eggs as the bird rose up from their midst. Even when the lichens only partly overlaid the eggs, by breaking their outline they made the eggs more difficult to detect as one peered down into the deep, dimly lighted well at whose bottom they rested. Indeed, when they merely served as a background for the eggs, and did not lie above them at all, these whitish lichens made the eggs more difficult to distinguish.

This second dendrocincla incubated no more constantly than the first. One morning, when I watched from 6:40 to 10:20 a.m., she divided her time as follows: off the nest 22 minutes, on the nest 57, off 4, on 13, off 43, on 23, off 56, on 2 minutes (this session was terminated by my approach to the nest). Increasingly long absences from the nest as the morning grows older seem to be customary with dendrocinclas, especially when they nest in sunny clearings. This bird also brought lichens and shreds of bark when she came out of the neighboring forest to resume incubation. She always entered the top of the palm stub head foremost, and probably she maintained this inverted position on her seven-foot-long climb down to the eggs. I never saw a second dendrocincla in the vicinity of either nest.

I watched nest 3 from 5:25 to 11:15 a.m. on April 11, and from 12:00 noon to 6:25 p.m. on the following day. In approximately 12 hours, the incubating parent took eight sessions, ranging from 16 to 89 minutes and averaging 57.0 minutes. Her nine recesses varied from 12 to 36 minutes in length and averaged 26.4 minutes. She was in the nest 68.3 per cent of the day. She incubated more constantly than the dendrocinclas that nested in hollow palm trunks open to the sky, largely because her absences were much shorter. Like the others, she often brought a flake of lichen or a shred of bark on her return to her eggs. She was not shy, and I watched her while sitting unconcealed about 30 feet away.

Like the first dendrocincla, this bird in the coffee plantation regularly left her eggs very early in the morning, while the light was so dim that I had to watch closely to see her dark figure shoot out of the doorway. Likewise, she remained active into the dusk of evening. Even if she had entered the cavity a short while earlier, when most birds were settling down for the night, she might fly out for another excursion in the twilight. Usually she repeated her mournful call many times as she approached and climbed up the trunk for her final return to the eggs. One evening, soon after the incubating bird had entered the nest, a second dendrocincla flew up and clung to the top of the stub above the cavity. Here it remained for a short while, nervously flitting its wings but making no sound. It did not go to the doorway. After its departure, the incubating parent looked out. This was the only time that I saw a second dendrocincla near any of the nests which I watched, although at this third nest I sometimes heard one in the distance while the parent was within.

In 1961, I watched this dendrocincla incubate the season's third set of eggs in the avocado tree from 5:17 to 11:53 a.m. on May 9, and from 11:57 a.m. until 6:32 p.m. on the following day. In 13 hours, the female took ten sessions on her eggs, ranging from 10 to 96 minutes and averaging 45.8 minutes. Her 11 recesses varied from 11 to 51+ minutes and averaged 29.3 minutes. She was in her nest for 60.9 per cent of the day. Although now she sat more constantly in the morning than she had done in the preceding year, on the afternoon of May 10, when rain fell much of the time, she was restless, coming and going more frequently. Again she brought additions to her nest on many of her returns, especially in the forenoon.

At this nest, the second egg was laid between 6:00 and 7:05 a.m. on May 2.

One egg hatched during the forenoon of May 22, the other between 6:00 p.m. on this date and 6:00 a.m. on May 23, after an incubation period of between 20½ and 21 days.

THE NESTLINGS

At my first nest, found in 1940, the dendrocincla incubated for most of May, and when the remaining egg failed to hatch, it was abandoned. The second nest had a remarkable history, to which we shall presently return. In the third nest, both eggs hatched on April 19, 1960, 13 days after I found them when incubation was already begun. The nestlings had tightly closed eyes and pink skin that bore long, sparse, gray down. The interior of the mouth was yellowish. Although the corners of the mouth were at first rather inconspicuous, in a few days they developed prominent white flanges. The nestlings' skin rapidly darkened. When newly hatched, the nestlings repeatedly raised their gaping mouths when I lowered a light into their chamber, but when they were two days old, as on all subsequent visits, they remained quiescent and would not lift their heads. They had evidently learned to gape in response to a specific stimulus, provided by the approaching parent, which I could not reproduce. The empty shells were promptly removed by the parent.

On the morning when the first egg hatched, the parent left the nest in the dim light at 5:32 a.m. At 6:04 she returned, stayed within for 8 minutes, then left with a piece of shell in her bill. By 11:22 a.m., she had brooded for seven periods, ranging from 8 to 40 minutes, averaging 25.4 minutes, and totalling 178 minutes. She brooded slightly more than half the time, or with considerably less constancy than she had incubated, although her second egg did not hatch until the afternoon of this day. In the first 6 hours of activity on April 22, she covered the three-day-old nestlings for seven periods, ranging from 3 to 24 minutes, averaging 13.9 minutes, and totalling 97 minutes. Brooding had already declined to 27 per cent of the morning. By April 28, when the nestlings were nine days old and were still rather naked, the parent did not brood at all during 6 hours of a dark, cool morning. But she attended the young by night until May 4, when they were 15 days old and well clad in brown plumage. Thereafter, the parent slept at a distance.

In 6 hours of the morning of April 19, when there was one newly hatched nestling, the parent brought food six times, each time a small insect, as far as I could see. Three days later, the two nestlings were fed only nine times in the same period of the forenoon; again their diet seemed to consist wholly of insects, one of which was brought in the parent's bill on each visit. On April 28, the two nine-day-old nestlings were fed 12 times in the first 6 hours of the day, or one feeding per hour per nestling. Now their meals were substantially larger and included seven small lizards that were brought on seven successive visits. On May 6, when the two nestlings were 17 days old, they received 16 meals, including seven lizards, in the first 6 hours of the morning.

Although these figures make it evident that the parent's visits with food were, on the whole, widely spaced, occasionally she fed the nestlings at a surprisingly rapid rate, especially in the evening twilight. On May 7, the female came with a meal five times in a quarter-hour after sunset, while rain fell steadily. Two days later, she brought four lizards in as many visits between 6:09 and 6:22 p.m. But her most remarkable activity was on the clear evening of May 11. At 6:13 p.m. the parent brought a lizard and passed it through the doorway to a nestling; this was the first

time that I saw her deliver a meal without entering the chamber. Then she went off, to return after 9 minutes with an insect, which she took inside. In the next quarter of an hour, she brought 12 more insects, many of which she caught in the air, on swift, graceful flights from the nest tree itself or from neighboring trunks. The prey appeared to be large, winged ants, flying in the twilight. While clinging to a trunk, the dendrocincla rubbed one of them beneath a wing, as though anting. Thus, from 6:05 to 6:38 p.m., the two nestlings received 14 meals, including one lizard and 13 insects. But on the following evening, in a moderate rain, the parent brought only a single lizard in this interval.

Sometimes the day's last meal was brought after the light had become so dim that I could see the object in the dendrocincla's bill only when she was silhouetted against the sky. I marvelled at her ability to find food so quickly in the failing light of evening, especially lizards, which apparently had been captured in the deep shade of neighboring woods and thickets. She also foraged successfully before sunrise. Thus, on April 30, she left the nest at 5:30 a.m., and 15 minutes later she returned with the first installment of the nestlings' breakfast, 2 minutes before her neighbors, the Golden-naped Woodpeckers, emerged from their nest to begin feeding their three hungry young. But while the Golden-napes then brought food at a very rapid rate, I saw the dendrocincla engage in such concentrated activity only in the evening, when the woodpeckers rested after a strenuous day.

I watched this nest, while it sheltered young, a total of 27 and a quarter hours. In this time the parent dendrocincla brought 76 meals, of which no less than 22 were small lizards. Some were anoles, whose bright yellow gular pouches protruded conspicuously while they were grasped in her bill. Because of their size, these lizards were the mainstay of the nestlings after their first week. Insects were, however, the most numerous items, and in addition there were a number of spiders. Only a single article was brought at a time. Often the parent foraged in the neighboring second-growth thickets, but sometimes she went off toward the forest, which was about 400 feet away and could be reached from the coffee plantation by flying over a pasture with scattered trees or through a shady dooryard.

During the first few days after the nestlings hatched, the parent evidently swallowed all their droppings, as I saw her remove none from the hole. After the young were a week old, she carried away their white fecal sacs in her bill. She kept the nest perfectly clean until the fledglings emerged from it.

At the age of 16 days, the nestlings were well covered with dark brown plumage, which made them hard to detect as one looked into their deep chamber. Unlike the loquacious young of some other hole-nesting birds, including Streaked-headed and Spotted-crowned woodcreepers, they did nothing to reveal their presence. I did not see them take food while their parent remained outside the cavity until they were 22 days old, and even then most meals were carried into the chamber for its secretive occupants, which did not, like some other woodcreepers and many woodpeckers, look out through their doorway while waiting for their food. It was only on their last day in the cavity that I heard, issuing from it, a weak version of their parent's squeaky, mournful call. They remained in the nest for the surprisingly long period of 24 days, and after their departure on May 13, they promptly left the coffee plantation. I did not see them again, for they failed to return to sleep in the hole. The female, however, often lodged there until August, but evidently she had one or

more additional dormitories which she used alternatively, for on some nights she was absent.

On the evening of August 4, I saw the dendrocincla carry a scrap of material into this cavity, suggesting that a second brood would be undertaken. But only a few shreds of bark were placed over the old, decaying nest, and no egg was laid there.

THE YOUNG AFTER LEAVING THE NEST

In 1961, the dendrocincla brooded her two nestlings in the avocado tree nightly until dawn on June 13, when the elder was 22 days old. That evening, after feeding them in the dusk, she drove a male Red-crowned Woodpecker from her old dormitory higher in the same tree and slept there, leaving her nestlings alone through the night for the first time. When I returned next morning, the doorway of the nest had been greatly enlarged, and the nestlings had vanished. At the end of the same day, the parent came once to the nest tree with food, which she then carried into a neighboring ravine, leading me to hope that at least one of the nestlings, which lacked only a day or two of the normal age for departure, had escaped whatever animal had attacked their nest. As it grew dark, the parent returned and entered the hole from which she had driven the woodpecker, came out, entered and left again, then in the dim light went in for the third time and stayed. I had never before seen her have such difficulty settling down for the night.

Next morning, I found a fledgling dendrocincla clinging upright on a trunk in the neighboring woods. It remained long in one spot, and while clinging scratched its head by raising a foot between the dropped wing and the body—"over the wing." Finally its parent arrived with food and, after voicing a few mournful notes, clung upright beside the fledgling and passed the insect to it. Before she returned with another meal, I advanced closer to the young bird. After a moment's hesitation, she dashed down and either struck the fledgling or alighted on its back, whereupon the two darted off swiftly together. Evidently this was the dendrocincla's expedient for quickly removing her offspring from an apparently dangerous situation.

Late in May of the following year, when the dendrocincla raised a brood in a bamboo stub after the loss of one set of eggs in the avocado, I found the dormitories of her two fledglings. One slept in the hollow decaying trunk of a pejibaye palm, about 50 feet high, in which earlier in the year a pair of White-crowned Parrots had nested. This old trunk stood at the edge of a little coffee plantation, about 50 yards from the dead avocado tree. Beyond the pejibaye was a patch of light second-growth woods, in which stood a dead cecropia tree the top of which had broken off, exposing the central hollow of the trunk. Here the other fledgling roosted. Both young dendrocinclas entered their dormitories through the open tops. Although well hidden after they had climbed down into the hollow stems, they slept exposed to the heavy rains of this season.

Alighting low on the tall pejibaye trunk after sunset, the fledgling which roosted there climbed slowly upward, the shortness of its bill, as well as the bird's clumsy movements, betraying its immaturity. I marvelled that it did not hurt itself on the many long, sharp, black thorns that still remained on the hard outer shell of the trunk. One evening when both of the young birds alighted on the pejibaye trunk, they threatened each other with their wings raised in a spectacular attitude. Then they separated, and each retired into its own dormitory.

The adult accompanied these young birds to their sleeping places and fed them

as they were about to retire. One evening, as the occupant of the pejibaye palm was climbing up its long trunk, she gave it, in rapid succession, about half a dozen insects which she caught in the air on rapid outward darts, in the waning light. Then, when it was nearly dark, she entered the dormitory in the avocado tree that she had occupied for so many months.

Evidently the young dendrocincla which slept in the cecropia trunk did not find its lodging comfortable. On the evening of May 27, it entered and left twice before it entered to stay for the night. On the evening of June 8, dendrocinclas came to both the pejibaye and the cecropia trunks, only to fly away again. This was the last time that I saw them there, although two evenings later I heard them in the distance. The female had led them to their dormitories and fed them for about two weeks after I first discovered where they slept. After that, the family seemed to disperse, to lead the solitary lives which dendrocinclas prefer.

REARING A NESTLING STREAKED-HEADED WOODCREEPER

The history of the second nest is somewhat involved, but as a result of frequent observations, and the careful study of the stratification of its materials which I made after the departure of the occupants, we may with some confidence retrace the course of events there. The site of this nest was in the lower part of a stately stilt palm, the top of which had evidently been broken off when the tract of woodland in which it stood had been cut and burned in the preceding year. While the hard outer layer of the trunk resisted decay, the soft tissues of the interior quickly rotted, leaving a hollow, erect tube about 11 feet long, propped 5 feet above the ground on the long, thick, spreading, spiny aerial roots. The lowest part of this tube was filled to a depth of 28 inches with dark brown earthy matter, evidently the remains of the central tissues, in which there were many big, shiny, brown beetles. Above this, many large pieces of hard bark, mixed with earthy matter, formed a layer 6 inches thick. These fragments of bark had evidently been carried in by a pair of Streaked-headed Woodcreepers before the dendrocincla brought anything to it. But 8 inches of loosely packed moss, and at least part of the layer, 2½ inches thick, of lichens and strips of fibrous bark, had undoubtedly been contributed by the dendrocincla before my attention was drawn to the palm stump by her emergence as I walked by it on June 1, 1942. From the truncate top of the stub a long fissure extended, gradually narrowing, far down the side of its hard outer shell. Too narrow for a dendrocincla to pass through, it was most useful to me. Inserting a mirror and a small light while I stood on a ladder, I could see, far below, a nest covered with whitish lichens, and in their midst, I believed, part of the surface of one white egg.

On a number of visits in the following days, I repeatedly saw the dendrocincla take a lichen into the trunk. It seemed to me that she was incubating, but all that my mirror and light revealed was a layer of lichens covering the nest. If the nest contained eggs, they were concealed by the lichens. Early on the morning of June 7, I began a continuous watch to learn whether the dendrocincla was in fact incubating. Presently a pair of Streaked-headed Woodcreepers approached through the clearing. One went to the side of the palm trunk, where it climbed slowly upward, nervously twitching its wings and uttering a sort of churring trill, very different from its usual clear trill. Reaching the top, it peered inside, then began to climb down the tube tail first. It did not descend more than a foot, as I could see through the

fissure in the side, and meanwhile its mate clung to a neighboring trunk. While the first woodcreeper was vacillating at the top of the tube, the dendrocincla flew down from the forest's edge, uttering her plaintive monosyllable as she came, and both intruders fled. Then the dendrocincla returned to the forest, neglecting her nest for at least an hour longer.

Late on the following morning, June 8, I happened to see a woodcreeper take a flake of bark into the stump. Looking in, I saw that the woodcreepers had covered the dendrocincla's white lichens with a layer of dark bark. At 10:45 a.m. on June 14, I found the woodcreepers at work, and during the next half-hour both of them carried into the hollow many flakes of bark, plucked from neighboring dead trees. The dendrocincla did not appear. The following morning, my mirror clearly revealed one pure white egg resting on the dark fragments of bark. There could be no mistake about its presence, for it was completely exposed, not partly or wholly covered with the materials of the nest, as dendrocinclas' eggs usually are. Later examination revealed an inch-thick layer of stiff bark flakes above the softer material which the dendrocincla had brought. But I found no eggs or fragments of shell buried beneath the bark, so possibly I was mistaken in believing that there was an egg on June 1.

At 5:10 p.m. on June 15, the day when the first egg appeared, the dendrocincla flew out of the stump as I approached. Half an hour later, she returned with a piece of lichen in her bill, evidently to pass the night with the egg. The following morning at 11:30 there were two eggs, with pieces of lichen lying beside them. The dendrocincla was now definitely in possession of the nest. While she incubated two days later, a Streaked-headed Woodcreeper started to enter the hollow, but on discovering that it was occupied, the newcomer promptly withdrew. The woodcreepers always retreated from the dendrocincla, and this was the last time that I saw either of them there. The topmost stratum of this layered nest contained only such materials as are gathered by dendrocinclas and not by Streaked-headed Woodcreepers. By bringing lichens, shreds of fibrous bark, and strips of monocotyledonous leaves, the dendrocincla raised the level of the eggs by 1½ inches during the 15 days that she incubated them. The top of her nest was arranged with whitish lichens occupying the center where the eggs lay and long, dark strips of bark curving around the periphery.

One egg disappeared before the end of June. I happened to be watching when, at 7:16 a.m. on July 1, the dendrocincla emerged from the top of the trunk with something white in her bill. Setting up the ladder, I dimly perceived a newly hatched nestling, far below my mirror in the deep well.

On July 7, when the nestling was six days old, I watched the palm stub from 6:30 to 10:00 a.m. In the 3½ hours, the parent brought food five times, but each time she dived into the hollow so quickly that the only object I could distinguish in her bill was a small lizard. She brooded four times, for 29, 3, 18, and then 36 minutes. Once she carried away a dropping.

Was the nestling a dendrocincla or a Streaked-headed Woodcreeper? As the days passed, this question occupied me increasingly. Yet even when the occupant of the nest was two weeks old and fast becoming feathered, the question remained unanswered. Whenever I looked into the deep tube by means of my mirror and light inserted through the fissure high in its side, I could at first distinguish nothing in the poorly illuminated interior. As my eye gradually became adjusted to the

obscurity and depth, the first details to become apparent were the broad yellowish flanges at the corners of the nestling's mouth. This was its one conspicuous feature; all else was shadowy and indistinct.

Fearing that the nestling would leave the nest before this question was settled, I decided to make a little window in the side of the trunk, so that I could insert my mirror and light nearer the object that I wished to examine. Standing on the ladder, I tried to penetrate the shell with a drill, but the hard cortex of the palm trunk stubbornly resisted. To drive the bit harder against the stubborn palm trunk, I increased the inclination of my ladder. When the tool still refused to cut into the resistant shell, I set my ladder still more slantingly. Suddenly the prop roots gave way: trunk, ladder, and man crashed heavily to the ground.

I turned my attention to the prostrate stub. A mere hollow shell, it was so light that even in my bruised and smarting state I could raise its upper end to the level of my eyes. Throwing in the full beam of my flashlight, I could see the nestling at the lower end, too far from my eyes to distinguish details. To measure the length of the tube, as an aid to placing my projected observation window in the most favorable position, I inserted a long green stipe cut from one of the tall bracken ferns that flourished in the surrounding burnt ground. This snake-like intrusion caused the nestling to scramble toward the opening. It came so close that I could clearly see the conspicuous, light gray stripes on its brown breast. This was the heavy marking of a *Lepidocolaptes*, not the faint, hair-like shaft streaks of the *Dendrocincla* which attended it. Its attempt to escape cut short by my face and the flashlight in the opening, the bewildered young Streaked-headed Woodcreeper scurried back to its nest at the bottom of the tube. Having disturbed it far more than I had intended, and having settled the important question, I pushed up the palm stub until its prop roots held it almost upright. Then I withdrew to a convenient log to rest and watch.

Before long, the foster parent flew down from the forest with an insect in her bill. Confused by the slight inclination of her formerly upright trunk, she flew from one to another of the surrounding stubs, voicing a high-pitched, rather sharp, long-continued trill. From within the trunk came a soft, liquid trill: the dendrocincla's trill was answered by a Streaked-headed Woodcreeper's trill. Voice as well as appearance attested that the nestling and its attendant were of different species. Soon the foster parent alighted on the upper side of the leaning palm trunk, peered in, then entered with food for the nestling, headfirst as she always did. Assured that the young bird would not be neglected as a result of the accident, I went home.

As I approached the palm trunk before sunrise next morning, I heard the nestling trilling within it. The dendrocincla brought its first meal of the day at 5:35 a.m., and by 9:05 she had fed it nine times, giving it a variety of insects, including a large brown moth. She would bring several articles in fairly swift succession, then remain absent for an hour or more—a method of feeding rather uncommon in my experience with birds. On subsequent mornings, she brought several small lizards and a number of green insects. The nestling now climbed far up the tube where I could clearly see, through the gap in the side, the streaks on its head, neck, shoulders, and breast. Its bill was curved more than the bill of its attendant. At the age of 19 days, it left the hollow palm trunk and doubtless accompanied its foster parent to the neighboring forest. I wondered whether it would be able to maintain contact

with her and receive food until it could take care of itself. Although the voices of the fledgling and its foster parent were certainly very different, doubtless during its last week in the nest each had become familiar with the other's call. Indeed, even without this preliminary conditioning, birds sometimes faithfully attend a fledgling of another species as it wanders through the trees.

While the nestling was growing up, and also during incubation, I never received even a suggestion that a second dendrocincla was interested in this nest. The single parent, evidently the female, was invariably alone.

SUMMARY

The Tawny-winged Dendrocincla lives in primary and older second-growth forests in the more humid lowlands of Central America and southern México. In southern Costa Rica, it is found from sea level up to 4000 feet and sparingly 1000 feet higher.

It forages nearer the ground than many woodcreepers and often joins the mixed flocks of birds that follow army ants. Sometimes two dendrocinclas are found in the same flock and appear to be mated, even in November, December, and January. More often, if more than one individual is present, one chases or even grapples with the other. It seems that dendrocinclas form pairs in the pre-laying period, but after incubation begins these break up and adults become intolerant of each other.

The Tawny-winged Dendrocincla subsists on insects, spiders, and small lizards. It prefers the easy foraging which army ants provide by chasing such small creatures into the open, but it does not eat the ants themselves. It often catches flying insects on long aerial sallies from the trunk to which it clings.

Clinging to trees, two dendrocinclas anted simultaneously, using insects, apparently large ants, driven from concealment by the army ants which these birds accompanied.

At all seasons, these dendrocinclas sleep singly in woodpeckers' holes or other cavities in trees. They enter and leave their dormitories in the twilight. One dendrocincla attacked Golden-naped Woodpeckers as they approached their lodgings in the evening, and even entered holes in which these and Red-crowned Woodpeckers were already ensconced, to drive them out. The dendrocincla is an extremely belligerent bird.

The Tawny-winged Dendrocincla's notes lack melody. The song is a high, sharp trill or rattling *churr*, often continued for a surprisingly long while. The call is a high-pitched monosyllable that sounds like a mournful complaint.

In the valley of El General, nesting begins in late February or March and continues into July. Nests were found in woodpeckers' holes, in the hollow centers of decaying palm stumps, and in the broken-off ends of stout timber bamboos. In the two last-mentioned situations, the eggs and young are exposed to the rain, and to hot sunshine if the nest is in a new clearing. In palm stubs, the eggs may rest as much as seven feet below the opening, at the bottom of a long tube. The entrances to the nests were from 5 to 20 feet above the ground.

The amount of nest building depends on the depth of the cavity which has been chosen. Green moss may be used to raise the level of a nest in a very deep hollow, but it is absent from shallower holes. Other ingredients of nests are rootlets, fibrous bark, fungal rhizomorphs, long strips of inner bark, pieces of papery bark, and whitish foliaceous lichens. The lichens are always prominent at the top of the nest, where the eggs lie. The most sustained building was witnessed in the evening

twilight, after most other birds had settled down for the night. The building dendrocincla was always alone.

Each of six sets contained two pure white eggs.

No more than one parent, evidently the female, was ever seen to take an interest in a nest with eggs or young. At nests in palm stubs exposed to full sunshine, long sessions of incubation, up to 1½ hours in length, alternated with almost equally long periods of neglect. A dendrocincla nesting in shaded woodpeckers' holes incubated more constantly, taking sessions which ranged from 16 to 89 minutes, recesses which varied from 12 to 36 minutes in length, and covering her eggs for 68 per cent of the day. In the following year, this dendrocincla incubated with a constancy of 61 per cent.

While the parent was absent, the eggs were often partly or completely overlaid by the loose material at the top of the nest, especially with foliaceous lichens or flakes of bark. There is some evidence that the dendrocincla covered them deliberately as she left, but possibly the loose pieces merely fell over the eggs as she rose up. When returning to her eggs, each dendrocincla continued to bring additional pieces of bark or lichen throughout the course of incubation.

At one nest, the incubation period was between 20½ and 21 days.

One female laid three successive sets of eggs in the same nest, from which the first and second sets were lost. Laying was resumed about 19 days after the loss of the first set and 11 days after the loss of the second. Apparently only one brood is raised each year.

Newly hatched nestlings are sightless, with long, sparse, gray down that fails to cover their pink skin. This skin darkens in the following days, and prominent white flanges develop at the corners of the mouth, the interior of which is yellowish. Even a newly hatched nestling was brooded only about half the time. Thereafter, brooding fell off rapidly and ceased in the daytime when the young were nine days old and still rather naked. The parent attended the nestlings by night until they were 15 days old and well clad in brown plumage, and at a later nest she did so until they were 22 days old.

Except for certain periods of concentrated feeding, which generally came in the evening twilight, the nestlings were fed at a slow rate. Two 17-day-old nestlings received only 16 meals in the first 6 hours of the day; but a few days later, they were fed 14 times in a half-hour after sunset. The parent could forage efficiently in dim light. Food was brought in the bill, a single article at a time. Insects were the most numerous items given to the nestlings, but after the young birds were a week old small lizards formed the bulk of their diet, which also included a few spiders. The nest was kept clean until the young left.

In contrast to the loquacious nestlings of *Lepidocolaptes* and some other hole-nesting birds, those of *Dendrocincla* are very quiet and secretive, remaining silent within their chamber instead of looking through the doorway and calling. One brood left the nest at the age of 24 days and did not return to sleep in it.

Two fledglings of another brood were led to sleep in separate hollow trunks, which had open ends that admitted rain. The female slept apart from them, in the dead tree where she had lodged over a period of two and a half years.

When a dendrocincla and a pair of Streaked-headed Woodcreepers claimed the same hollow palm stub, the latter were easily driven off by the former, but in her absence they built a nest in the stub and laid two eggs. One of these was hatched by

the dendrocincla, which raised the nestling without help. She always started to descend the seven-foot-long tube headfirst, in an inverted position. When older, the nestling answered her sharp trill with a clear, soft trill, quite different in quality. It left the nest when 19 days old.

GENERAL SUMMARY OF INFORMATION ON THE DENDROCOLAPTIDAE

The approximately 60 species of woodcreepers or woodhewers form a homogeneous family which is confined to the American continents and closely adjacent islands. Like the antbirds and manakins, these heat-loving birds scarcely extend beyond the tropics either to the north or to the south; although a few species reside high in the mountains, the great majority are found in lower and warmer regions. This family is composed exclusively of scansorial birds which climb up the trunks and along the thicker limbs of trees, hence most of its members occur in forested areas, although a few are present in savannas with scattered trees.

In appearance and mode of foraging the woodcreepers resemble the creepers (Certhiidae) of northern lands, but most of them are larger. Their most obvious adaptation for climbing is the long, graduated tail, which is composed of 12 stiffened feathers, the shafts of which project beyond the broad vanes and are turned inward at the tip, the better to serve as a prop. The length and stoutness of the projecting tips of the shafts varies considerably intergenerically, being great in *Glyphorhynchus* but slight in *Dendrocincla*, which has special modes of foraging that do not involve climbing. Unlike the woodpeckers, which they resemble in their scansorial habit, woodcreepers have three toes directed forward and only one turned backward. The forwardly directed toes are united for the length of their first and second phalanges. The bills of woodcreepers exhibit considerable diversity. All are narrow rather than broad, but some are straight and fairly stout whereas others are slender and curved. Extreme types are the short, laterally compressed, wedge-shaped bills of *Glyphorhynchus* and the slender, compressed, strongly curved bills of *Campylorhamphus*, which resemble sickles or scythes and may exceed 2 inches in length.

The woodcreepers range in size from about 5 to 13 inches. In plumage the family is monotonous, all its members being clad in shades of brown and olive, without any bright colors. Often the tail, rump, and wings are brighter, more chestnut or rufous, than the foreparts of the body. Variety is achieved by longitudinal streaking with lighter and darker shades, especially on the head, neck, shoulders, and under parts. Transverse bars of dusky or black impart distinction to the large woodcreepers of the genus *Dendrocolaptes*. One of the most handsome of the Central American members of the family is the Black-striped Woodcreeper, which on the head, neck, back, and breast is blackish with large oval spots and streaks of pale buff, while the lower back, rump, wings, and tail are bright rufous-chestnut. In this family, the sexes are commonly indistinguishable.

Woodcreepers appear never to form flocks of their own kind, although one or a few often join a roving mixed party of small woodland birds. Streaked-headed Woodcreepers, Spotted-crowned Woodcreepers, and apparently many other species, live in pairs throughout the year. Most members of this family seem to reside permanently where they breed, but the "Climbing Wood-hewer," one of the few species that ventures beyond the tropics, is a summer resident in the region of Buenos Aires, Argentina (Hudson, 1920, 1:236).

Woodcreepers subsist largely if not wholly on insects and other small invertebrates, but they occasionally take a small lizard or frog. Most of their food is found as they creep up the trees in an upright position, or else outward along the branches, according to whose inclination their bodies may become horizontal or even somewhat inverted. As they proceed in this fashion, they peer and probe into crevices in the

bark, loose flakes of which they sometimes pry off with their bills, and they lift up or pull off tufts of moss or lichens to see what lurks beneath. When they have gone as far upward on a trunk or outward on a limb as the hunting is profitable, they fly down to a lower point on a neighboring trunk and repeat the process. Woodcreepers with extreme types of bills have special modes of foraging. The Wedge-bill incessantly strikes the bark with its short, sharp bill, apparently picking off innumerable creatures too small to be seen from the ground. The scythebills use their long, curved beaks to probe between the clustered fruits of palm trees and beneath the sheathing bases of their fronds (Carriker, 1910:658). They also poke their bills into deep crevices in furrowed bark and between woody vines that have twined around each other. The Ivory-billed Woodcreeper sometimes forages on the ground, either in woodland (Dickey and van Rossem, 1938:323) or on coastal mud flats at a distance from forest (Willis, 1960*b*). Rarely a woodcreeper digs into soft, rotten wood for food.

Some woodcreepers join the mixed companies of small birds that follow army ants. Clinging upright to the lower part of a trunk, the woodcreepers watch for an insect driven from its hiding place by the ants, then dart down or outward to snatch it from the ground or the surrounding foliage. Seizing their prey, they carry it to a convenient trunk, devour it, and await another victim. The dendrocinclas are persistent followers of the army ants, the Barred Woodcreeper frequently accompanies them, and other members of the family resort occasionally to this convenient method of feeding.

Although the calls and songs of woodcreepers are, like their vocal organs, structurally simple, the clear, sweet tones of many of them and the energy and persistence of their delivery, give them a high place among the bird notes of the tropical American forests. Their songs are often heard at dawn, and from time to time through the day, but they are delivered most freely as the birds seek their resting places in the evening twilight, when the forest's deepening gloom makes them most impressive. Foremost among the Central American woodcreepers as a songster is the Brown-billed Scythebill. Its song begins as a fine, clear, ascending trill, to which is soon added a loud, ringing *tewe tewe tewe tewe tewe we we we we we we*. The most remarkable feature of this brilliant performance is that the trill continues after the louder notes have begun. The woodcreeper seems to sing two different songs simultaneously; when I first heard a scythebill, I thought that two individuals were performing together, one trilling while the other sang louder ringing notes. The perfect synchronization of these two songs, and the frequent repetition of this wonderful song when only one scythebill was in sight, finally convinced me of my error. Snethlage (1928:547) held the Red-billed Scythebill to be the best songster among the woodcreepers of northeastern Brazil.

In the breeding season, the Buff-throated Woodcreeper, clinging unseen high in a tree, tirelessly repeats clear, far-carrying, somewhat plaintive notes, a dozen or more in a series and all in nearly the same key. Other memorable songs of members of this family are the long-drawn melodious trills, soft and clear, that the members of a pair of Streaked-headed Woodcreepers give responsively; the fine, rapid, ascending trill of the Wedge-billed Woodcreeper; and the brief, sweet notes of the Black-striped Woodcreeper. The Tawny-winged Dendrocincla and its congeners are inferior songsters, whose somewhat harsh churrs or rattles make up in length what they lack in mellowness of tone. The Spotted-crowned Woodcreeper is also a poor songster

with a weak, squeaky voice, quite different from the clear trill of its lowland counterpart.

Nuptial feeding seems not to have been observed in woodcreepers, and little is known of their courtship.

Woodcreepers appear always to nest in cavities, never in structures which they build in the open, yet they are not known to excavate holes for themselves. Although they sometimes occupy a hole which woodpeckers have made and abandoned, and rarely a bird box, they prefer a cavity formed by decay in a dead trunk, or sometimes a cranny in an irregular living trunk. In either case they prefer an inconspicuous entrance barely wide enough for them to squeeze through. A substantial proportion of the recorded nests of woodcreepers was low, sometimes within a yard of the ground, probably because low nests are more easily found by ornithologists rather than because they are more abundant than high ones. In Costa Rica, the Streaked-headed Woodcreeper prefers an elevated site, up to 80 feet, but it will accept a fairly low one if it is otherwise satisfactory. The little Wedge-billed Woodcreeper seems to favor a low cavity, within a yard or two of the ground. The Tawny-winged Dendrocincla not infrequently nests in the center of a decaying palm stump, at the bottom of a tube which opens upward and provides no shelter either from rain or the rays of the sun when it is overhead.

Unlike woodpeckers, woodcreepers build a nest in the bottom of their cavity, taking in a great quantity of material if it is spacious. In the Streaked-headed and Spotted-crowned woodcreepers, the nest is composed of many flakes of stiff or corky bark, with no softer material and with nothing to bind the pieces together. The Wedge-billed Woodcreeper makes a softer nest of fibrous materials. The Tawny-winged Dendrocincla chooses fibrous bark, papery bark, whitish foliaceous lichens, and similar materials, which rest on a filling of moss if the nest cavity is too deep. In the Streaked-headed Woodcreeper, both sexes build, and doubtless this is also true of the Spotted-crowned and Wedge-billed woodcreepers, as both adults continue to carry in materials while incubation is in progress. Once I watched a Plain-brown Dendrocincla carry 53 billfuls of green moss into a hollow stub in an hour and a quarter; the bird seemed to work alone, as there was never more than one individual in sight.

Woodcreepers lay sets of two and less often of three eggs. Sets of three have been recorded for *Dendroplex picirostris* (Cherrie, 1916:268-269), *Glyphorhynchus spirurus*, and a few other species. The eggs of woodcreepers are usually ellipsoidal or oval, with scarcely any difference in the shape of the two ends. They seem always to be pure white.

Incubation is performed by both parents in the Streaked-headed, Spotted-crowned, and Wedge-billed woodcreepers, but at five nests of the Tawny-winged Dendrocincla, I found no evidence that a second parent was in attendance at any stage. A pair of Wedge-billed Woodcreepers took sessions on the eggs which averaged an hour in length; they kept their eggs constantly covered throughout a morning. The larger Streaked-headed and Spotted-crowned woodcreepers took shorter sessions, rarely exceeding 45 minutes and averaging from 15 to 40 minutes. In these two species, the two parents together kept their eggs covered for only 60 to 80 per cent of the observation periods. The sessions of three Tawny-winged Dendrocinclas ranged from about 15 minutes to 1½ hours, but they were separated by relatively long absences. The eggs were covered 68 per cent of the time in a shaded nest,

considerably less in nests exposed to sunshine in clearings. In all the species mentioned in this paragraph, the parents continue to bring contributions to the nest while they incubate; in the dendrocincla the eggs are more or less covered by the loose, light-colored materials of the nest lining while the parent is absent.

At a nest of the Spotted-crowned Woodcreeper the incubation period was 17 days, and at a nest of the Tawny-winged Dendrocincla it was 21 days. When a dendrocincla incubated eggs of a Streaked-headed Woodcreeper, the incubation period was about 15 days.

The nestlings of *Lepidocolaptes*, *Glyphorhynchus*, and *Dendrocincla* are hatched with gray down which does not cover their pink skin, and the interior of the mouth is yellow or yellowish. In the Streaked-headed and Spotted-crowned woodcreepers, both parents brood the nestlings and feed them with adult and larval insects, spiders, and the like. Feathered nestlings of the Streaked-headed Woodcreeper were fed at the rate of four times per nestling per hour. At the age of 13 days, two nestlings of the Spotted-crowned Woodcreeper were given 22 meals in 1½ hours. A Tawny-winged Dendrocincla, attending two nestlings without help from a mate, usually fed them infrequently, but once she brought them 14 meals in half an hour after sunset. She gave the nestlings many small lizards in addition to insects and a few spiders. Woodcreepers carry food to the nest in their bills, one article at a time. Streaked-headed and Spotted-crowned woodcreepers at first swallow the nestlings' droppings or carry them off in their bills. After the young birds can climb up and take their nourishment through the doorway, the parents, no longer obliged to enter the cavity, neglect the sanitation of the nest. A Tawny-winged Dendrocincla, however, kept its nest clean until the young left.

Parent woodcreepers apparently never give distraction displays.

As they grow older, nestlings of the Streaked-headed and Spotted-crowned woodcreepers frequently utter weak versions of their parents' characteristic songs or calls. In both of these species of *Lepidocolaptes*, the nestling period is approximately 19 days. Young dendrocinclas, which are much more silent and secretive, remain in the nest for 24 days, and after their departure their parent leads them to sleep in other cavities, always one to a hole. In coloration, juvenal woodcreepers differ little from their parents.

Helpers at the nest are unknown, but a Tawny-winged Dendrocincla hatched and reared a Streaked-headed Woodcreeper in a hollow palm trunk into which both species had carried nest material.

Adults of the Streaked-headed, Spotted-crowned, Wedge-billed, and Buff-throated woodcreepers, and of the Tawny-winged and Plain-brown dendrocinclas roost singly in cavities in trees, usually those formed by decay. They are among the last of the diurnal birds to retire in the evening and the first to become active at daybreak. The dimness of the light when they enter and leave their holes makes it very difficult for the observer to find these dormitories. The two species of *Lepidocolaptes* and the Tawny-winged Dendrocincla, for which alone long series of observations on roosting are available, sleep in holes throughout the year. Often these cavities are of such form that rain enters through the top, which suggests that concealment is more important to the woodcreepers than is dryness.

FAMILY PICIDAE¹

RED-SHAFTED FLICKER²

Colaptes cafer

The Central American forms of the Red-shafted Flicker are sufficiently distinct from the more northern races to have been once classified as a separate species, *Colaptes mexicanoïdes*. This woodpecker is about 11 inches in length. The forehead, crown, hindhead, and hindneck are deep rufous-chestnut. The back, shoulders, and much of the wings are evenly barred with black and light brown. The rump and upper tail-coverts are white, and the latter are broadly barred with black. The tail feathers and larger remiges are blackish, with shafts that are mostly bright orange or red. The sides of the head and neck, as likewise the throat and foreneck, are fawn gray, adorned in the male with bright red malar stripes. The chest bears a large black crescent. The more posterior under parts are dull white, shading laterally into pale pinkish gray, and sprinkled with numerous small, roundish or cordate spots of black. The lower side of the wings is largely buff-pink or salmon-pink, and the under side of the tail is chiefly rufous-orange. The female resembles the male, except that her malar stripes are cinnamon instead of red.

The Red-shafted Flicker ranges from southeastern Alaska and the more southerly parts of western Canada over the western half of the United States and the highlands of México to northern Nicaragua. Since so much has been written about the more northerly representatives of the species, I shall confine this brief account to what I have learned about its habits in Central America, particularly in Guatemala. In this country, I found the Red-shafted Flicker well distributed over the highlands, ranging from 5000 to 11,000 feet above sea level. It was fairly common in the more open parts of the mixed woodland of pines, oaks, and many other broad-leafed trees on the Sierra de Tecpán, between 7000 and 9000 feet. But nowhere did I find it more abundant than on the high massif of the Sierra Cuchumatanes, where its large size and its loquacity made it one of the most conspicuous birds on the grassy plateau and the rocky ridges which rose above this extensive tableland. Here the flickers lived among alders, pines, and low junipers. At the time of my visit, in mid-September of 1934, the many dead pine trees, which had succumbed to a blight of some sort, provided numerous, although unstable, sites for nest cavities and dormitories. Here the flicker far outnumbered the Hairy Woodpecker, the only other picid which I saw, or which was likely to occur at this altitude. The flicker's abundance around 11,000 feet suggested that it ranged even higher in these poorly explored mountain areas.

Like their northern relatives, the Guatemalan flickers are sociable birds, and in September, October, and November I found them usually in parties of three or four. Evidently these were parents with the young of their latest brood. Often my approach

¹In this family I have arranged the species in the order of their increasing sociability, as shown by their nesting and sleeping arrangements. The chief difficulty has been with the piculets, and I have arbitrarily placed them last of all. Further studies of the piculets, especially of the many South American species of whose habits scarcely anything has been recorded, may yet reveal a degree of sociability not inferior to that of the Acorn Woodpecker.

²Since this account was written, Short (1965) has presented reasons for considering *C. cafer* and *C. auratus* as being conspecific.

made them rise from the ground, where they probably had been gathering ants, a favorite food. One which rose from the path ahead of me flew only 20 feet to the trunk of a neighboring pine, where it clung upright, hardly 5 feet above the ground and fully exposed. Here the bird remained intently regarding me, motionless except for its slightly shaking head, as long as I kept my eyes fixed upon it. But the moment that I moved it disappeared behind the trunk, up which it climbed to the higher branches, whence at length it flew.



Fig. 23. View near the northern edge of the plateau of the Sierra Cuchumatanes, Department of Huehuetenango, Guatemala, at 10,500 feet, showing alpine meadow, blighted pines, and mixed woods of pine and dicotyledonous trees in the background. Here lived Red-shafted Flickers, Hairy Woodpeckers, Brown Creepers, Golden-crowned Kinglets, Slaty Flower-piercers, Meadow-larks, Guatemalan Juncos, and resident Savannah Sparrows. August 24, 1934.

Even in November, the flicker's loud, mellow, cheerful *wic wic wic wic wic* floated through the crisp early morning air, over fields whitened with frost, bringing to one recently come from a northern land memories of spring, at a time when the signs of the seasons were confusingly mixed; for, despite the penetrating nocturnal chill, sheltered glades supported an abundance of bright blossoms, especially of composites suggestive of autumn. The flicker's jubilant calling continued through February, when oaks and alders were tasselled with long catkins in true vernal style, although months of frost and increasing drought had left only a poor remnant of flowering herbs. When the sun stood high in the bluest of skies, the flicker's loud, rolling call was replaced by a quiet *wic wic*, as though he conversed with his companions in confidential tones.

NESTING

On March 17, 1933, I found a male flicker beginning to excavate a nest chamber on the Sierra de Tecpán, at an altitude of 8500 feet. His site was the stub of a lateral branch of a pine tree, at a height of about 30 feet. Hanging below the decay-

ing stub, which ascended at an angle of about 45 degrees, he was drilling into its lower surface. At the beginning, I found only the male at the still shallow depression. On March 22, I first saw the female at the hole, which was being deepened very slowly. Clutching the rim of the cavity with her feet, she hung below it, with only her head and neck inside as she worked. After every few pecks, she withdrew her head to look around. In the hour that I watched, she labored for only 13 minutes, and her mate did not appear. Each partner carved while the other was out of sight, as I have often found in other woodpeckers. As late as April 8, the flickers were still hammering at this cavity.

On April 14, in the same locality, a boy showed me a nest in the decaying heart of a living alder tree growing in an open pasture. The irregular orifice, which apparently had been little altered by the flickers, was only 5 feet above the ground, and the chamber extended 16 inches below this opening. Although the hollow may have been enlarged by its tenants, it had evidently not been made by them. Four pure white eggs lay on the unlined bottom. The shells, glossy as the finest porcelain, were water-marked by slightly wavy lines, which ran both longitudinally and transversely. They measured 31.0 by 21.4, 31.0 by 21.0, 30.2 by 21.4, and 30.2 by 21.4 mm. The male incubated these eggs through the night, and by day he attended them in alternation with his mate—an arrangement which, as I later found, is also followed by the Yellow-shafted Flicker. By April 20, the eggs had vanished from the low, exposed site.

The pair of flickers which carved a nest chamber in March hatched its eggs in April. But with the first hard rains in mid-May, the rotten stub, heavy with water, fell to the ground. I found the three fully feathered young flickers apparently uninjured by their 30-foot fall. All three resembled the female in plumage. They could hardly fly, and when I picked them up they squawked loudly and struggled hard to escape, pecking and biting with vigor. If I held two of them face to face, each directed its pecks at the other; yet, when they rested close together without constraint, they were perfectly friendly. When I placed them on a stump, they alternately pecked at the wood and called to their elders in the treetops. I left them in an oak tree, so that the parents might continue to attend them.

In early June, I found a third nest, in which nestlings were still being fed. It was about 75 feet up in a blasted tree standing in a maize field.

SUMMARY

In Guatemala, the Red-shafted Flicker occurs from about 5000 feet to at least 11,000 feet above sea level. It is found chiefly in open woods of oaks and other broad-leaved trees with an admixture of pines or, at higher elevations, in open stands of pines and alders. Late in the year, flickers live in family groups of usually three or four individuals; apparently these are parents with full-grown offspring. They often forage on the ground.

Loud calling begins in November and continues through February. In March, the flickers begin to carve their nest chambers, working alternately; each works while its mate is at a distance. The Red-shafted Flicker also breeds in cavities made largely or wholly by decay. Three nests ranged in height from 5 to about 75 feet. One nest contained four pure white eggs in mid-April. The male attended these through the night, but by day the sexes incubated alternately. A late nest still held nestlings in early June.

GOLDEN-OLIVE WOODPECKER¹

Piculus rubiginosus

This beautiful woodpecker is about eight inches in length. Its back and wings are a most attractive shade of olive-green with a golden tinge. Its tail is brownish olive, the central feathers becoming blackish toward the end. Its under parts are yellowish olive with transverse yellowish bars which become broader and less sharply defined on the abdomen and flanks. As in most woodpeckers, the male and female are alike in appearance except for the markings of their heads. On the male's nape is a large area of bright crimson, which extends forward along the sides of the pileum to the base of the bill, enclosing the slate-gray of the crown and center of the forehead. His grayish brown cheeks are bordered below by broad crimson malar stripes. The female has a crimson nape but lacks the conspicuous crimson malar stripes of the male.

The Golden-olive Woodpecker ranges from México to northern Argentina and is highly variable. I found it fairly common in the coffee plantations on the Pacific slope of Guatemala. Here the trees of the original forest had been left to shade the coffee, which was set out after the undergrowth was cleared away and the canopy thinned. In October, these woodpeckers were usually in pairs and were rather difficult to approach. In Costa Rica, the Golden-olive Woodpecker is most abundant in the highlands. Carriker (1910:585) found it from 1500 to 6000 feet above sea level, but the greatest numbers were found between 2000 and 4000 feet in the Reventazón Valley on the Caribbean side of the country. In the region of El General on the Pacific slope, I have seen it no lower than 3500 feet. In the vicinity of Vara Blanca on the northern or Caribbean side of the Cordillera Central, the Golden-olive Woodpecker was rather rare around 5500 feet. Here it lived in the heavy, epiphyte-laden forest and in adjacent clearings with scattered trees.

In this locality, in about the middle of February, I began to hear, especially in the early morning, the far-carrying call of the male. This consisted of a high-pitched, clear, powerful note, very rapidly repeated to form a long-continued roll or trill, all in approximately the same key. It was easily distinguished from the shorter, weaker, slower roll of the Hairy Woodpecker and the queer, wooden rattle of the Smoky-brown Woodpecker, which were the other chief picids at Vara Blanca. Clinging in some high treetop, the Golden-olive Woodpecker repeated his loud trill over and over. The call note of both sexes is a high, loud, sharp *bee*, and the birds also utter a dry *churr*.

From August of 1937 until the following March, a female slept alone in old holes in decaying stubs in a narrow clearing in the forest. Her first lodging, about 20 feet up in a tottering trunk, was occupied nightly for two months after I found her. After this trunk fell, she moved to the abandoned roost hole of a female Hairy Woodpecker, head-high in a neighboring slender stub. Early in March, I discovered that a male Hairy Woodpecker slept in a chamber freshly carved in the top of the same low stub, about 6 feet above the cavity in which the Golden-olive Woodpecker still roosted. But before the end of the month, the latter was sleeping in the

¹ This life history is an abridgement of Skutch, 1956.

newer and higher hole, the Hairy Woodpecker having gone elsewhere. I do not know whether his desertion was voluntary or whether his larger neighbor had somehow evicted him, possibly merely by ensconcing herself with the cavity before his arrival in the evening. This Golden-olive Woodpecker was almost fearless of me. She would enter her dormitory while I stood in plain view fairly near it, and after she had settled within, it was difficult to make her come out.



Fig. 24. Upper Tropical Zone forest near Cañas Gordas, Costa Rica, at about 3800 feet above sea level. In this woodland and adjacent clearings, Golden-olive Woodpeckers were abundant.

NESTING

On April 5, 1938, I found a pair of Golden-olive Woodpeckers incubating in the hole where the female had of late been sleeping, and where the male Hairy Woodpecker had formerly passed his nights. This cavity was 13 feet above the ground, in a slender and very rotten stub standing amid tall, rank grass in a steep hillside pasture. I could not examine it until two days later, when I had assistants hold a ladder. My mirror then revealed four, glossy, pure white eggs, resting on clean chips at the bottom of the hole. I did not jeopardize the nest by attempting to remove them for closer examination.

Now that the female woodpecker's dormitory had been converted into a nest, the male occupied it by night. The female returned to sleep in her earlier lodging 6 feet lower in the same stub. However, she slept there only a few nights and then moved to a more distant abode that I failed to find. In using the female's rather than the male's dormitory as a nest, the Golden-olive Woodpeckers did just the reverse of a pair of Red-crowned Woodpeckers that I had watched earlier. I was not

certain of the origin of the hole in which the Golden-olive Woodpeckers nested. Possibly they had excavated it themselves and the Hairy Woodpecker took possession of it for a while, to be turned out later by the rightful owners. The size of the doorway suggested that the hole was carved by the larger Golden-olive Woodpeckers.

By day, the male and female sat alternately on the eggs. Despite the lowness of their nest, both were extremely confiding and did not fly out when I stood directly below their doorway, even after I had made a sound which caused them to look out. When I came with two helpers to hold the ladder for me, we found the male woodpecker in charge of the nest. After I drew his attention by tapping on the trunk, he gazed calmly down on the three of us. It was necessary to clear a space at the foot of the stub to set up the ladder, and for a while the bird watched me chop down the grass and weeds so close below him. But before I finished this work, he lost courage and flew away. The female's behavior was most variable. Sometimes she watched me set up the ladder beneath the nest and even let me climb part way up before she fled. At other times a slight tap on the trunk would send her off.

Seated on a distant stump on the hillside without concealment, I began to watch this nest as it grew light at 5:30 a.m. on April 15. There was no sign of activity at the hole until 7:15, when the female suddenly flew to the top of the stub and uttered a single, low, wiry note. The male, which had not previously revealed himself in the doorway, now looked out for the first time, then silently flew off. The female at once entered the nest. Four hours slipped by without my having a glimpse of her in the nest or of her mate on the outside. Beginning at last to suspect that the male might have replaced her on the eggs, at a moment when my attention strayed, I clapped my hands and called to bring to the doorway whichever member of the pair was within. When these sounds failed to obtain a response, I advanced and tapped lightly on the trunk. Instead of merely looking out, as she usually did in similar circumstances, the female came out and flew away. But after only 6 minutes she returned to the nest, to sit for another hour. Through much of her long morning session of nearly 5 hours' duration, she hammered lightly on the inner wall of her chamber.

At 12:12 p.m., the male at last returned and clung beside the doorway. The female flew away and the male entered at once. At 1:34 the female returned and alighted beside the doorway, giving a low, wiry note I had heard early in the morning. The male silently departed, and the female entered. I was now obliged to be absent for a little over an hour while I visited some other nests. The female was still within the cavity when I returned at 2:42, and she sat until her mate replaced her at 3:05. At 4:50 she again came to the stub and voiced the same low, wiry notes as before. She waited before the doorway 2 or 3 minutes for her mate to emerge, but he did not even show his head. Then she went in, but promptly came out and flew away. After her departure, the male looked out, then settled back upon the eggs. At 5:03 the female returned once more, sounded the wiry note, then entered while her mate was still inside. He at once made his exit and flew off. At 5:54 he returned, clung beside the doorway and uttered a low note, and the female departed. Then the male entered to pass the night on the eggs.

The female woodpecker's long morning session of nearly 5 hours surprised me greatly. Her two afternoon sessions lasted 91 and 51 minutes, while the two afternoon sessions of the male continued for 82 and 118 minutes. Considering the woodpeckers' day to extend from 5:45 a.m. to 6:15 p.m., an interval of 12.5 hours, and neglecting

the interruption of 6 minutes for which I was responsible, the female incubated for 439 minutes and the male for 311 minutes of the day. Had her mate yielded the nest to her when she arrived at 4:50 p.m. to relieve him, the female might have had a still larger percentage of attendance to her credit. At no other woodpeckers' nest which I have watched continuously has the female incubated for such a large part of the day.

Three of the eggs hatched on April 16; the fourth hatched on the following day. The newly hatched nestlings had tightly closed eyes and pink skin without any trace of feathers. Their parents were negligent in removing the empty shells, allowing parts of them to remain in the nest for at least five days after the nestlings had hatched. Two of the young woodpeckers vanished a few days after hatching, evidently having lost out in the competition with their nest mates for food. This is a common occurrence among nestling woodpeckers, and it appears to be in part a consequence of the parents' inability to see the nestlings well at the bottom of the deep cavity and to distribute the food equally among them. Eight days after they hatched, the two survivors, which had grown with wonderful rapidity, were sprouting pinfeathers.

After the nestlings hatched, the parents became more wary than they had been while they incubated, and they would fly from the hole with far slighter provocation. I tried to watch the nest from a blind set close in front of it, but the female delayed so long in approaching that I finally decided to remove the offending brown tent and to look on without concealment from a more distant point. On April 27, after the cessation of a cold rain, I took my station on the hillside and watched the parents attend their two eleven-day-old nestlings. In the 4 hours and 40 minutes from 6:50 to 11:30 a.m., the male visited the nest only three times, the female only twice. Presumably the adults fed the nestlings on each visit, which would make the rate of feeding little better than once per hour for the two young birds. Once I discerned what seemed to be a small particle of food projecting from one side of the female's bill as she entered the nest, but otherwise the parents came with no visible food. The feeding of the nestlings was evidently by regurgitation, but since this was done within the cavity, I could not watch it. The female still made her first morning appearance at the nest at about 7:15, as she had done while she incubated. Thus the nestlings received their first meal of the day rather late. They were now brooded very little during the day; the female remained in the nest for periods of 10 to 9 minutes only, while the male stayed for 7, 7, and then 8 minutes. And the parents did not warm the nestlings even for the whole of these brief intervals but spent part of the time looking through the doorway. From time to time, they carried away droppings.

Another nestling died after its feathers had begun to sprout, leaving only one alive out of the four that hatched. At the age of 21 days, the lone survivor began to appear in the doorway to receive food. It was well feathered, resembled the female, and was without much doubt a young female. On May 10, when the young bird was 24 days old, I devoted 5 hours of the morning to watching the parents attend her. I began my vigil at dawn, and as the light increased I could distinguish the male's head in the top of the chamber. He still passed the night in the cavity, but perhaps he clung to the side of the hole above the nestling rather than actually brooding her. At 5:58 a.m. he flew out, and immediately the nestling's head appeared in the doorway. She continued to watch and wait for her breakfast for nearly 2 hours more, for it was 7:45 before the male returned with her first meal of the day.

He brought nothing that I could see in his bill, but on arriving he clung to the outside of the trunk beside the doorway, placed his bill in the nestling's mouth, and proceeded to regurgitate food to her. The feeding was completed in two installments, each lasting a few seconds. At its conclusion, he flew away. Three quarters of an hour later, he came again with a second and apparently more copious meal. The young woodpecker, which had been watching through the doorway, leaned far out to receive it. As the male flew off, the nestling voiced a low trill.

The adult female first appeared that morning at 8:55. Clinging to a neighboring tree, she uttered the sharp, staccato *beee*, and then a rapid trill. Thence she proceeded to the entrance of the nest, with nothing visible in her bill, and fed the nestling by regurgitation in a number of brief installments. After this, she flew off and did not return during the next 1½ hours. At 9:05 the male appeared for the third time. From a neighboring tree he called and trilled, while the nestling answered with a much weaker trill. She stuck out her long, slender, white tongue, as though in anticipation of the food she was about to receive. But this time the meal was short. After the male left, the young bird scratched and pecked the inner wall of the chamber. Through the doorway, I could see her hang backward in the top of the cavity to preen her breast feathers. In 20 minutes the male was back again and fed her more liberally, in four courses. Thus, in the first 4½ hours of the woodpeckers' active day, the single nestling received only five meals, of which the male brought four.

Now that the adults could feed their nestling through the doorway, they no longer entered the cavity and removed droppings, as they had done earlier. In consequence, the bottom of the chamber was soon covered with an accumulation of filth. This probably was not detrimental to the young woodpecker, which now no doubt passed day and night clinging to the wall of the deep cavity, rather than resting on the bottom, as she had done when she was younger.

On the afternoon of May 10, the young woodpecker looked down while we set the ladder below her. She watched me climb up, and even permitted me to touch her bill, before she retreated into the bottom of the hole. As I was ascending to the topmost step of the ladder and balancing myself in a difficult position, my mirror rubbed against the stub and made a grating noise, which frightened the woodpecker more than had my approach. Suddenly darting from the nest, she turned down the slope toward the woods in the ravine. Her flight was slow and labored, but without a pause she covered about 25 yards, in a course which at first was inclined downward, but toward the end veered slightly upward. She came to rest in a tangle of vines that covered a small tree within the forest's edge. Since other woodpeckers of about the same size (such as Golden-naped and Golden-fronted woodpeckers) stay in the nest a month or more, I was surprised that this young Golden-olive Woodpecker could fly so well at the age of only 24 days.

The young woodpecker was fully feathered and her fresh, new plumage was colored like that of the adult female. Soon after her premature departure from the nest, I watched to see whether her parents would try to bring her back to the nest cavity, for the sun was sinking low. The female did not again appear in the vicinity, but at about 6:30 p.m. the male returned to the hole. Clinging before the doorway, he peered inside and all around, as was his custom before entering, but he showed little concern over the nestling's absence. He uttered not a syllable to call her back, as parent Golden-naped Woodpeckers might have done, but he silently retired into

the sheltering hole, while the young bird remained in the open, exposed to the rain.

Four days later, I found a young female Golden-olive Woodpecker, attended by her parents, high up in a moss-burdened tree at the forest's edge. Although she was about 1000 feet from the nest that I had watched, I believe that this was the fledgling that had been reared in it, for Golden-olive Woodpeckers were not abundant in this region, and each pair wandered over a wide area.

For a number of nights after the nestling flew out, the male continued to lodge in the nest cavity, but I never again saw the young woodpecker near it. Doubtless, as in the Red-crowned and Hairy woodpeckers, the young Golden-olive slept clinging to a trunk in the open, until she succeeded by her own unaided efforts in finding an unoccupied cavity suitable for a lodging.

The only other nest of the Golden-olive Woodpecker which I have seen was in a dead, branchless trunk, standing in the midst of a swampy area covered with bushes and low trees, in the well-wooded valley of the Río Pastaza below Baños, Ecuador, at an altitude of 4200 feet above sea level. On October 18, 1939, this inaccessible hole contained, as far as I could learn, a single well-feathered male nestling, which spent most of the time looking through his doorway. In an hour and a half, each of the parents fed him twice, by regurgitation, and it is perhaps significant that the male returned to the nest in slightly less time than the female. Although the adults delivered food while clinging below the doorway, at the conclusion of a meal they pushed past the nestling to enter the cavity and clean it. The fact that the head markings of this nestling resembled those of the adult male, whereas those of my Costa Rican nestling were like those of the adult female, showed that in this species young in their first plumage wear the colors of adults of the same sex.

LINEATED WOODPECKER

Dryocopus lineatus

This large woodpecker is somewhat over 12 inches in length. The upper parts of the male, including the wings and tail, are mainly black. His high-crested head and his hindneck are bright red and conspicuous from afar. The region around the eye and much of the cheeks are slate-colored. A white or whitish stripe, beginning at the base of the bill, runs back over each cheek, along the sides of the neck, and over the shoulders. The lower cheeks are crimson; the chin and throat are streaked with black and white; and the foreneck, chest, and upper breast are plain sooty black. The more posterior under parts are pale brownish buff or clay-color, more or less distinctly barred or spotted with sooty black. The under wing-coverts are buffy yellow. The female resembles the male except that her forehead and the forepart of her crest, as likewise the malar region, are black instead of red. In both sexes, the iris is pale yellow or nearly white. The bill is blackish in the race *mesorhynchus* inhabiting Panamá and southern Costa Rica, but it is pale horn-color or yellowish white in the race *similis* which ranges from northwestern Costa Rica to southern México. About the Gulf of Nicoya, where the two forms meet, I have seen individuals with bills intermediate in hue.

The species ranges over much of the tropical portion of the American continent from northern México to northwestern Perú, Paraguay, and northern Argentina. A most adaptable bird, in Central America it is found throughout the length of both coasts. It is found in the most humid regions as well as the most arid, where along the watercourses and in the river bottoms the trees grow big enough to provide sites for its nest. In both Guatemala and Costa Rica, this woodpecker lives from sea level up to 3500 feet, if not higher; in Costa Rica, I found it nesting at 3000 feet. In México, it occasionally occurs as high as 5000 feet (Griscom, 1957:29). In the more heavily forested districts, it prefers the older second-growth woodlands and clearings with scattered trees, especially if many of these have been killed by fire, to the depths of the high rain forest itself. At all seasons, it lives singly or in pairs, never in flocks. Its flight is strongly undulatory.

FOOD

Lineated Woodpeckers are fond of ants, especially those which dwell in the hollow trunks and branches of the guarumo (*Cecropia*) trees that spring up swiftly in forest clearings and denuded lands of all sorts, in humid districts at lower and middle altitudes throughout tropical America. I have often watched these woodpeckers perforating the soft wood that surrounds the wide central cavity of the thinner trunks and branches—no difficult undertaking for bills as strong and sharp as theirs. Then they busily extract from the interior objects which are doubtless either the *Azteca* ants or their larvae and pupae. From time to time, they interrupt this activity to collect the little ants which run confusedly over the bark. Or they may merely hammer on the branch, without perforating it, until the ants come pouring out through the doorways, which are situated at the upper end of each internode. Then the woodpecker eagerly picks the ants off and devours them. The trunks and branches of these trees often show great traumatic swellings where they have been pierced by

the woodpeckers; smaller branches and even the tops of young trees may break across where they have been perforated by the birds' bills. The guarumo provides not only spacious chambers for the accommodation of the ants, but also a special food in the form of little white corpuscles rich in protein (the "Müllerian bodies") that are produced in successive liberal crops on the peculiar hairy cushions at the bases of the long petioles of the ample, palmately lobed leaves. In return for so much



Fig. 25. A guarumo or trumpet tree (*Cecropia* sp.), a swiftly growing second-growth tree which the Lineated Woodpecker often visits, and injures, in order to extract the ants which inhabit the hollow stems.

generous hospitality, the *Azteca* ants have been supposed to protect the tree from the depredations of injurious creatures of various sorts. But at best they form a rather ineffective garrison, and I have often wondered whether they ever render any service to the tree that adequately compensates for the tremendous damages they indirectly cause by attracting the Lineated Woodpeckers (Skutch, 1945c).

These woodpeckers also pry the bark in flakes from dead trees and dig into trunks and stems to extract insects and larvae other than ants. In Honduras, I once was led by a loud tapping to a Lineated Woodpecker in a stand of wild cane (*Gynerium*) beside a river. The bird was clinging to the upper side of a leaning cane in which he was drilling holes. I watched him until he became aware of me and flew off. Going then to examine what he had done, I learned that he had pierced

the cane to the pith in several places. When split open, the interior of the stalk disclosed a slender white larva over an inch in length, and an empty cocoon in which evidently a similar larva had metamorphosed and escaped. Did the woodpecker know in advance just where to bore in order to reach something edible, or did he try again and again until his industry was rewarded?



Fig. 26. Apex of a young shoot of a guarumo tree, cut open to show the hollow internodes inhabited by *Azteca* ants, a favorite food of the Lineated Woodpecker.

On September 15, 1960, the excited calls of the Golden-naped Woodpeckers in a tree of *Clusia rosea* in the garden drew my attention to a Lineated Woodpecker in this tree. When I first glimpsed the larger woodpecker, it seemed to be carrying a long, curved twig. Closer scrutiny revealed that the woodpecker was a male, and that the apparent twig was his lower mandible, which was bent from the base, so that it crossed the upper mandible well behind the tip of the latter. Then it continued to curve upward and leftward so far that it seemed to be three or four times the normal length. The Lineated Woodpecker hung back downward beneath an apple-sized *clusia* pod that was opening, just as the Golden-naped Woodpeckers did, but the pod was apparently empty.

For the next five weeks, this unfortunate woodpecker continued to visit the clusia tree. Sometimes he hung for many minutes beneath a single opening pod and laboriously extracted some of the seeds enclosed in bright red arils, of which woodpeckers, honeycreepers, and other birds are exceedingly fond. Whether the handicapped woodpecker removed the seeds with his upper mandible or his tongue I could not tell. His overgrown lower mandible impeded him greatly, and even after he had obtained a few seeds, he had trouble working them back into his mouth so that he could swallow them. Once, while continuing to hang back downward, he supported the seeds on his foreneck until he could take them into his mouth. In consequence of his almost daily visits, the Golden-napes became reconciled to his presence in their favorite food tree and would even gather clusia seeds while he was there. I last saw this Lineated Woodpecker on October 23, when, after 24 hours of rain, he looked slightly bedraggled.

Since a deformity of this nature does not develop in a day, it is evident that the woodpecker managed to survive with it for a period considerably longer than the five weeks that I had him under observation. Obviously he could not peck into wood with such a mandible. Yet he did not appear emaciated and, except after the long-continued rain, his plumage was in good condition whenever I saw him.

VOICE AND MECHANICAL SOUNDS

The Lineated Woodpecker's most common utterance is a loud, mellow, far-carrying *wic wic wic wic wic*, by which the male and female answer each other. This pleasant, stirring call is one of the vernal bird notes of Central America and is heard chiefly from December (in the south, at least) until the end of the dry season in March or April. At a distance, the call sounds much like that of a flicker. While attending their young, although rarely at other times, the parents utter a peculiar loud churr, sounding like *kay rar-r-r-r-r*, or sometimes *k'rroo*. This phrase is punctuated by sharp monosyllables that resemble a high-pitched human sneeze. Before they leave the nest, the young woodpeckers deliver both the *wic wic wic* and the powerful rolling call, in voices slightly weaker than those of the adults.

In addition to these vocal notes, both the male and female beat out rapid, rolling tattoos on resonant dead stubs, sometimes responding to each other in this fashion instead of with their voices. This tattoo serves to distinguish the Lineated Woodpecker from the other big, red-crested woodpecker of Central America, the Pale-billed Woodpecker, which rarely drums a tattoo but beats two loud, staccato taps.

ROOSTING

Although the Lineated Woodpeckers remain paired throughout the year, they lodge at all seasons in separate holes. From February until June of 1936, a female slept nightly in a decaying trunk in a clearing at the edge of the forest on the ridge between the Buena Vista and Chirripó rivers, in El General. The stub, about 20 feet in height, was a mere hollow shell, with its internal cavity open to the outer air through several large gaps. Arriving in the evening, usually well before most birds of other kinds had settled down to rest, the woodpecker would climb over the outside of her dormitory, tapping loudly on the resounding shell and peering in through the gaps, as though to make quite sure that no snake or other unfriendly creature had hidden itself within during her day-long absence. Then she would slip in through the particular opening that she used for her doorway and would spend a while looking

out, before she disappeared for the night. In the morning, she awoke late and then would gaze out through one of the openings for many minutes before emerging. Sometimes, before flying off in search of food, she would beat a loud tattoo against the top of her hollow shell; this was answered by her mate at the edge of the neighboring forest, where evidently he slept.

After June, many months passed before I again saw a Lineated Woodpecker enter this stub. But the following April, a female, probably the same individual, lodged there for a while. She was just as cautious about entering the stub as she had been in the preceding year.

In June of 1940, I watched a female retire in the evening to sleep in a similar hollow trunk, on a cleared ridge close to the forest in another part of El General. Arriving after sunset, she clung to the side of the trunk and began to tap with her bill. She climbed all over it, up, down, and around, hammering loudly here and there, and peering again and again into the gaps in its outer shell. After continuing this for about 10 minutes, she went at last to the opening that she considered her doorway—evidently the entrance to an ancient hole of either her own kind or the Pale-billed Woodpecker. She stuck in her head a little way and promptly withdrew it. She did this many times over, at each repetition going in a little farther, until finally she entered, when the light was growing dim. Then she pushed forth her head and looked out and around again and again, before at last she settled down to rest in the deepening dusk.

Although this woodpecker entered the trunk through a doorway that had probably been made by a woodpecker, her dormitory was far more spacious than a woodpecker's nest. The whole top of the stub appeared to be hollow, and there was a long, irregular gap down the side, through which she might well have gone in. In the related Black Woodpecker of Europe, the female often roosts in a hole with several entrances, although the male prefers a lodging with a single doorway (Blume, 1961:27).

On April 4, 1937, I watched still another Lineated Woodpecker retire at nightfall into a large hole at the very top of a tall, decaying trunk in a clearing at the forest's edge. A male, apparently the mate of this bird, seemed to wish to enter a hole in a low trunk near my observation post, but he feared to go in while I watched.

THE NEST

In southern Central America, the Lineated Woodpeckers begin preparations for nesting very early, and I have known them to start carving their holes in the first days of November. In northern Central America, the few available records indicate a somewhat later beginning of the breeding season. The spacious nest chamber is carved in a dead tree or in the dead top of a living tree, and all such trees that I have found have been near woodlands in clearings, pastures, or in fringes of trees along watercourses flowing through cultivated districts. Eleven nests of the dark-billed race in southern Costa Rica ranged from 9 to nearly 100 feet above the ground, but only one was below 30 feet. Two nests of the light-billed Lineated Woodpecker in the Motagua Valley of Guatemala were much lower. One was barely 6 feet above the ground in an old, rotting wooden pile of a washed-out railroad trestle near the junction of the Morjá, Jubuco, the Motagua rivers. On two sides of the nest was open water, on the other two, tall grass with scattered low trees. The second Guatemalan nest was 10 feet up in a tall, branchless, charred trunk standing alone in a hillside pasture.

As in other woodpeckers, the cavity is carved out by the male and female working alternately. That in the trestle had a round doorway $3\frac{1}{2}$ inches in diameter. The excavation extended to a depth of $13\frac{3}{4}$ inches below the lower edge of the orifice. At its widest point, somewhat above the bottom, it was 7 inches in diameter from front to back and 5 inches from side to side, thus being elliptical rather than round in cross section. The second Guatemalan nest had a doorway $3\frac{1}{4}$ inches in diameter and it was 18 inches deep. The chamber measured 6 by $4\frac{1}{2}$ inches in transverse diameter. As in other woodpeckers, the nest is unlined, and the eggs rest on loose chips in the bottom.

THE EGGS

The first Guatemalan nest contained four eggs and the second held three. The glossy, immaculate white shell was so translucent that one could readily see the position of the small yolk within, and later it was possible to count the pulsations of the embryonic heart. The yolk always rotated to the highest part of the egg, whether a side or either end was held uppermost. The eggs in the first set measured 30.6 by 21.8, 30.2 by 21.4, 31.8 by 21.8, and 32.5 by 21.4 mm. Those in the second set were 26.2 by 22.2, 27.8 by 22.2, and 30.2 by 21.0 mm. The last two eggs laid in this set were somewhat lopsided and misshapen—a rare condition in birds' eggs.

Of the two Guatemalan nests, the eggs were laid in one in early March, and in the other in early April. The high nests in Costa Rica were not directly examined, but as nearly as could be calculated from observation of the parents' behavior or the known dates of departure of the young, eggs were laid in them as follows: January (or possibly late December), 7; February, 1; March, 1; April, 2. With one exception, these nests were situated in the valley of El General, 2000 to 3000 feet above sea level.

Belcher and Smooker (1936:798) reported one set of two and one of three eggs, found in Trinidad in April.

INCUBATION

As soon as the nest cavity has been carved, the parents spend much of the day guarding it, although it still contains no egg. This precaution is necessary, because the commodious chamber is greatly coveted by a variety of other birds, from swallows to toucans, which nest or sleep in holes in trees but are unable to make them. Both sexes alternate in this duty, and the guardian may either rest within the cavity, usually looking out through the doorway, or cling to the outside of the trunk close by the entrance, choosing the shady side if the day is warm and sunny. From time to time, the bird may gather up a billful of chips from the bottom and throw them out through the doorway, although active carving has ceased days earlier. At first, no bird occupies the cavity at night, but one member of the pair arrives early in the morning, and while clinging in front peers cautiously through the doorway from every angle, often continuing this careful inspection for several minutes. Then it may beat a loud tattoo to bring its mate from the neighboring woods, and it may call *wic wic wic wic* if the other is slow to appear. On its arrival, the newcomer also inspects the interior of the cavity while clinging in front. Later, one may enter the nest to keep guard.

After a few more days have passed, the male spends the night in the new hole. The female comes early to replace him, and then they take turns at guarding through the day. Now they attend the nest much as though they were incubating, with the

difference that they look through the doorway or remain clinging beside it, instead of staying in the bottom. If an intruder approaches, the guardian presents a formidable beak in the aperture. I saw one do this when an inquisitive Pale-billed Woodpecker came to inspect a cavity in which a pair of Lineated Woodpeckers were preparing to nest. The larger visitor, on seeing the hole so effectively guarded, gave two loud taps on the trunk beside the entrance, then flew away.

After the set of eggs is complete, the male and female take turns in the nest much as before, only now they stay more constantly out of sight. The male regularly takes charge of the eggs through the night, while the female sleeps at a distance, doubtless in some old hole or hollow trunk such as has already been described. She comes early in the morning to replace her mate, and then the two sit alternately through the day, for 2 or 3 hours at a stretch. The changeover is effected in silence and without ceremony. The woodpecker coming to take its turn alights on the trunk; the mate which has been sitting leaves; then the newcomer enters. I have never seen one member of the pair go into the nest before the other comes out, as sometimes happens with Golden-naped Woodpeckers and Olivaceous Piculets.

These woodpeckers often approach and enter their hole with the greatest caution, and this was especially true at the low nest in the pile beside the rivers, at least while I watched it, concealing myself as well as I could amid the tall grass 100 feet away. Flying up to take a turn on the eggs, the woodpecker would often cling behind a pile beyond its own and peer cautiously around the sides, now to the right, now to the left, alternately, doing this several times over. Satisfied that there was no danger, it would proceed to its own pile and cling below the doorway. Here it peered to the left, to the right, on top of the pile, and inside the cavity, again and again, with an almost ludicrous excess of caution. It put in its head and withdrew it a number of times, then at last it slipped in. Such careful inspection of the cavity is often made even when the new arrival has just seen its mate emerge, which should assure it that no snake or other enemy can be lurking within.

From the low nest in the rotting pile, the top was inadvertently broken by the boy who found and showed it to me. He wedged the pieces of decaying wood in place to cover over the cavity, but in the course of incubation they fell away, leaving the chamber roofless. These big, shy woodpeckers continued to incubate for a while in their low nest exposed to the sky, but finally they abandoned it before the eggs hatched. To study the other low nest that I found in the charred trunk in the pasture the following month, I removed a segment of the front wall with a saw and chisel; this was before I had learned how to study nests in cavities by means of mirrors and flashlights. Although the alteration was made when only the first egg had been laid, the woodpeckers completed their set and started to incubate. After each inspection, I carefully replaced the removable segment of wall and wedged it securely in, but one morning I found that it had fallen or been torn out, and the eggs were gone. With the loss of these low nests, I was unable to learn the period of incubation.

THE NESTLINGS

I have not seen newly hatched Lineated Woodpeckers, but they are probably sightless and perfectly naked, like other very young woodpeckers. At first the young birds are brooded much, but after they grow older the parents merely guard them, clinging in the top of the chamber and looking through the doorway. At the approach of any creature that they do not trust, the adults draw back inside, ready to defend

their home with their powerful bills. When the parents come to the nest with food, there is never anything visible in their bills, for they feed the nestlings by regurgitation.

After the young woodpeckers are strong enough to climb up and look out through the doorway, some parents become very noisy as they approach the nest. Before proceeding to the orifice, they cling to a neighboring portion of the trunk and repeat over and over the peculiar rolling *kay rar-r-r-r-r*, punctuated at intervals by a sharp note like a sneeze. This call is rarely given except by the parents of older nestlings or of fledglings, or by the feathered young themselves, and it has at times drawn my attention to nests which otherwise I might not have discovered. One adult male with nestlings almost ready to fly would not go to feed them while I watched his high hole from the bank of the river which it faced, and for well over an hour he clung to the top of the stub above the nest and repeated interminably this peculiar combination of loud, far-carrying sounds. After a while, his mate arrived and added her voice to his. They continued these imprudent calls until I despaired of seeing them feed the two nestlings, both of which were thrusting their heads through the doorway in anticipation of a meal, and I went away leaving them undisturbed.

Early in 1940, a pair of Lineated Woodpeckers had a nest about 30 feet above the ground in a charred, branchless trunk, standing conspicuously in a newly made hillside clearing, beside the cabin I then occupied in the valley of the Río Pacuar, a tributary of the Río Térraba. Here I could watch it from a window, but for more careful observation I set a blind on the back of the sharp ridge. From there I could look into the nest from about its own level; behind me was the dark green background of the forest that clung to the flanks of the steep ridge across the river. Possibly because of the unusually exposed situation of this nest, the adults were at all times exceedingly quiet and circumspect in its vicinity, rarely uttering a note even after their nestlings were feathered, and never entering their hole when they were aware of my presence. The nestlings had apparently hatched early in March, and by March 19 the parents spent much time looking out of the opening of the hole, whence I inferred that the young no longer required much brooding but were merely being guarded. By March 26, the parents were delivering food through the doorway, without entering. On April 2, for the first time I saw the nestlings looking out of the entrance. As far as I could learn from the ground, there were only two, both females.

On the following day, April 3, I watched this nest from the blind from 5:20 to 10:54 a.m. and from 2:30 to 6:05 p.m., a total of 9 hours. The male, which spent the night in the nest, first looked through the doorway at 5:28 a.m. and flew at 5:52. Two minutes later the female arrived, fed a nestling through the doorway, then pushed in and immediately came out with a dropping in her bill. This was the first of the nine meals received in as many hours by the two young birds. Woodpeckers which feed their offspring by regurgitation come with food far more seldom than do those that carry particles visible in the bill. I could never see anything in the mouths of these parents; when an adult arrived at the nest, it would place its bill into a nestling's open mouth and regurgitate with the violent shaking of the head characteristic of this process. The nourishment was passed to the young woodpecker in from one to five, but most commonly two, separate acts of regurgitation, with intervening pauses in which the parent removed its bill from the nestling's mouth. I could not learn whether a single young bird received all the food brought by a parent on a visit to the nest, or whether it was divided between them, in the manner of hummingbirds. The nestling that was looking out of the opening sometimes made a

squeaky-buzzy sound when food was brought. After delivering the meal, the parent, usually the female, would enter the cavity to remove a dropping.

The division of labor by these parent woodpeckers was interesting. The female brought most of the food, coming to feed six times to the male's three. But in the 9 hours of my watch, the male spent 4½ hours in the nest; the female spent only 5 minutes there. The well-feathered nestlings did not require brooding, as it was a warm day. While in the chamber, the male passed the time looking out through the doorway; more rarely one of the nestlings occupied this coveted position, while the male clung to the inner wall of the cavity on one side. A few times the male and one of the nestlings had their heads framed in the round orifice together. His purpose in remaining in the nest was evidently to protect the nestlings rather than to brood them. Doubtless the enemies against which he guarded were chiefly the Fiery-billed Araçaris, which at this season sought the holes of the larger woodpeckers for their own nests or dormitories and frequently occupied them as soon as they were deserted by the makers and original tenants. They went the rounds of the long-littered clearings that cut ever more deeply into the primeval forest, examining all the cavities in the charred dead trees that remained upright, to test their eligibility as sleeping and breeding chambers for themselves. In the course of the day, the great-billed birds twice visited the trunk that I watched. Whether in the absence of the guardian parents they would have harmed the nestling woodpeckers, I do not know, but I doubt that they would have molested young so large. Still, the adults were taking no chances.

On their first visit, early in the morning, a pair of araçaris flew up and clung to the top of the woodpeckers' trunk. The male woodpecker that was inside drew down into the cavity. Next a third araçari arrived, looked cautiously into the hole, and left without attempting to enter. Another araçari, less prudent, then came and pushed its great red bill through the doorway. I heard a sharp *click* as the parent woodpecker struck it with his own bill, whereupon the intruder promptly departed. The flock of araçaris went off without revisiting the nest, and after a while the male woodpecker showed his head in the entrance again. A few days earlier, I had seen an araçari repulsed from the doorway by a similar sharp peck on its bill from the parent within. When, late in the afternoon, a pair of araçaris again came in sight, the adult male again made himself invisible in the lower part of the chamber. But when one of the intruders clung to the trunk well below the nest, the female, arriving just then, drove it away.

The female, which as we have seen, brought most of the food, seemed afraid to approach the doorway of the nest while her mate was within, or when she was uncertain whether or not he was present. Arriving to feed the nestlings, she would alight on the upper part of the trunk and cling there, often for many minutes, until she saw her mate depart, or until one of the nestlings, which also drew their heads in at her arrival, looked out again and began to call. I believe that she hesitated to go to the doorway because of the danger of being mistaken for an intruder and treated accordingly. When an araçari flew up to cling to the trunk, the guardian parent would withdraw out of sight into the cavity and would prepare to deliver a sharp blow to the trespasser's bill. His own mate often approached the nest hole from a direction in which the male could not see her as he looked through the doorway. He would first become aware of her arrival by feeling the impact as she flew against the trunk, just as at times he was first apprised in this fashion of an araçari's

arrival, and he would draw down into the cavity in the same manner. After a while, if no araçari appeared at his doorway, he would cautiously peer out, and if he saw his mate he would fly away, leaving her to feed the nestlings.

At 5:35 p.m., the male, which had retired for the night, did not leave the nest when his mate came to the doorway after clinging for half an hour to the top of the trunk which contained the nest hole. Accordingly, she flew away without delivering the day's last meal that she had apparently brought for the nestlings. The male stayed quietly in the hole as daylight faded and brought my interesting vigil to a close.

The male passed the night of April 5 to 6 in this nest with the two nestlings, but on the morning of April 8 I learned that the nestling had slept alone. I use the singular, because I think it likely that one of the young woodpeckers had already departed, for that morning I watched the nest continuously from 5:30 to 9:30 and saw nothing to suggest the presence of a second occupant. In these 4 hours, the female fed the nestling twice, at 6:26 and 8:42 a.m., while the male failed to appear at all. Probably he was attending the other young woodpecker which had flown away. On both visits, the female fed the nestling from the outside of the nest hole. She brought one large meal the first time and two meals on her second visit. She did not enter the cavity to clean it.

The remaining nestling was exceptionally noisy, in sharp contrast to the discreet silence that the parents habitually preserved in the vicinity of their nest. She frequently voiced the loud, mellow *wic wic wic* and also the equally loud *kay rar-r-r-r-r*, at the same time stretching far out of the doorway to look around for the approach of a parent with food. She pecked at the wood around the orifice and in the top of the cavity. As the morning advanced, she became quieter and rested out of sight in the nest.

On the following night, the nestling again slept alone. Soon after sunrise next morning, April 9, I saw her fly from the hole. The adult female had come to feed her, but instead of going to deliver the food at the nest, she flew off to a dead tree in front of it. Thereupon, the young woodpecker leaned far out of the doorway, then launched boldly forth and flew up the hillside, directing her course obliquely toward the neighboring forest. Although she had never before been able to spread her wings, she now flew strongly in the undulatory fashion of her kind, and covered about 50 or 60 yards before coming to rest low on a dead trunk in the clearing. Here she was joined by the female and both birds climbed circling around the stump.

When I returned to the nest site a little later, I found the fledgling just within the forest's edge. Although woodpeckers' nests are often in a clearing, it seems that young Lineated Woodpeckers are led on leaving the nest, to the nearest woodland. It has been my experience that, when young woodpeckers are reared in a clearing, they invariably desert it almost as soon as they take wing. I did not again see the member of this brood which departed first, but the other passed much of the morning within the edge of the forest nearest the nest, climbing over the trunks, pecking at the bark, and from time to time calling loudly for nourishment. That evening, neither parent nor fledgling came near the nest to sleep in it. The hole remained untenanted for at the most two nights, and on the third, four of the Fiery-billed Araçaris which had so long coveted it made it their lodging. Later, five araçaris slept in it; this seems to be the maximum number of these great-billed birds that can crowd into a Lineated Woodpeckers' hole.

My first Costa Rican nest of the Lineated Woodpecker was also used as a dormitory by four Fiery-billed Araçaris four or five days after the young woodpeckers had abandoned it. Meanwhile, Gray-breasted Martins, and probably other birds also, had entered to investigate it as a possible nest site. At nest 5, the nestling woodpeckers were not accompanied by the male during their last night or two in the nest. After their departure, they did not return to roost in the nest cavity, but the male resumed his habit of sleeping in it, at least for a few nights. From these and additional observations made at other nests, I conclude that it is the custom of the male Lineated Woodpecker to sleep with the nestlings until their last few nights in the nest cavity. After their exit, the male may resume his use of this hole as a dormitory, but more often he does not return to it. The fledglings do not, like young Golden-naped Woodpeckers and Olivaceous Piculets, return to sleep in the nest. Apparently, they roost in the open until they succeed in finding unoccupied cavities to serve them as dormitories, in the manner of Red-crowned Woodpeckers, Hairy Woodpeckers, and Ivory-billed Woodpeckers (Tanner, 1941).

In El General, I have not known more than two young Lineated Woodpeckers to be reared in a nest, but since among woodpeckers it frequently happens that some of the young in each nest fail to fledge, it is certainly not impossible that in this region Lineated Woodpeckers lay sets of more than two eggs, as they do in other parts of their range. From four nests in El General, the young left between February 20 and 27, from one nest they left in early March, and from three others in April or May. I think it more likely that the late nests were replacements of earlier ones that had been lost rather than second-brood nests. The young which flew from the nest on April 9, for example, could hardly have been the second brood of parents whose first brood had been fledged in late February.

Young newly emerged from the nest resemble their parent of the same sex, but their plumage is slightly duller. While watching two immature birds which had been some time out of the nest and appeared to be brother and sister, I noticed that the eyes of the male were bright yellow, whereas those of the female were brownish.

SUMMARY

The Lineated Woodpecker is widespread in the lowlands of continental tropical America. It is found not only in humid regions but even in arid districts where trees of fair size are confined to watercourses and river bottoms. It occurs up to 3500 feet above sea level and occasionally to 5000 feet. It prefers older second-growth woods and clearings with scattered trees to the interior of heavy forest. At all seasons, it is found singly or in pairs.

This woodpecker is very fond of ants and their pupae, which it extracts from the hollow stems of *Cecropia*, often severely damaging the trees. It pecks into dead trunks and sometimes into living stems in search of insect larvae.

Its call is a loud, mellow, far-carrying *wic wic wic wic wic*. Parents attending young utter a peculiar loud churr, *kay rar-r-r-r-r*. Both sexes beat long, rolling tattoos on resonant dead stubs.

Adults sleep singly in hollow trunks, which they enter with great circumspection, usually early in the evening. In the morning, they become active later than most birds.

In Costa Rica, Lineated Woodpeckers sometimes begin to carve their nest cavity early in November. The male and female work alternately. The spacious chamber is situated in a dead trunk or the dead top of a living tree, at heights ranging from 6

to nearly 100 feet, but the high sites are preferred.

Eggs are laid from late December or January to April but, at least in El General, most sets are laid in January. Two sets in the Motagua Valley of Guatemala consisted of four and three, pure white, glossy eggs.

As soon as the nest chamber is completed, the parents alternately guard it through much of the day, to prevent its appropriation by the many birds that covet it for nesting or roosting. At this stage, the adults either rest within the cavity, looking through the doorway, or else they cling to the trunk beside it. After incubation begins, they remain more often out of sight in the bottom of the cavity. The male remains in the nest through the night, and by day the partners alternate every 2 or 3 hours. The changeover is effected without ceremony.

The nestlings are fed by regurgitation at rather long intervals. In 9 hours, two feathered young were fed six times by the female parent and three times by the male. But the female spent only 5 minutes in the nest, whereas the male was within the cavity for 4½ hours. Since the young no longer required brooding, he merely guarded them. On several occasions, a Fiery-billed Araçari, which thrust its great beak into the nest, received a sharp blow from the parent woodpecker.

The male parent spends the night with the nestlings until a day or two before they depart from the nest. At one nest a fledgling left early in the morning and flew strongly on her first flight. The young do not return to sleep in the nest; apparently they roost in the open until they can find holes for themselves. The male may resume his use of the nest cavity as a dormitory, but more often he goes elsewhere to sleep. The hole is then, as a rule, promptly occupied by araçaris or other birds.

Apparently one a single brood is reared in El General. Young in juvenal plumage resemble the parent of the same sex.

PALE-BILLED WOODPECKER

Phloeocastes guatemalensis

This large, high-crested woodpecker is about 13 to 14 inches in length. The male's head is entirely bright red. His upper parts, including the wings and tail, are plain dull black. On each side of the neck is a whitish stripe which extends to the back, where it converges with that of the opposite side. The foreneck and upper chest are dull black, and the more posterior under plumage is light buff, broadly and evenly barred with sooty black. The lower surface of the wings is largely buffy yellow, and the under side of the outer tail feathers is yellowish olive. The female is slightly smaller in size; she has a black band which extends from her forehead to the front of her tall red crest; her chin and throat are black. In both sexes, the strong bill is whitish; the bright yellow eyes are set in a circle of blackish bare skin; and the legs and feet are blackish. In general aspect, this woodpecker is not very different from the slightly smaller Lineated Woodpecker. In the latter, however, the white lateral stripe extends through the cheek to the base of the bill, whereas in the Pale-billed Woodpecker it scarcely invades the red of the head. Moreover, these white stripes converge on the back of the Pale-billed Woodpecker but remain widely separated on the Lineated Woodpecker. These two red-crested species are easily distinguished by their vocal and mechanical sounds.

The Pale-billed Woodpecker is found on both coasts from northern México through Central America to western Panamá. It avoids some of the drier regions with low trees where the Lineated Woodpecker is at home, but it extends higher into the mountains. I saw a single bird, evidently a straggler, at 5400 feet in the Cordillera Central of Costa Rica, and Ridgway (1914:178) cited a record of its occurrence at 5500 feet in the Mexican State of Sinaloa. In Costa Rica, it nests up to at least 3000 feet.

This is the woodpecker that I have most often met in the forests of El General. Sometimes it enters neighboring clearings with scattered trees, especially if they have been killed by fire, but it is less abundant in such clearings than is the Lineated Woodpecker, which in turn rarely goes far into the heavy forest. But the Pale-billed Woodpecker is a true bird of the forest and often forages in the shady depths of the woodland. A male and female are almost always found together, but unless there are dependent young, larger groups are not seen. Its flight is strongly undulatory.

FOOD

With its powerful bill the Pale-billed Woodpecker attacks decaying trunks, breaking off large flakes, sometimes several inches in length. One morning, I watched a pair hammering at an old, decaying palm trunk in the dimly lighted understory of the forest. They seemed to extract small objects which I could not distinguish. After they flew away, I examined the rotten trunk and found it infested with termites, which doubtless the woodpeckers had been eating.

Sometimes a woodpecker works very hard for its food. One day, at the edge of a banana plantation, I found three Pale-bills in a spreading inga tree. They appeared to be a pair with a full-grown young male. While the adult male hammered vigorously at a living bough about 4 inches thick, the young bird clung close by,

incessantly repeating a high, bleating note. From time to time he went to peck at the holes that his parent had made, but in an ineffectual manner. When he came too close to his hard-working parent, he was admonished with a peck. At intervals the young woodpecker stretched his wings sideward and upward, revealing the primrose yellow of the under coverts. After at least 20 minutes of continuous hard toil, the parent extracted something from the center of the limb and passed it to his offspring. Then the three woodpeckers flew away.

The Pale-billed Woodpecker varies its diet with fruit. On an afternoon in May, I watched a male eating the small, black berries of a low tree of the melastome family. Clinging to a slender limb, he plucked berry after berry from a many-branched panicle.

VOICE AND MECHANICAL SOUNDS

The most common utterance of the Pale-billed Woodpecker is a loud, bleating sound, unlike that of any other woodpecker that I know, but Sutton and Pettingill (1942:19), who heard in northeastern México notes evidently quite similar to those of Costa Rican representatives of the species, compared it to the call of the Ivory-billed Woodpecker. The members of a breeding pair of Pale-billed Woodpeckers voiced low, whining notes as they met at the nest, and once the male, coming to replace his mate on the eggs, gave a most peculiar call, not very loud, which I wrote as *keeu keeu keeu keeu keeu*. A male which seemed to be prospecting for a nest site uttered a low, whining or moaning sound as he clung to a dead trunk.

Instead of the rolling tattoo typical of woodpeckers, the Pale-bill beats a loud double tap—*rap rap*—which is one of the distinctive sounds of the Central American lowland forests. If the woodpecker continues drumming, it nearly always spaces its double taps so widely that they do not run together and produce a longer roll. The only exception to this rule that I have noticed was made by the above-mentioned male which uttered the whining or moaning sound. While voicing these notes, he tapped on the dead trunk three or four times together, but more softly than usual. After continuing these varied sounds for several minutes, he flew off through the neighboring woods very rapidly, without the usual pronounced undulations, making a sharp, rattling noise as he went. This happened at the end of July; by November of the same year, a hole had been carved in this trunk and incubation was in progress.

ROOSTING

Pale-billed Woodpeckers sleep singly in large holes like those in which they nest. Early in February of 1942, I found a male's dormitory, about 30 feet up in a massive, rotting trunk in the midst of the forest. After cautiously peering into his chamber, he entered in the evening while there was still much light in the under-wood and many sylvan birds were still active. In the morning, he delayed in his dormitory while other birds sang and foraged.

At about 5:00 p.m. on March 22, when the forest was gloomy and wet from the afternoon showers, I found a female looking out of his hole. After she had delayed with her head framed in the doorway for more than a quarter of an hour, her mate flew up through the woodland with resonant wing beats and alighted on the dead trunk above the hole. Thereupon the female emerged and flew away. As she

departed, I heard a few bleating notes, but I could not tell from which of the two they came. After she had gone, the male entered the hole for the night.

Three days later, on a clear evening after a shower, I watched this hole again. At about 5:30, the male and female woodpeckers appeared in the neighboring trees at about the same time. Both pecked sporadically at the bark. Presently the female went to the hole and, with much hesitation, entered it slowly. For several minutes she remained within, her head in the doorway. But when the male alighted on the top of the trunk and backed down toward the hole, she came out. He entered for the night, while she flew away over the treetops. On the evening of March 27, he came alone; his mate did not appear. His time of retiring was irregular, for on some evenings I found him inside at about 5:20, but on others he did not arrive until 5:45, when the light was growing dim beneath the trees. He continued to lodge in this hole until mid-April, more than two months after I first found him roosting here.

On April 20, no woodpecker came to this hole in the evening and it remained vacant. But the next time that I watched it as the day ended, on May 10, the female arrived, and after much cautious peering through the doorway, she entered and remained for the night. Thus, at last, she gained possession of the lodging which evidently she had long coveted. Possibly her mate had in the meantime carved a new and sounder dormitory for himself. The female's succession to a hole which her more industrious mate abandons when he has prepared another for himself seems to be not uncommon in woodpeckers; I earlier saw this happen in the Red-crowned Woodpecker. But the female Pale-bill did not occupy her mate's dormitory for long, and before the end of May I found it abandoned. I kept this hole under observation, however, and in early September I noticed a twig that bore a few dead leaves projecting through the doorway. When I clapped my hands, the sleepy little face of a kinkajou (*Potos caudivolvulus*) looked out (Skutch, 1960b).

On February 6, 1944, I found another female Pale-billed Woodpecker's dormitory. It was in a decaying stub beside a brook at the forest's edge. When I arrived at 4:53 p.m., the woodpecker was already within, her flaming head and whitish bill conspicuous in the round doorway. Although the narrow valley where the dormitory was situated was already in shadow, the trees on the low ridge which she faced were in full sunshine, and bird activity was high. After I had watched her for 40 minutes, the woodpecker descended lower in her chamber, where even her light bill was no longer visible. Much daylight remained and many birds were still active. On February 9, this woodpecker entered her dormitory at 5:11, although the sky was lightly overcast, instead of clear as on February 6. By March 11, this dormitory was abandoned.

NEST AND EGGS

According to Griscom (1957:44), the Pale-billed Woodpecker breeds in southern México from December 8 to June 2. In El General, this woodpecker nests at a season when I have found no other species of the family so engaged. On October 9, 1945, I watched parents attending a full-grown young bird, which must have hatched at the beginning of September at latest, from an egg that was evidently laid in August. I have found two nests with eggs in mid-November, and on December 5 I discovered an inaccessible hole with either eggs or young nestlings. I have no evidence of breeding by the Pale-billed Woodpecker between January and July, when five or six other kinds of woodpeckers nest in El General. Apparently, this

woodpecker finds the beginning of the dry season the most favorable period for attending its fledglings, and to bring them forth at this time, it must start to nest toward the end of the wet season.

The three nests that I have seen were in dead trunks that stood in clearings in the forest, at heights of about 20, 28, and 40 feet above the ground. The lowest nest, which alone was safely accessible, had a wide doorway $3\frac{1}{2}$ inches in horizontal diameter by 4 inches in vertical diameter, and the cavity extended $12\frac{1}{2}$ inches below the orifice. This seems rather shallow for so large a woodpecker, and possibly it was carved no deeper because of the hardness of the wood. I have not watched the excavation of the nest cavity, but Sutton (1952) stated that both sexes share in this labor.

My first and lowest nest held two white eggs on November 14, 1936, and no more were laid. They rested on some fine particles of wood in the bottom of the chamber, where I could just touch them with my finger tips. I have found no other record of the eggs of this species, but in Trinidad, Belcher and Smooker (1936:798) found a set of two eggs laid by the related Black-and-White or Crimson-crested Woodpecker. Two eggs is an unusually small set for a woodpecker.

INCUBATION

On November 16, at 12:15 p.m., I began to watch my first nest, in which the male woodpecker was then attending the eggs. At 1:05 he looked through the doorway, scratched himself, and after a few minutes climbed out, to cling below the entrance and look around. After a brief intermission, he returned to his task. For the next 3 hours, during which a hard shower fell, he remained steadily at his post. At 4:03, when the sunshine was breaking through the clouds, the woodpecker again emerged, and this time he climbed to the top of the tall, bare trunk, where he stretched his wings and scratched. After resting here for a few minutes, he began to climb downward, tail first. He failed to notice a wide old hole directly below him; his tail slipped into it and he almost fell. But he caught himself and continued downward to his nest, which he re-entered at 4:12 p.m., after an inspection which lasted several minutes. He looked out when his neighbors, the Golden-naped Woodpeckers, arrived to enter their dormitory higher in the same trunk. Aside from these short intermissions, he incubated steadily from some time before 12:15 p.m. until nightfall, and all this while he ate nothing. I did not see his mate.

As day broke at 5:25 on the following morning, I resumed my watch. Ten minutes later, the woodpecker looked through his doorway as the Golden-napes left their lodging high above him. Then he descended to the eggs and sat steadily until, at 7:12 a.m., his mate silently flew up and alighted beside the doorway. As the partners met, I heard a low, whining note. Then the male flew away and the female entered the hole. For nearly $4\frac{1}{2}$ hours, she remained steadily within, rarely coming to look through the doorway for an interval of about 5 minutes. At 11:38, the male suddenly alighted beside the entrance and uttered the peculiar low *keeu keeu keeu keeu keeu keeu* that has already been mentioned. He erected his high crest to its fullest extent. The female came through the doorway with her red and black crest also standing straight up, then she flew away. The male then laid back his crest to the usual position (by no means flat) and entered. I then went off, but on a visit of inspection at 1:25 p.m. I found him still present. In the 24 hours from 12:15 p.m. on November 16 to 12:15 p.m. on the following day, he had been constantly

in or near the nest for all but 4 hours and 26 minutes of the forenoon, when his mate was in charge. These woodpeckers not only made fewer changeovers than other woodpeckers that I have watched, but they spent little time looking through their doorway. After a thorough inspection of the hole and its surroundings when they arrived to incubate, each climbed in and remained down out of sight.

On the morning of November 24, I found the female in this nest at 7:10, and she was still present when I returned at 9:15 a.m. to see whether the eggs had hatched. They were still intact. After my visit of inspection, she promptly returned to them and continued to sit, while I watched, until 11:42 a.m., when the male, voicing a single low note, came to replace her. Both partners erected their crests momentarily as they passed each other at the doorway. At 4:35 p.m. of the same day, I found the female again within, although a week earlier, when I had watched continuously, she was absent throughout the afternoon. Possibly the imminence of hatching caused a change in the schedule of incubation.

THE NESTLINGS

By the early afternoon of November 26, one of the eggs in this nest had hatched. On December 1, I found the empty shells of both eggs still present, and to judge by their appearance both had hatched, yet there was only one nestling. I managed to lift out the surviving young woodpecker for examination. It had grown enormously in the few days since it had hatched. Its pink skin was quite naked, but the black rudiments of its contour feathers showed through the transparent skin, and the tips of the sheaths which enclosed its remiges and rectrices were just pushing out from its wings and tail. Its heel pads were studded with prominent papillae. But the feature of the nestling which most engaged my attention was the white lump or knob at each corner of its mouth, which projected even beyond the swelling on the side of its head that represented a tightly closed eye. These knobs were far more conspicuous than the mouth-corners of any other nestling that I had even seen. Indeed, they were no mere salient folds of white or yellow skin, like the corners of the mouth of many passerine nestlings, but solid, rounded lumps, attached wholly to the base of the lower mandible, which, as in other woodpeckers, was both longer and wider than the upper mandible. There was a conspicuous white "egg tooth" at the tip of the upper mandible and a much smaller one at the point of the lower mandible. Since the lower mandible projected well beyond the upper, it must also have come into play in breaking through the shell, and accordingly it was armed for its task.

When I replaced the young woodpecker in its deep hole and looked in with my mirror, without illuminating the interior, these two shining white knobs at the sides of the mouth were the most conspicuous features of the nestling. It frequently raised its gaping mouth, in the manner of passerine nestlings. The interior of the mouth lacked bright color; it was pale pink, like the skin over the body. When feeding the nestling in the dimly lighted chamber, the parents were evidently guided to its mouth chiefly by the knobs at its sides.

When I returned on the following day, the young woodpecker had vanished. But the empty shells still lay in the hole, six days after the first egg hatched. Otherwise, the bottom was perfectly clean. A large black snake, 6 or 7 feet long, that crossed my path as I was leaving the ravaged nest, may have been the culprit, but I was not certain that it could climb 20 feet up a smooth, barkless trunk a foot in diameter.

In March of the following year, a pair of Fiery-billed Araçaris started to incubate in this hole, but they were no more successful in rearing a family than the original occupants had been.

I have found no other nest of the Pale-billed Woodpecker in a trunk that appeared strong enough to support a climber or a long and heavy ladder. On December 30, 1959, I saw a young female leave a higher nest. She resembled the adult female in plumage, but the knobs at the corners of her mouth were still prominent, and her bill was somewhat dark. She lost no time in ascending to the tops of the tall trees in the neighboring woods. She was fed by the parents with food carried in the bill rather than by regurgitation.

SUMMARY

The Pale-billed Woodpecker inhabits the heavier Central American forests and adjacent clearings, from sea level up to somewhat over 5000 feet. It lives in pairs at all seasons.

It extracts insects and their larvae from dead and sometimes living wood, prying off large flakes with its strong bill. It varies its diet with berries.

The common utterance of the Pale-billed Woodpecker is a loud bleating, and it voices also low whining and moaning sounds. It beats two strong, staccato taps, never a rolling tattoo.

Adults roost singly in holes like those in which they nest, in the midst of the forest or at its edge. They often retire very early in the evening, although they are not consistent in this, and in the morning they become active later than most birds. A female sometimes preceded her mate to his dormitory in the evening, but she left as he approached. After he abandoned it, she slept there.

In El General, the Pale-billed Woodpecker breeds from August to December. Three nests were in dead trunks, at heights ranging from 20 to 40 feet. The single accessible nest contained two pure white eggs in mid-November.

A 24-hour record of incubation showed that the female attended the eggs continuously for about 4½ hours in the forenoon. The male attended the eggs the rest of the time and slept in the nest at night. When the eggs were near hatching, however, the female was found in the nest in the late afternoon.

The newly hatched nestling is pink-skinned and sightless. Its heels are protected by pads studded with prominent papillae. At the corners of the mouth are great white knobs that probably guide the parents when delivering food. These knobs persist until the young leave the nest.

HAIRY WOODPECKER¹

Dendrocopos villosus

The wide-ranging Hairy Woodpecker varies from under seven to over nine inches in length; the far-northern races are the largest and the tropical races, which here chiefly concern us, the smallest. The dark areas are black; the light areas, white in northern races, are more or less strongly tinged with brown in the Central American forms. The back of the male's head is adorned with a patch of red, which color the female wholly lacks.

The Hairy Woodpecker ranges from near the northern limit of trees in Alaska east to Newfoundland and south to Florida, the Bahama Islands, México, and Central America as far as western Panamá. Throughout Central America, it occupies a broad altitudinal zone extending from about 4000 to at least 11,000 feet above sea level, and its occurrence at even greater heights is to be expected, since in México it has been recorded at 12,000 feet (Griscom, 1957:39). It appears to live as low as 4000 feet only where the mountain slopes are exposed to the prevailing winds and hence unusually cool and humid for the altitude. In the valleys and on the more sheltered slopes, it is rarely found lower than 6000 feet. Near Vara Blanca on the northern or windward slope of the Cordillera Central of Costa Rica, an excessively humid region exposed to the full sweep of the northeast trade-winds and subject to long-continued storms of wind-driven mist and rain, I found Hairy Woodpeckers abundant at 5500 feet. Here they dwelt among heavy subtropical rain forests, where the towering trees were burdened with an amazing profusion of epiphytic plants of many kinds. At higher altitudes in Costa Rica, these woodpeckers inhabit heavy forest dominated by huge oaks, and higher still they live among the stunted trees near timberline.

In the Guatemalan highlands, Hairy Woodpeckers are at home in woodlands of oak and other broad-leaved trees, or among forests composed largely of pine, as well as in the remnants of the magnificent stands of cypress on the high mountain tops. On the plateau of the Sierra Cuchumatanes in the Department of Huehuetenango, I found them on the lightly wooded ridges that rose above the level alpine meadows. Here they frequented the pine trees which, at the time of my visit in September, 1934, had been killed in large numbers by some sort of blight. At an elevation of about 11,000 feet, they were far less in evidence than the Red-shafted Flickers.

As to the Hairy Woodpecker's way of finding food, there is little to be written about the southernmost representatives of the species that has not been said for the northern races. They are everywhere the same industrious peckers into dead and dying trees. In Guatemala, I watched a female tear apart old pine cones in search of insect larvae that hid beneath the scales. Here, at the higher altitudes, these woodpeckers roam through the woodlands in the motley flocks of resident and wintering wood warblers, vireos, flycatchers, and other small birds. For some months after the young become independent of parental care, each woodpecker appears to avoid the company of others of its kind, and it is rare to find more than one of

¹ This life history is an abridgement of Skutch, 1955.

them in a flock of other birds. By late November or December, however, they have mated and travel in pairs, either in the mixed flocks or by themselves.

In voice, too, the Hairy Woodpeckers of Central America resemble their northern relatives. Their most common utterances include a sharp *bip*; a longer, fuller, stronger *beep*; and a rapid, high, clear *bic-bic-bic-bic-bic*—a variant of the picarian rolled note or churr. Both males and females beat rolling tattoos on resounding dead wood. At Vara Blanca, I first heard this drumming about the middle of February.

Most woodpeckers are territorial birds, and it is rare to find two nests of the same species in sight of each other. But, as a rule, the boundaries between territories are established by methods that elude the birdwatcher. Once, however, I witnessed a dispute between two male Hairy Woodpeckers, which were apparently endeavoring to settle some difference over boundaries or conflicting claims to territories. It was on April 18, 1938, in the pasture below my cottage at Vara Blanca. Here there were a number of dead trunks close together, and fallen dead branches, portions of which rose above the herbage that covered the ground. The two antagonists clung to a thick branch, or to the side of a trunk near its base, a foot or two apart, and thrust forward their heads until body, neck, head, and bill all lay nearly in a straight line. In this posture, they twitched their bodies rapidly up, down, and sideward, continuing this simultaneously for a few seconds. When one stopped, the other also stopped.

Then they would prance about, or come as near to prancing as is possible on a surface that is vertical or almost so, both at the same time, for a period of several seconds. Next, perhaps, one would fly over the other and cling to the trunk an equal distance on the opposite side of his opponent; with their relative positions reversed, they would proceed much as before. After a while, the two woodpeckers would rest for a minute or two, only a foot or two apart. Then one of them would fly to a nearby trunk or branch, and soon the other would follow. As the second came near the first, the latter would sometimes spread his wings in a defensive attitude, thus displaying the black and white bars on the lower surfaces, and the display would continue in the same fashion. Only rarely did one bird come into contact with the other as the two moved about and flew over each other, and then they barely touched, in the lightest and most inoffensive manner.

Thus the dispute moved from one trunk or branch to another, then back again to the first. They always kept near the ground, rarely rising as much as 10 feet above it. Perfect silence was preserved by the contestants, which seemed quite oblivious of me. For nearly an hour this elaborate play continued, with alternate intervals of activity and motionless repose, while the two protagonists clung possibly a foot apart. At last they flew off. Like so many of the conflicts of birds, theirs had been almost without contact; neither contestant lost a single feather.

At Vara Blanca, I found ten dormitories of Hairy Woodpeckers. The birds invariably slept alone, but in August two females, probably young birds, occupied holes only ten feet apart in the same low stub in a pasture. The doorway of the lower hole was only as high as my head. From early August until the following February or March, another female slept 15 feet up in a rustic post that supported a telegraph wire beside a muddy mountain road. Tame and confident, she was not frightened from her low hole by travellers passing before her doorway. Her tenancy of over six months was terminated only by the fall of the decayed pole. Other Hairy Woodpeckers which slept in low cavities were equally fearless; they would sometimes

enter the cavity while I stood watching at a distance of only three or four paces. Indeed, in these mountain fastnesses still scarcely invaded by man, the birds as a whole were far easier to approach and to watch than I have ever found them elsewhere.

A male Hairy Woodpecker roosted in a hole in a high stub at the forest's edge from September until at least the end of the following January; in February the stub fell. Although I found seven dormitories of females and only three of males, the two newest cavities were occupied by males, and the only hole that I actually saw being made, before the start of preparations for breeding, was carved out and used for sleeping by a male. Some of the chambers in which females roosted were very old and dilapidated, with chinks in the walls. Like other members of the family, these woodpeckers retired early, especially on rainy evenings, and they became active late in the morning.

NESTING

Above Tecpán in the Guatemalan highlands, at an altitude of nearly 9000 feet, I found a pair of Hairy Woodpeckers beginning a hole, evidently destined to contain eggs, on February 7, 1933, at the height of the dry season. On March 21 I discovered, in the same locality, another hole, which apparently already held nestlings. At Vara Blanca, the first preparations for nesting were noticed on March 3, 1938, when I watched a pair just beginning to carve a hole. This hole was never completed, possibly because the woodpeckers found the wood too hard toward the center of the trunk, but a pair in a neighboring hole were incubating by March 28. This was at the driest time of the year in an excessively rainy region that had no real dry season. In both Guatemala and Costa Rica, the Hairy Woodpeckers nest earlier than the majority of the birds around them.

The seven nests that I have seen in Central America were in dead trunks or posts, either in the woodland or in clearings near it. In height they ranged from 11 to about 60 feet above the ground. Male and female take turns at carving out the nest cavity. Sometimes each continues the task rather steadily for 25 or 30 minutes, but often the period of work is considerably shorter. When the mate arrives to take over the carving, the one which has been toiling promptly flies away to forage at a distance, instead of waiting close by while the other labors, in the manner of trogons, puffbirds, jacamars, barbets, and motmots. In April I watched a pair of Hairy Woodpeckers carving a hole to replace another they had lost. They dawdled at their task through the early morning, but at about 10:00 they began to work steadily and continued until noon. Another pair also worked hard through the middle of the day. The loosened chips were never carried away but were always dropped from the doorway, which was from $1\frac{3}{8}$ to $1\frac{1}{2}$ inches in diameter.

One of my two accessible nests was, as soon as completed, stolen from the woodpeckers by a pair of Blue-throated Toucanets, which, after enlarging the doorway, laid their own eggs in it. The other nest within reach of a ladder was 11 feet up in a telegraph pole beside a mountain road, and it contained three white eggs when found on April 16. This is the only set of eggs of the Hairy Woodpecker found in Central America of which I have knowledge. In the daytime, the male and female incubated alternately; by night, the male alone occupied the nest. One morning at dawn, I saw the female come to replace her mate on the eggs, but he, not caring to leave so early, repulsed her with pecks from the doorway. He delayed in the nest

for 34 minutes longer, or until 6:14 a.m. Then, hearing the female call *bip* in a neighboring tree, he flew forth. Seven minutes later, the female entered the hole to incubate.

In the nest in the telegraph pole, only a single egg hatched, on April 24. The pieces of empty shell remained in the hole for at least two days. The nestling was naked and had tightly closed eyes. Like other woodpeckers, it bore at each corner of the mouth a prominent white knob. It was fed by both parents with food carried in the bill, from which at times parts of insects projected and were easily seen. Both parents took turns at brooding the nestling by day, but the male alone remained in the nest through the night. When the nestling was six days old, its pinfeathers began to sprout. At the age of 17 days, it was partly feathered and already displayed a patch of red on its head. At three weeks of age, it was well clothed with plumage and closely resembled the adult male.

By his tenth day, the young woodpecker had become quite vociferous and cried much in a high-pitched voice when a parent visited his nest. By the time he was feathered, he rapidly repeated a sharp, clear, metallic note, and he also uttered the churred call of the adults. When 26 days old, he began to look through the doorway and call for food with a sharp *bip* or a rapid series of these notes, only slightly weaker than the corresponding notes of the adults. The parents now passed food to him while they clung outside the nest hole. Except at mealtime, the young woodpecker was now less noisy than he had been a few days earlier. Both parents removed droppings and kept the nest clean for at least 17 days after the nestling hatched. But about the time the young woodpecker was clothed with feathers, they relaxed their attention to the sanitation of the nest, and it soon became foul on the bottom. Before the nestling departed, the waste matter had accumulated to a depth almost sufficient to bury an unhatched egg that still remained in the hole.

The young woodpecker flew from the nest on May 22, at the age of 28 days. While I watched that afternoon, the male from old habit came to the post with a long larva dangling from his bill. Not finding the young bird in the nest, he called, received an answer from the neighboring thicket, and flew off in that direction with food. Neither a parent nor the fledgling came that evening to sleep in the nest cavity, which thenceforth remained deserted.

From a nest 60 feet up in a tall dead trunk standing in a pasture, I watched the last fledgling, a male, make his exit at about 11:00 a.m. on May 8. He flew very well and descended to a small yos tree that stood down the slope from the nest. Here he climbed about and pecked at the bark just as though he had long engaged in these activities. Both he and the other fledgling wore red patches on the head, brighter than those of the adult male, whose plumage was worn. That evening the adult male retired alone into the empty nest. The cloud-mist that covered the mountain made it difficult to follow the movements of the two young woodpeckers, but apparently they remained out in the rain.

Late in the afternoon of the third day after these two young birds left the nest, I again found them with their parents on a dead trunk near the nest tree. The fledglings hammered at the decaying wood and picked up particles which apparently were not edible, for they were dropped. But at least they were trying to find food for themselves. They flew back and forth between the trunks with surprising speed. I decided to try again to learn where they passed the night. At 5:45, when the sky was dark with clouds and a drizzle fell, the adult female entered a hole in the top

of a living guarumo tree. Then the adult male vanished, evidently to sleep in the nest cavity, as he had done three nights earlier. However, this opened on the side of the trunk facing away from me and I could not see him enter.

After their parents had retired, the two young woodpeckers continued to climb over the trunks in the slow rain and the waning light. Although there were a number of old and unoccupied holes made by woodpeckers and barbets in these trunks—one of them in the guarumo tree, directly below that into which the adult female had gone to roost—the young birds took no notice of them. I lost sight of one of the young woodpeckers while keeping my eyes on the other. As the light failed, he ascended to the top of a tall tree and climbed restlessly over its branches, pecking here and there, and taking special interest in a shallow hollow in the midst of a small cushion of moss. Still, he did not sleep in this. At last he settled down, clinging upright to an upright bough, just beneath a horizontal branch that sprung from it. Although these branches were themselves thin, the moss that enveloped them afforded the young woodpecker a degree of shelter from raindrops that fell vertically. But he was unprotected on three sides and exposed to all the winds that blew that stormy night, while his parents slept not far off in their snug lodgings. The parents showed exactly the same indifference to their offspring as I had earlier found in Red-crowned Woodpeckers. What a contrast between this neglect and the careful attention which Golden-naped Woodpeckers and Olivaceous Piculets give to their fledglings' comfort for the night!

SUMMARY

The Central American races of the Hairy Woodpecker are found in a broad altitudinal zone between 4000 feet, in situations where the mountain slopes are unusually cool and humid, to at least 11,000 feet. At 5500 feet they were found in heavy subtropical rain forest and at higher altitudes in heavy forest dominated by huge oaks. At very high elevations they live among the stunted trees near timberline.

Like the northern races, the southern representatives of the species subsist on insects and insect larvae chiseled from the bark and wood of dead and dying trees. After the breeding season these woodpeckers are solitary, but pairs have been formed by late November or December. The vocalizations and drumming of these birds are similar to those of their northern relatives. The birds sleep alone in holes, but these may be as close as 10 feet apart.

Seven nests were found in dead trunks, or in poles, from 11 to about 60 feet up. Both sexes carve the nest cavity. One nest contained a set of three eggs. Both sexes incubated, in alternation, but the male occupied the nest at night.

The single nestling hatched from these eggs was fed by both adults. Droppings were removed by the adults for about the first 17 days of the nestling period. The young bird left the nest at the age of 28 days; the nest cavity was thenceforth deserted.

At another nest, the departure of the second of two fledglings was observed. The adult male spent the night in the empty nest hole. On the third day after their departure from the nest, the two fledglings were hammering on decaying wood but they were not successful at finding food. Late in the afternoon the adults retired, leaving the fledglings to find their own shelter. At least one young bird slept out in the open, largely exposed to rain and high wind.

GOLDEN-FRONTED WOODPECKER

Centurus aurifrons

The genus *Centurus* contains a number of small and middle-sized woodpeckers whose upper parts are conspicuously barred with black and white or black and yellowish. The adult males have more or less red on the top of the head, and sometimes this extends to the hindneck, which in other species is orange, yellow, or some dull color. The females resemble the males except that the red or yellow is less extensive, confined to the hindhead or nape, or else it is wholly absent from these regions. The under parts are pale brownish, grayish, or yellowish, usually with an area of yellow or red on the abdomen. Over much of continental America, from eastern and central United States to Colombia, Venezuela, and the Guianas, the birdwatcher is likely to meet some form of this attractive genus at low and middle altitudes wherever there are trees large enough to provide nest sites. Endemic forms occur on a number of the Greater Antilles and Bahama Islands.

Centurus aurifrons, as now understood, contains a bewildering array of intergrading forms which range from Oklahoma and Texas to Costa Rica and were formerly divided among several species. In Guatemala, where I knew it well, it extends from both coasts into the highlands and is found in districts with copious rainfall no less than in arid valleys where cacti and low, thorny trees are the dominant vegetation. It was abundant among the shade trees of the coffee plantations about the shores of Lake Atitlán, at 5000 feet above sea level, but in my travels over the country I never found it much higher than this.

The form of the Golden-fronted Woodpecker which I studied, *C. aurifrons pauper*, is confined to the humid Caribbean lowlands of northeastern Guatemala and northern Honduras. This attractive woodpecker measures about eight inches in length. The male has the whole crown, hindhead, and nape bright poppy red. His forehead is whitish, not golden-yellow as the name of the species leads one to expect, for the "golden front" is confined to inconspicuous patches behind the nostrils. On his back and shoulders the white bars are much narrower than the black ones with which they alternate; his rump and upper tail-coverts are pure white. His tail and wings are mostly black, but the latter have white bars, especially on the coverts. The sides of his head and his under parts are light shades of gray and brown, and there is a patch of yellow on his abdomen. His bill is blackish, his eyes orange or red, and his feet olive-greenish. The female resembles the male, except that her crown is grayish white and the red is confined to the back of her head.

This woodpecker is at home in clearings and plantations with scattered trees and in light second-growth woods. It avoids the interior of the heavy rain forest that was the original vegetation of the region where it dwells. In 1932, I found it abundant on Alsacia Plantation, which extended along the Río Morjá, a tributary of the Río Motagua, back into the foothills of the Sierra de Merendón, a range which forms the boundary between Guatemala and Honduras. Here the Golden-fronted Woodpecker was by far the commonest woodpecker, and its nests were found more readily than those of any other woodpecker in any region where I have studied birds.

In flight the Golden-fronted Woodpecker rises and falls as it alternately flaps and rests its wings. It sometimes perches crosswise on a slender twig in the manner of a passerine bird, but more often it clings to a trunk in the usual picarian manner.

FOOD

Unlike some other animals with a high degree of structural specialization, woodpeckers are quick to take advantage of any promising source of nourishment. This is especially true of the Golden-fronted Woodpecker, which forages in the most diverse manners, often performing feats for which it appears to be poorly fitted. Although much of its food consists of insects and their larvae pecked out of bark and wood in the conventional woodpecker fashion, it not infrequently darts into the air to snatch insects on the wing, with a bill that seems too narrow to be efficient in this mode of capture. It often eats berries, and it enters the banana plantations to feast on ripe fruit that the cutters have missed. Sometimes I surprised these woodpeckers foraging on the ground, possibly for ants, although I could not make sure.

VOICE AND MECHANICAL SOUNDS

The call of the Golden-fronted Woodpecker is a loud, rolling *krr-r-r-r*, similar to that of the Red-bellied Woodpecker of the United States and other members of its genus. It also utters, sometimes in flight, the notes *tsuka tsuka*, which reminded me of a call of the Banded-backed Wren, although its tone is softer. Another call is a low, rather harsh *krrr*. This woodpecker sometimes beats a rolling tattoo on a dry, resonant trunk or branch.

NEST BUILDING

On April 1, 1932, I found at "Alsacia" a nest of the Golden-fronted Woodpeckers with feathered young. These nestlings flew away a day or two later. Since laying and incubation require at least two weeks and the nestlings stay in the nest a full month, it is evident that this pair began to breed in February, if not earlier. They attempted to rear three broods and were still engaged with the third in July. Thus, in the lower Motagua Valley, the breeding season extends from early February well into July, and possibly it is even longer.

The nests are placed in fence posts, within 5 feet of the ground, or in dead trees standing in bushy pastures or above low, second-growth thickets. Sometimes the nests are at a considerable height. In May, I gave a good deal of attention to a pair of woodpeckers which were carving a new hole 6 feet above that in which their previous brood had been destroyed by fire ants. The wood of the slender, barkless trunk was soft, and their task did not appear to require great exertion. On May 11, when the cavity was 7 inches deep, I watched both in the morning and afternoon without seeing them at work.

Next day I had better luck. As I crept through the bushy pasture to a place of concealment in tall weeds, at 9:50 in the morning, I heard vigorous tapping from inside the cavity, which was already large enough to conceal the working bird. After the sound had continued for 5 minutes, the male emerged and hung on the shady side of the vertical trunk, panting, to rest from his labor, for the day was extremely warm. After a 2-minute recess, he re-entered the hole and continued his chiseling. He worked for 4 minutes longer, then came to the entrance, still with open mouth, called *krr-r-r-r*, *krr-r-r-r*, and without waiting for a reply descended into the cavity to resume his task. His mate, in the distance, responded with the same call several times repeated, and was answered by the male from within the hole. At length she

flew to the entrance of the hole and he climbed out to make way for her. She entered and brought up, in rapid succession, ten billfuls of small chips, each time sticking her head out of the entrance to let them fall to the ground. Sometimes, between bringing up billfuls, she climbed out of the doorway only to turn around and slip right in again, for no apparent reason. After she had thrown out enough of the debris, she proceeded to chisel inside the cavity. But soon she stopped to throw out more wood particles, and after a few minutes she flew away.

For the next 24 minutes work was suspended while both members of the pair stayed out of sight. At 10:35 a.m. the female returned and clung before the doorway, looking around carefully. Satisfied at last that no enemy was in view, she entered and began to peck. She spent only 9 minutes at the nest, chiseling a little, but much of the time throwing out chips or resting with her head in the opening, panting. At 10:44 she emerged, called, was answered by her mate in the distance, then went off. Twenty-six minutes elapsed before he reached the doorway, where he peered cautiously from side to side and into the cavity, before he entered. Finally he slipped in, only to turn around and push his head out for another survey before getting down to work. Although he stayed inside for 14 minutes, he spent most of this time gazing through the doorway. At 11:24 the female flew to the entrance and repeated several times a low, rather harsh *krrrr*, a common note of greeting quite different from the loud, resonant, rolling call. Whereupon the male emerged and flew off, and after a minute's delay she followed him. Nine minutes passed before she returned, entered the hole and threw out a billful of chips, chiseled a little, looked out with mouth agape for a few minutes more, then departed.

During my 2-hour watch the male worked the harder, as I judged by the tapping sounds that emanated from the trunk while he was within, but the female threw out all the loosened material—an interesting division of labor. While one member of the pair was at work in the cavity, the other usually stayed at a distance, but it was not too far off to hear and answer its mate's calls. In this the woodpeckers differed from the trogons, jacamars, motmots, and kingfishers that I was studying at the same time, for with these the resting partner waited close by until its turn to resume work came, and if it flew to a distance the excavation of the burrow or chamber would cease as soon as the other discovered that it had been left alone. Despite their desultory way of working, these woodpeckers finished their hole and had begun to lay only 14 days after the failure of their earlier nest.

A completed nest chamber had a round doorway $2\frac{1}{4}$ inches in diameter. It extended 10 inches below the lower edge of this aperture and was 4 inches in diameter near the bottom. Since the bottom of the cavity may be carved out in preparation for later broods, it becomes deeper as the season advances and may reach a depth of 15 inches. The chamber is never lined, and the eggs rest on a bed of fine chips.

THE EGGS

At "Alsacia" in April and May I examined four nests, each with four eggs. One set, first seen on April 8 when incubation was well advanced, may have been a first laying; the other three were either second broods or replacement layings. The eggs, which are laid on consecutive days, are short and blunt, pure white, and

glossy. Those of one set measured 22.2 by 19.1, 22.2 by 19.8, 22.2 by 19.4, and 23.0 by 19.1 mm.

INCUBATION

Even before laying began, the male slept in the nest cavity. In one instance, I found him doing so five days before the first egg appeared, but from observations I later made on other species of woodpeckers, it is probable that the male Golden-fronted Woodpecker may use the hole as a dormitory for a much longer period before it becomes a breeding nest. By day, one or the other of the parents was often to be found in the eggless hole, looking through the doorway rather than sitting in the bottom. At other times, they watched the hole while clinging to a neighboring shaded trunk. Since woodpeckers' holes are coveted by numerous other birds as breeding sites, the value of guarding them even before laying begins is obvious.

The male continued to sleep in the nest through the period of laying and the whole course of incubation. At four nests I never found a female present by night at any stage of the breeding cycle. However, the female came to replace her mate early in the morning, and throughout the day the two alternated in the nest. Nest holes were so deep that a sitting bird could not be seen from the outside, but any unaccustomed sound caused it to climb up and look through the doorway, and here it remained, with its head framed in the round aperture, until its suspicions were allayed. If I approached too near the woodpecker promptly darted forth, but if it saw nothing alarming it resumed incubation. In the warmest part of the afternoon, especially if the nest stub were exposed to full sunshine, an incubating bird sometimes left the hole and spent part of its period of duty clinging upright to the shady side of the trunk or even to a neighboring tree. Doubtless in these circumstances the eggs remained sufficiently warm without being covered.

The female incubated in the late afternoon, and often as the sun declined she would look out expectantly for her mate. After sunset he arrived to replace her on the eggs. Sometimes he called *tsuka tsuka* as he approached, and she greeted him with a long *kr-r-r-r*, delivered with her head in the doorway. Then she emerged and with undulating flight sought her sleeping quarters at a distance. After descending into the nest, the male usually climbed up to the entrance once or twice to survey his surroundings before he finally settled on the eggs for the night.

In the nest which I watched the woodpeckers carve out, there were two eggs on May 18 and four on May 20. On May 31 this hole contained one egg, one newly hatched nestling, and the shells of two eggs that had hatched. This left one nestling and one egg to be accounted for, and I do not know what happened to them. Thus hatching started only 11 days after the set was complete, but since I was not sure whether the last egg of the set had hatched, the full incubation period remains unknown. Probably it is about 12 days. At two other nests, the hatching of the eggs was spread over at least two days, which suggests that when the male sleeps in the nest during the period of laying he actually incubates the eggs. Probably in this interval they are warmed more or less by day also, with the result that the embryos of the earliest eggs start to develop well in advance of that of the last in the set.

THE NESTLINGS

Immediately after hatching, the young woodpeckers were, if possible, of even more bizarre appearance than the newly hatched young of the kingfishers that I was

studying at the same time. Their heads especially attracted attention (fig. 27). The tightly closed eyes protruded grotesquely well beyond the general contour of the head. The upper mandible was not only considerably shorter than the lower, as in kingfishers of corresponding age, but it was also much narrower. The terminal portion of the upper mandible was covered with a conspicuous, hard, white, shield-like eggtooth, near the center of which was a small, sharp protuberance that was apparently the principal instrument for breaking the shell at hatching. There was a similar but smaller white area on the projecting tip of the lower mandible. The

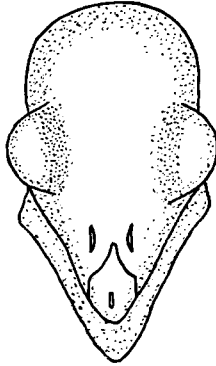


Fig. 27. Head of two-day-old Golden-fronted Woodpecker viewed from above, showing the bulging, tightly-closed eyes, the broad lower mandible with projecting corners, and the shorter, narrower upper mandible with a prominent white eggtooth at its tip. From a field sketch by the author. Enlarged.

nestlings' skin was pink, without the least down or rudiment of feathers. Their heels were studded with prominent papillae or callous projections, which protected them from abrasion as the nestlings shuffled about on the rough floor of their nursery. They made a low, buzzing sound and uttered a soft, clear *peep*. The parents did not remove the empty shells for some days.

When the nestlings were two days old, I detected the first trace of feathers, ten little white points projecting from the end of the uropygium, the rudiments of the tail. By eight days of age, the upper mandible had caught up with the lower and nearly covered it, except for the enlarged and projecting corners of the latter. Their remiges and rectrices were just pushing out, but otherwise the nestlings were still quite naked, although the dark rudiments of the contour feathers were visible through the transparent skin. Their eyes were still tightly closed, but a day later, or nine days after hatching, the eyelids began to separate.

The feathers remained ensheathed until the nestlings were 16 or 17 days old, then they expanded rapidly, so that in a day or two the young birds became fairly well feathered. At the age of three weeks, when the nestlings were fully clad in plumage, the males had bright red crowns, whereas on the females this color was confined to the back of the head. By this time the nestlings could climb up the vertical wall of their chamber and look out through their doorway.

The foregoing was the course of development of many of the nestlings, but all did not live to become feathered. At one nest, in which the fourth egg hatched on

April 14, I noticed a day later that one nestling, apparently the youngest, looked weak and shrivelled. By April 17 it had vanished, doubtless having been unable to compete for food with its older nest mates. At this time one of the three survivors seemed to be falling behind the others and becoming shrivelled, and I thought that it would perish. But it managed to live, although its development was greatly retarded, and it was still nearly naked when its two nest mates were fairly well clothed with plumage. Possibly it would have survived to fly, if the whole brood had not been destroyed by ants when the nestlings were about three weeks old. At another nest in which four young hatched, only three lived to become feathered.

Golden-naped Woodpeckers likewise seem rarely to rear as many nestlings as they have eggs, and the same has been true of a number of other tropical woodpeckers that I have studied. In northern birds whose eggs tend to hatch on successive days, so that the last-born are handicapped in competing for food with their older and stronger nest mates, it is held that this system has the advantage of adjusting the number of living progeny to the abundance of food in any particular season. When food is plentiful, the parents may succeed in rearing all their nestlings, whereas in years of scarcity the younger ones soon starve, permitting the adults to concentrate their care on those which they have a chance of bringing through alive. But with these tropical woodpeckers, there is no reason to suppose that the supply of food when the observations were made was less than normal, and their habitual failure to rear their whole brood suggests lack of adjustment between the number of eggs in the set and the parents' capacity to take care of their young.

It was impossible to see the contents of the Golden-fronted Woodpeckers' deep holes by applying an eye to the doorway, which was likewise too narrow to admit an exploring hand. I had read somewhere that the proper way to study a woodpecker's nest is to cut, with saw and chisel, from the front of the enclosing wall, a segment which can be removed for each inspection and afterward replaced. Accordingly, I applied this method to my first woodpecker's nest. It was satisfying to take the eggs and later the young woodpeckers in hand for close examination and measurement. But when the nestlings were three weeks old, fire ants, which had invaded the crevices in the outer layers of the dead trunk, found their way into the nest through the imperfectly sealed opening that I had made. Two of the nestlings died in the nest, while the third jumped out prematurely, to find the same fate awaiting it among the ants wandering over the ground.

About this time, I was faced with the problem of seeing the contents of a trogons' nest in a termitary, still occupied in its outer layers by the insects; and to cut out a segment of the hard, alveolar carton would, it appeared, place the birds' eggs in great jeopardy. After much thought, I devised a mirror and electric light, which enabled me to view the contents of the trogons' chamber. After I made this simple apparatus, it proved to be useful for a number of closed nests of other kinds. Thereafter, I opened no more woodpeckers' holes, but contented myself with looking in with light and mirror. As I have found with other species of birds, the unaltered nests fared better than those which had been opened and closed again. The chief disadvantage of my new method was that often, when I looked at older nestlings, one was so completely covered by the others that I could not be certain how many were present.

The males brooded the nestlings through the night. One male, when his three young bristled with pinfeathers, ceased to cover them in the bottom of the nest, but

slept each night hanging upright in the top of the hole, his feet clutching the rim of the doorway, his head turned back and buried in his plumage. If I advanced quite noiselessly to a position in front of the nest, which was in a tall fence post, I could surprise him slumbering in this attitude when I switched on the flashlight, but if I rustled the leaves on the ground with my feet he would awaken and stare into the dazzling beam with his red-capped head framed in the round orifice. Since the cavity was 15 inches deep, he was well out of contact with the nestlings, but he served as a buffer between them and the outer world.

Thus he passed five or six nights, until his nestlings were about three weeks old and well feathered, when he left them alone in their nursery. Now at last I could look in at the young birds in the night, when I could see far more clearly in the weak light of a small flashlight than while the sun was shining. All three of the young woodpeckers, two males with red crowns and one female with the red confined to her hindhead, lay side by side, facing the same way. Two slept with their bills pointing straight forward, but one of the males had turned his head until his bill pointed upward. Their black, white-striped backs and shoulders, closely pressed together in the narrow chamber, covered the bottom with one continuous pattern.

Whenever I visited this nest by day, the adult male became greatly agitated and clung to a fence post only 3 or 4 yards from me, bobbing his head up and down as he called *quit it, quit it*. His mate always stayed at a greater distance and appeared less concerned. When I examined the ill-fated nest which the ants had destroyed, the situation was just the reverse, for here the female was by far the more demonstrative. On the morning when the first two nestlings hatched, she merely flew excitedly from tree to tree in the vicinity, calling *tsuka, tsuka* as she emphatically bobbed her head but made no feint of attack. Thereafter, her boldness increased daily. Dropping from a perch in a tall tree to one side of the nest, she steered so straight toward me that for a moment it seemed that her sharp, chisel-like bill would pierce my cheek or transfix an eye, but when she was within arm's length she swerved sharply to one side, darted by, and curved up to a high perch on the other side of the nest, from which she repeated her menacing dive in the reverse direction. Sometimes she would drop straight down toward me from a branch above my head, as though intending to strike. On one of her swoops, her wing actually brushed the hand I had raised to the entrance of the nest. Her mate made only verbal protests, either while clinging well beyond my reach in the top of the dead nest tree, or else from a still safer distance.

At a third nest, neither parent became much excited when I visited their nestlings. Both clung quietly to a young ceiba tree which grew beside the stub that contained their nest, watching me in silence. Rarely the female would fly half-heartedly toward me, never coming very close. Since there are these interesting individual differences in the behavior of the parents, doubtless there are nests at which both parents guard their young zealously, but I failed to find such a pair.

During their final days in the nest, the young woodpeckers, now well feathered, took turns clinging in the top of the nest with their heads in the doorway, waiting for their meals. The parents, arriving with food, clung below the entrance and passed it to them. From an early age, the nestlings received food held visibly in their parents' bills rather than regurgitated to them, in the manner of a number of other species of woodpeckers. The young left this low nest in the fence post when they were 30 days old. Each then rather closely resembled its parent of the same sex,

but the bills of all were noticeably shorter and, probably for this reason, appeared to be thicker. None returned to roost in the nest. After their departure, the bottom of the chamber, which for weeks had been so completely covered by them that I could not see it, was found to be covered with filth, in which maggots writhed. When the nestlings of another nest were still very young, I noticed that all droppings had been removed.

SEQUENCE OF BROODS

When found on April 1, the low nest in the fence post contained nestlings, which two days later had apparently flown. By April 21 this hole held four eggs, which hatched from May 1 to 3. The three surviving nestlings departed on May 31 and June 1. By June 19 the cavity had been cleaned of the filth which these nestlings had left and also deepened, and fresh chips covered the bottom. On June 21 there was one egg in this nest, and to my surprise the male did not pass the night with it. Two days later I left to visit the arid region higher in the Motagua Valley, and when I returned on July 6 I found that the nest had been hacked open and destroyed. From these observations, it appears that with good luck the Golden-fronted Woodpecker may rear three broods between February and August. The interval between the departure of one brood and the laying of the first egg of the next set appears to be two or three weeks.

SUPPLEMENTARY OBSERVATIONS ON THE GOLDEN-FRONTED WOODPECKER OF COSTA RICA

The southernmost form of the Golden-fronted Woodpecker, *Centurus aurifrons hoffmanni*,¹ which until recently was classified as a distinct species, inhabits Nicaragua and Costa Rica. In the latter country it is found in the highlands on the Caribbean slope to an altitude of nearly 7000 feet, and it is also present in the northern part of the Pacific lowlands. In the southern Pacific lowlands it is replaced by the Red-crowned Woodpecker. The Golden-fronted Woodpecker is very common in the semiarid woodlands of Guanacaste and in the coffee producing regions of the Central Plateau and Caribbean slope down to at least 2000 feet, below which, in the more continuous forests of the foothills, it appears to be less abundant. It does not require heavy timber, and among the coffee plantations, light copses, and scattered trees of much of the Meseta Central it is the only woodpecker that one is likely to meet. In appearance, this small form of the Golden-fronted Woodpecker differs from *C. aurifrons pauper* chiefly in having yellow rather than red on the nape in both sexes. In the male, the red of the crown may blend into the yellow of the hindneck or it may be separated from it by an occipital band of yellowish gray. The vocabulary of this woodpecker also resembles that of its northern relatives and consists largely of *churrs*, which are sometimes loud and sometimes soft.

ROOSTING

Hoffmann's Golden-fronted Woodpecker lives in pairs throughout the year. In November of 1935 I found a pair in some low trees in a pasture near the foot of the Tablazo Mountains, on the southern side of Costa Rica's Central Plateau at an altitude of about 4500 feet. In these trees were several woodpecker holes, which appeared to have been recently carved, although the breeding season was evidently

¹ Since this chapter was written, Selander and Giller (1963:240) have argued for the restoration of *hoffmanni* to specific status.

long past. Suspecting that these cavities were intended for use as dormitories, I watched them at daybreak, and one morning I saw a male and a female emerge from the end of a dead, truncated branch, about 15 feet above the ground. Investigation showed that the upper part of the stub contained a shallow cavity with two openings, one of which was the gap left where the branch had broken off, and the other a round doorway that the woodpeckers had carved in the lower face of the limb. Probably because they had seen me watching them, these woodpeckers did not sleep in this cavity in the immediately succeeding nights, and I could not find their new lodging. A similar instance of a male and female sleeping together in a hole with two entrances is reported of a newly mated pair of Green Woodpeckers (Blume, 1961:31).

Near Las Cañas, Guanacaste, in November of 1937, I watched a single Golden-fronted Woodpecker enter a hole in a dead stub of a roadside tree in the evening twilight. In late August and early September of 1938, on the hacienda "Las Cóncavas" near Cartago at an altitude of 4600 feet, I found four of these woodpeckers sleeping in as many holes in low trunks in and around the edges of a grove of small trees in the midst of pastures. Unlike the earlier pair, these birds all roosted singly, although by day I generally met Golden-fronted Woodpeckers in pairs at this season. Also unlike nearly all other woodpeckers that I have watched, they retired very late in the evening and emerged from their holes quite early in the morning, so that neither when they went in nor when they came out was there enough light to distinguish their sexes with certainty. From these observations and those on the Red-crowned Woodpecker that are given in a later section, I infer that the male and female which I found sleeping together in November had adopted an arrangement unusual in their species. Possibly, since the cavity which they occupied had two doorways, it was taken to be the equivalent of two chambers. More probably, they slept together for warmth, for the shoulder of the mountain where they lived was windy and cold at this season. On the chilly morning when I watched for their emergence, they lingered in their protected nook unusually long even for woodpeckers, which are typically late risers.

NESTING

At "Las Cóncavas," I found two nests in aguacatillo trees (*Persea caerulea*) in 1937. The first, 16 feet above the ground in the dead top of a small, living tree standing in a pasture, held three white eggs on June 22. The second, 12 feet up in a very similar site, contained two nestlings whose feathers were just sprouting on June 29. At the first nest, the male and female took turns at incubation by day, and the male was in charge of the eggs through the night. His long nocturnal session began surprisingly late in the evening and ended early in the morning. On the cloudy morning of June 27, the female came to relieve him at 5:17 a.m., about 20 minutes after the abundant Gray's Thrushes had begun their magnificent chorus in the dim light of dawn. At 5:42 the male returned to replace his mate, which probably had not eaten before she went on the nest, and only then was there sufficient daylight to reveal his bright red cap. In the evening, the female remained on the eggs until 5:59 p.m., when she left on hearing her mate's call. At 6:07 he went into the nest and stayed until, at 6:20, I could hardly distinguish his doorway in the fading light and all birds had become silent. Although there were two old woodpeckers' holes in the tree where this pair nested and a number more in

neighboring trees, the female did not roost in any of them but flew off to the west until out of sight.

Not far from this nest, another male slept in an old and somewhat ruinous hole. He was not breeding and might well have belonged to an earlier brood of the nesting pair.

SUMMARY

In Central America, the Golden-fronted Woodpecker inhabits both humid regions and arid country with cacti and thorny scrub. Where rainfall is high, this woodpecker is found in plantations and light second-growth woodland rather than in the heavy forest. In Guatemala it resides from sea level up to at least 5000 feet, and in Costa Rica it occurs from sea level to nearly 7000 feet.

Versatile in its manner of foraging, the Golden-fronted Woodpecker extracts insects from wood and also catches them in the air. It varies its diet with fruits.

Its vocal notes include a loud rolling *krr-r-r-r*, a short harsh *krrr*, and a soft *tsuka tsuka*. It beats a tattoo on resonant dead wood.

In the lower Motagua Valley of Guatemala, the breeding season extends from at least February to August, and three broods may be reared, sometimes in the same hole. The nest cavity may be low in a fence post or high in a dead tree. It is excavated by both sexes working alternately, and it may be completed in less than two weeks.

Four sets in the Motagua Valley consisted of four eggs. The male and female incubate alternately through the day. By night the eggs are covered by the male, which may begin to sleep in the nest before laying starts. Hatching may begin 11 days after the set is complete and is spread over two days or more. The incubation period is at least 12 days.

At hatching, the sightless, perfectly naked young have the lower mandible both longer and broader than the upper mandible. At the age of three weeks they are well covered with plumage, which resembles that of the parent of the same sex. They remain in the nest for about 30 days.

The young are fed by both parents, with food carried in the bill. The parents at first keep the nest clean, but they neglect sanitation after they can feed the nestlings through the doorway without entering the hole, with the result that before the young fly the bottom of the nest becomes covered with maggot-infested filth. The male attends the nestlings through the night. When his offspring were becoming feathered, one male passed five or six nights sleeping above them in the top of the chamber, his feet clutching the doorway. During their last week in the nest, these young slept alone. After their first flight, they did not return to the nest.

There are great individual differences in the demonstrativeness of parents when the nest is visited by man, sometimes the male, sometimes the female, exhibiting greater zeal in its defense.

The younger members of a brood die or develop more slowly than the older ones. The parents appear unable to rear young from all the eggs which they lay.

In Costa Rica, Golden-fronted Woodpeckers remain mated through the year. Usually they roost singly in holes, but both members of one pair occupied, in November, a hollow stub with two openings. This nest was on a cold, windy mountainside in the highlands. Unlike most woodpeckers, Golden-fronted Woodpeckers may retire in the dusk and leave the dormitory in the dim light of dawn.

RED-CROWNED WOODPECKER

Centurus rubricapillus

This small woodpecker is about six and a half inches in length. In the male, the forehead is dull brownish white and the crown and hindneck are bright red. The back is broadly barred with black and white, and the lower rump and upper tail-coverts are white. The tail is black with white bars and spots on the middle feathers. The black wings are also marked with white. The sides of the head and the under plumage are shades of buffy gray, with a patch of bright red on the lower abdomen. The female resembles the male, except that her crown and hindhead are light buffy gray and only her hindneck is red, of a shade less intense than that of the male. In both sexes, the bill is black; the eyes are brown; and the legs and feet are gray.

The Red-crowned Woodpecker ranges from the southern half of the Pacific slope of Costa Rica through Panamá and Colombia to Venezuela, British Guiana, Trinidad and Tobago. A lowland bird, it extends upward to 5000 feet on the Pacific slope of extreme southern Costa Rica, to 2800 feet in the Coastal Range of Venezuela (Schäfer and Phelps, 1954:87), but rarely over 1000 feet in the Santa Marta region of Colombia (Todd and Carriker, 1922:241). In northern South America and adjacent islands, the Red-crowned Woodpecker prefers more or less arid country with low and open vegetation. On Tobago, where it is very common, it lives in the coconut plantations and other cultivated areas, and on Patos, near Trinidad, it is abundant among the tall cacti which cover most of the tiny islet (Belcher and Smooker, 1936:797). In the Santa Marta area it also dwells in arid country with many giant cacti, in which it often carves its nest cavity. In northeastern Venezuela it is abundant at the edge of the deciduous woods (Friedmann and Smith, 1950:493). In the Coastal Range of Venezuela it is likewise said to be a xerophilous bird (Schäfer and Phelps, *loc. cit.*). But in the valley of El General, where I am most familiar with it, the Red-crowned Woodpecker inhabits clearings in the heavy rain forest, which until a few decades ago covered most of the country.

FOOD

In addition to the small invertebrates which it extracts from decaying trunks and branches, the Red-crowned Woodpecker eats a variety of fruits, including the small black berries of *Miconia*, the seeds of *Alchornea latifolia* and of species of *Clusia* which are enclosed in bright red arils, and the green fruiting spikes of *Cecropia*. Although fond of bananas and resident in the neighborhood, it was long before these woodpeckers came to my feeding shelf in a tree by the house. For years this shelf had been provided with fruit daily, and 21 other kinds of birds had become regular or occasional attendants before I saw the first Red-crown eating there. Perhaps one reason why four years passed before these woodpeckers became habitual visitors is their aversion to standing on a flat surface. The first whose arrival I witnessed alighted on one of the branches that supported the table and backed slowly, hesitantly down toward it. When at last he reached its level his tail slipped under the edge, for the board did not make contact with the limb. This seemed to upset the woodpecker, for he climbed up the branch for a foot or two. Then he again backed down,

and again his tail went beneath the table. At last, after much hesitation, many approaches and reversals, the woodpecker discovered that he could reach a banana while clinging upright to the edge of the table, without the necessity of standing on a horizontal surface. Clinging so, he partook of the banana for a minute or two, while tanagers and other birds came and went.

When the woodpecker returned next day, he approached the board with the same retrograde movement, the same hesitation and reversals, that I had witnessed on his first visit. When, on reaching the table, he found no banana that he could touch while clinging upright to its edge, he hung for a moment beneath it, back downward. But after a little while he stood on the board and ate the fruit as the Golden-naped Woodpeckers had already learned to do. On his later visits in the same day, he went more directly to rest on the board and eat. This was in June of 1946, and in the succeeding years, the Red-crowned Woodpeckers have frequently come to feast on the bananas and plantains that we provide for them and the other birds. Sometimes they carry away pieces for their nestlings, and later they may bring their fledglings to the table. But they are not so regular in their attendance as are some of the passerines, their visits appearing to depend on the seasonal availability of other foods.

VOICE AND MECHANICAL SOUNDS

The call of the Red-crowned Woodpecker is a drawled rattle or churr, *krr-r-r-r*, which is uttered with a number of variations. Often it is high-pitched and long-continued. Both sexes beat tattoos on resounding dead wood, but in my experience they do so rather sparingly. One day while I watched a pair attend nestlings, a second pair approached, and once the intruding male went to look into the nest. The resident male chased the trespasser around and around in wide, irregular circuits, above or through the treetops, the two flying rapidly in an undulatory course and sometimes churring as they went. The resident female did not chase the intruding male but threatened him with uplifted wings when he came into the nest tree. Later the resident male displayed, raising and spreading his white-barred, black wings, stretching forward his neck, and uttering a queer, indescribable note as he bobbed his head up and down. This dispute stimulated much drumming by both of the parents.

ROOSTING

Red-crowned Woodpeckers are mated throughout the year. By day I have repeatedly seen a male and female keeping company even in December, and at night they often roost in neighboring holes. But I have never found an adult male and female sleeping in the same hole, nor two adults of the same sex roosting within sight of each other. Like other woodpeckers that I have studied, with the exception of the Acorn Woodpecker, the Red-crowned Woodpecker has well-defended territories.

In 1936 and 1937, when I resided at Rivas in the narrow valley of the Río Buena Vista on the northern side of the basin of El General, I enjoyed exceptionally favorable conditions for studying woodpeckers, toucans, woodcreepers, tityras, and other hole-nesting birds. Not long before my arrival, the rain forest, on a long, steep slope above the settlement, had been felled for planting maize. The laborers had left a number of trees standing above the wreckage of the forest, and these were

killed when fire was set to clear the land for sowing. After these gaunt, charred relics of the woodland began to decay and soften, woodpeckers of four or five kinds carved holes in them for sleeping or breeding. The absence of leafy trees above the secondary vegetation that soon covered the slope permitted an unobstructed view over the whole clearing, so that a woodpecker could scarcely enter or leave any of the holes unperceived by an attentive observer. Thus it was often possible to follow simultaneously the movements of the several members of a family, as one can rarely do amid the luxuriant vegetation of the humid tropics.

From February, 1936, to May, 1937, I followed the activities of the single pair of Red-crowned Woodpeckers (henceforth known as the "hillside pair") that roosted and nested in this hillside clearing. When I first found them, they were feeding nestlings on the southern side of the clearing. Their nest was in one of three holes in a small burio (*Heliocarpus excelsior*), a swiftly-growing tree the wood of which is about as soft as that of the better-known balsa (*Ochroma*). In the evening of March 1, I concealed myself in a thicket to watch the family retire. At 5:37 p.m., the male flew up and entered the nest hole with the nestlings, which uttered their weak, buzzing call as he joined them. Turning around, he thrust his head through the doorway and continued to look out over the darkening valley. Soon the female arrived, and for a long while she rested motionless on the upper side of one of the higher limbs of the dead tree. Finally, at 6:03, she bestirred herself and dropped down to the hole from which I had seen her emerge in the morning. As usual, she peered through the doorway to make sure that no intruder lurked within, but then, oddly enough, instead of entering headfirst and then turning around, as her mate had done, she tried to insert herself tail foremost into the cavity, a feat which I had never before seen a woodpecker attempt. But her feathers caught on the rather sharp rim of the opening, causing her much annoyance. She made several trials of this mode of entry, and on the last one her right wing got caught on the outside and would not follow the rest of her body. Obviously, woodpeckers are poorly adapted for entering holes tail foremost.

After almost leaving her wing behind, she abandoned her attempt to enter her lodging of the preceding night in this unconventional manner and turned her attention to the third of the holes which the tree contained. The latter was in the main trunk well below the nest with the young. This she also insisted on entering in her whimsical retrograde fashion, and finally she succeeded in working her way in. But for some reason this chamber failed to satisfy her, and she came out to fly off to the north, where doubtless she knew another cavity that would provide a night's lodging.

After his mate's departure, the male settled down in the nest, and I no longer saw his head in the doorway. But before long he was aroused by the violent shaking of his slender trunk. Sticking his head far out, he turned it sideways to peer into the topmost leafless branches with one eye, and there he beheld three brilliant Fiery-billed Araçaris which, on their way to their sleeping quarters, had paused here. The araçaris flew back and forth among the naked boughs, alighting heavily, and one struck its great bill loudly against a branch. Sallying forth, the male woodpecker darted above the toucans, uttering his long-drawn *kr-r-r-r-r*. Soon the intruders straggled off toward the more massive trunk in which they slept, and the woodpecker returned to his nestlings.

We shall later give attention to the behavior of the two fledglings which on

March 23 and 25 left this nest. Suffice it to say at this point that they soon disappeared from the clearing, while their parents continued to reside there, from time to time changing their quarters. In the next 12 months, the male occupied no less than nine different holes, the female at least eight. There were doubtless other lodgings which I did not record, as while breeding was not in progress my visits at dawn or nightfall were rather widely spaced. The cause of these frequent changes of domicile was sometimes the falling of the branch or tree which contained the cavity, but at other times the cause of the change was not evident. The most widely separated of the dead trees where, in the course of the year, I found either member of the pair sleeping were about 500 feet apart. Most of the dead trees were slender trunks of the burío or some other species with soft wood in which woodpeckers could easily carve holes, so that usually my first intimation that a new hole was needed was the sight of the male's red head in the doorway of a cavity already large enough to serve as a dormitory. While the Red-crowned Woodpeckers changed their lodgings frequently, a family of Golden-naped Woodpeckers roosted from one breeding season to the next in the same hole, more laboriously carved in the harder wood of a more massive trunk, in the same hillside clearing.

Although I sometimes found the male Red-crowned Woodpecker at work, I never saw his mate engage in excavating a hole. Certainly he almost always slept in the newer and sounder chamber. At least six of his dormitories appeared to be freshly carved, but only once did the female install herself in a new hole, and it is possible that he had made it for her. More often, she took possession of an old hole which he had abandoned. Sometimes she contented herself with what appeared to be a most inadequate shelter, such as a hollow in the very top of a tall trunk which opened skyward and admitted October's torrential rains. While she lodged uncomfortably here, her mate enjoyed a snug new hole which he carved for himself 2 feet below her. These dormitories, about 60 feet above the ground, were the highest that I found. The lowest were about 20 feet up. Although the male and the female never occupied the same hole, they often slept in the same trunk.

The male woodpecker was usually the first to retire in the evening and the last to come forth in the morning, although occasionally the order of going to rest or emerging was reversed. With the notable exception of the Golden-fronted Woodpeckers of the Costa Rican highlands, I have found that members of this family in general take long periods of rest, so that one finds them ensconced in their chambers, in both the morning and the evening, while many kinds of neighboring birds with less commodious lodgings are active. In the rainy month of October, the male Red-crown often retired between 4:00 and 5:00 p.m., an hour or more before nightfall, and rested quietly, looking out over the slowly darkening landscape. Once, when I found him so at 4:15 p.m., he remained with his head in the doorway, without going forth to feed, until he descended into the hole for the night, and he did not emerge until 5:50 a.m. next morning, after his mate and his neighbors, the Golden-naped Woodpeckers and the Fiery-billed Araçaris, had become active. This long period in the hole can hardly be ascribed to broodiness, for the nesting season was months off.

While the male rested in his chamber in the evening, his mate often pecked idly here and there on neighboring dead trees, or clung motionless to a branch, until the light grew dim, when she, too, sought her shelter for the night. One evening she discovered that by tapping on the hard, white diaphragm across the end of a broken-

off, hollow branch of a guarumo (*Cecropia*) tree, high above the ground, she could produce a loud, sharp noise, and she occupied herself in this manner for a few minutes. On reaching her dormitory, she usually went in tail first, and with practice she acquired far greater proficiency in this mode of entry than she had displayed on the first evening that I watched her retire. The male more rarely entered his hole backward. In the morning, although the female so often left her nest before her mate, she did not always go to forage before him. Thus on October 17 she emerged from her chamber at 5:30 a.m. and clung to the top of her trunk near her doorway until, after 20 minutes, he came forth from his lodging beneath her and both flew off together.

In those periods when I spent much time with these woodpeckers, particularly during and immediately after the breeding season, they became almost indifferent to my presence beneath them. But if I were absent for several weeks, I found that when I next watched them in the evening they were distinctly shyer and hesitated to enter their holes in my presence. In these circumstances, one evening the male went to rest in his mate's dormitory, and she in his. The reason for this reversal of their usual arrangement appeared to be that the male preferred the female's chamber because it opened on the side of the trunk away from me, and she, coming later, had to be content with the one that remained empty.

In mid-afternoon in May, while a heavy shower fell, I found the male taking shelter in his dormitory, but the female was not in her hole. The following afternoon, at about the same hour, both woodpeckers were absent from their holes during a hard rain. Whether or not a bird seeks protection from a diurnal rain in its dormitory may depend, among other things, on how far from home it happens to be when the shower begins. Since their well-oiled feathers shed water very well, it is not necessary for these woodpeckers to seek shelter in a hole when it is raining.

On February 9, 1948, I found another pair of Red-crowned Woodpeckers lodging in a tall, fire-killed stub of a muñeco tree (*Cordia*), surrounded by lower stump sprouts, at the edge of a pasture. In the top of this stub, about 35 feet above the ground, were two woodpecker holes, about one vertical foot apart, the upper one facing west and the lower one south. After sunset, I watched a male woodpecker enter the lower hole. A little later his mate went to the upper hole and, after clinging beside it for a good while, pushed in tail foremost. Here they stayed for the night.

On February 14, both of these woodpeckers had entered their respective holes by 5:10 p.m., well before sunset, although their tree was in the shadow of the forest on a neighboring elevation. They lingered for a good while looking out with their heads in their doorways. On February 25, however, the male did not enter his hole until 5:29, when he went in headfirst. On this evening I did not see the female. On February 27, the male flew up to his stub just as I was passing it, at 5:20 p.m. He remained clinging in front of his doorway, churring, while I walked across the pasture to watch from a distance. For the next 20 minutes he delayed his entrance, but toward the end of this period he pushed in through the opening until he was almost inside, then he drew out again rapidly, doing this over and over. Finally, at 5:41, he turned around and deliberately pushed in tail first. He was apparently somewhat apprehensive because he saw me watching him. After he retired, I went in search of his mate and found her looking out of a hole 20 feet up in a dead *Inga*, another tree with soft wood, about 100 yards from her former and her mate's present lodging.

They continued to occupy these widely separated dormitories until at least March 15, after which I lost track of them. Apparently they went elsewhere to breed.

On June 6, 1961, I found a female Red-crowned Woodpecker roosting in the dead avocado tree where a Tawny-winged Dendrocincla nested and slept in three consecutive years. The hole into which she had retired had been carved and occupied as a dormitory by a male Golden-naped Woodpecker, but the family of Golden-napes had earlier moved elsewhere. On June 11, a male Red-crowned Woodpecker was carving a hole higher in the same avocado tree. At 6:20 p.m. on this date, the male was looking out of the hole where the female, evidently his mate, had been sleeping. After a while, he emerged and climbed up the trunk, whereupon the female, which I now first noticed, climbed down and slipped into her dormitory. The male entered the hole that he had been carving earlier in the day. Not content here, he soon returned to the lower hole, which the female vacated as he approached. She ascended the trunk and went into the upper hole. Again the male emerged and went to the upper hole, whereupon the female obligingly shifted to the lower one. Soon, however, the male returned to the lower hole, and she re-entered the upper one; in these positions they settled down for the night. Thus the male was clearly dominant over the female. He did not, as far as I saw, peck at or threaten her, but she quietly slipped out while he was a few inches away, leaving him the hole of his choice. Both birds usually entered tail first. Next day, the branch of the avocado tree broke off at the male's new hole, ruining it. He then slept in the chamber which the female had formerly occupied, and she went elsewhere. But his tenancy of this hole was brief, for a day later he was driven out by the dendrocincla.

NEST AND EGGS

In El General, between 2400 and 3000 feet above sea level, Red-crowned Woodpeckers begin to breed in February or early March and continue until May or June, sometimes, perhaps regularly, attempting to rear a second brood. The hillside pair started nesting only a few days later in 1937, when January and February were unusually wet, than in 1936, when these months were dry. In 1937 this pair began to incubate about February 16 and their young left the nest on March 29. The preceding year the young departed on March 23 and 25. Red-crowned Woodpeckers breed consistently earlier than their neighbors the Golden-naped Woodpeckers, which seldom lay their eggs before late March or April, but they breed later than three other woodpeckers of the same region, the far larger Lineated and Pale-billed woodpeckers and the much smaller Olivaceous Piculet.

Often the female Red-crowned Woodpecker lays her eggs in her mate's dormitory, which, as we have seen, is usually newer and sounder than her own. This was true of the first brood of the hillside pair in 1937 and of their second brood in both 1936 and 1937. In the case of the first brood of 1937, the male had been lodging in the cavity for more than two weeks before laying began in it. At the end of February of 1937, I found another pair, the male of which roosted in a newly made hole and his mate in an older one, both in the same wayside tree. By March 5 incubation was in progress in the hole where the male had lodged. Since the male's dormitory so often becomes the receptacle of the eggs, it is natural that he should take charge of them by night.

Although in the case of the hillside pair all the hole-carving that I witnessed was done by the male, the female may help to prepare a nest if one is needed during

the breeding season, just as happens in the Golden-fronted Woodpecker. On March 16, 1940, I found a male Red-crown lodging in a new hole only 15 feet above the ground. Three days later, at 4:00 p.m., the female was looking out of this cavity, which suggested that it would be used for breeding, although it still contained no egg. In a rainstorm on March 23, the branch broke across the middle of the cavity; this was not surprising, for the birds had left a very thin shell of wood surrounding their chamber to support the terminal part of the upright dead branch. Soon after this, the pair of woodpeckers started a new hole just below the ruined one, and both sexes worked at it. One morning I watched the female chisel steadily for 45 minutes, and she was already at work when I arrived. This chamber was abandoned before completion.

The holes in which I have found Red-crowned Woodpeckers attending eggs or young were situated from 11 to about 75 feet above the ground, but only one was below 25 feet. They were in dead trees or dead branches of living trees. Nearly always a tree with soft wood, such as *Heliocarpus*, *Inga*, or *Nectandra*, is chosen for the nest site, and this, coupled with the usually advanced stage of decay of the tree, makes a prudent person desist from trying to reach it. One nest tree fell after a brood had left, providing me with an opportunity to measure the nest chamber. The doorway was $1\frac{3}{4}$ inches in diameter and the cavity extended for 9 inches below it. Rather irregular in shape, it was widest about halfway down, where its diameter was $3\frac{3}{4}$ inches.

One egg in a fallen nest was pure white, glossy, and measured 23.8 by 17.1 mm. Although I have not known more than two young to be reared in a nest, the set of eggs is probably larger than this, for woodpeckers seem rarely to succeed in rearing all of their brood.

INCUBATION

By January 29, 1937, the male of the hillside pair had established himself in the dormitory which was destined to become the breeding nest, high up in a slender trunk near the center of the clearing. On February 4 he first showed his head in his doorway at 5:44 a.m., nearly half an hour after the Orange-billed Nightingale-Thrushes and Black-striped Sparrows began to sing in the day's first light. After a while, the Red-crown uttered a loud *krr-r-r-r* as he looked out of the entrance, and at irregular intervals he repeated this rolling churr. Formerly, this male had rested silently in the top of his chamber until the time came for him to emerge. Finally, at 6:18, an hour after the dawn chorus began, he flew out and away. But in 5 minutes he returned, entered his hole, and this time stayed down out of sight. A few minutes later, the female arrived and clung in front of the doorway, looking in. In a minute or two, her mate came out and flew away, whereupon she entered his hole at 6:27 and for 6 minutes she stayed inside, most of the time looking out. Then she left to follow her partner far down the slope to the southwest. The male's calling from his dormitory before emerging in the morning, his return soon after, and his mate's new interest in this chamber, all presaged its use as a breeding nest.

A week later, on February 11, the male had not shown his head in his doorway by 5:55 a.m., half an hour after the dawn chorus. At this time the female flew across from her own dormitory and entered his, only to come out immediately and cling to the trunk beside the doorway. Here she remained until he emerged 2 minutes later and climbed up one of the ascending branches at the top of the tree.

Then she promptly entered and stayed out of sight, while the male continued to cling motionless in the treetop. Presently he called twice and flew off to the south. For 28 minutes the female remained in the bottom of the cavity; then she came to the doorway and spent 4 minutes looking out. At 6:29 she came forth, flew to the top of a neighboring tree and called. Finally, at 6:38 she flew northward, doubtless in search of food. The male had not yet returned.

Revisiting the clearing at 10:00, I found both woodpeckers absent, and I waited half an hour until the male arrived and entered the hole. Soon I began to hear tapping from the trunk, and presently he came to the doorway and threw out chips. For the next half hour he continued to chisel in a rather desultory fashion, judging by the sounds that I heard, and from time to time he came to the doorway to throw out loosened particles. Then he stuck his head out and called a few times, after which he flew away. All this while the female stayed out of sight. The male was evidently enlarging his chamber in preparation for a brood.

In the succeeding days the female continued her early morning visits to her mate's dormitory, and by February 17 the long periods which both sexes spent in the hole left no doubt that they were incubating. On February 23, I started to watch at 12:40 p.m., continued until 6:00 when it was growing dark, resumed my vigil at 5:45 a.m. next morning, and carried on without interruption until 12:40 p.m., thereby making a complete record of the activities at this nest over a period of 24 hours (assuming that nothing unusual happened during the night).

At 6:13 a.m. on February 24, the female flew up the hillside, alighted in a neighboring tree, and churred. Her mate, which had passed the night in the nest, did not reveal himself in the doorway. She came to the entrance to the cavity and clung in front of it. The male tapped inside and finally looked out. At 6:15 he left, and 2 minutes later the female entered the nest hole. At 5:32 on the preceding evening, the male had replaced his mate for the night. Thus his nocturnal session continued for 12 hours and 43 minutes. During the day, the female took six sessions lasting 61, 76, 80, 2, 52, and 75 minutes, with an average of 57.7 minutes. The male's sessions, alternating with these, lasted 105, 38, 22, and 83 minutes and averaged 62 minutes. Since the male happened to be present when I began and ended my watches in the middle of the day, he must be credited for sitting 57 additional minutes, not included in the above, since these sessions were not timed in full. Thus, between the male's first departure in the morning and his final return in the evening, he spent a total of 305 minutes in the nest, his mate spent 346 minutes, and the nest was left unattended for five short periods, totalling 26 minutes. The two sexes together kept the nest occupied for 96 per cent of the day.

Sometimes the woodpecker which had been incubating became impatient, left the nest and called before its partner came in sight, and then a few minutes might elapse before the other took charge of the eggs. More often, the bird on duty waited in the hole until it saw, or at least heard, its approaching mate, or even until the latter had reached the doorway. But the new arrival never entered the hole until after the other had come out. I never saw the female enter the nest tail first, as she so often did when entering her dormitory. Sometimes, in woodpeckers of which several grown birds sleep in the same cavity, including Golden-naped Woodpeckers and Olivaceous Piculets, one member of the pair enters to take over incubation before the other has left, and the two may stay inside together for a few minutes, but in species which sleep singly, it is most exceptional for the two to be together in the

hole, however briefly, at any time. The one occasion on which I saw a member of this pair go into the cavity before the other had left was early in the morning of February 11, before incubation began, when the female entered without waiting for her mate to emerge. Then she came out so promptly that I suspected her unusual behavior had drawn an admonishing peck from the male.

Usually the incubating partner rested out of sight in the bottom of the hole, but toward the end of a long session it might spend much time looking through the doorway, as though impatient for its mate's return. Rarely it would climb out of the hole and then would go right in again. Sometimes while incubating the male hammered or pecked inside the nest, thereby breaking the tedium of his session. For the rest, the day passed uneventfully, except that from time to time one of the woodpeckers chased a pair of Masked Tityras, which alighted in the top of this tree on the way to or from their own nest higher on the hillside. The longest interruption of incubation, lasting 12 minutes, was caused by this disturbance.

A pair which in 1953 nested in a dead branch of a living burio tree in our garden incubated far less methodically and constantly than the hillside pair. Instead of waiting for his mate's arrival on the morning of March 24, the male, after much looking through his doorway, flew away at 6:00 a.m., leaving the eggs unattended. At 6:17 he returned to the nest, but a minute later his mate came and replaced him. She incubated for 36 minutes, the longest uninterrupted session that we recorded in the course of the morning. Thereafter, the woodpeckers were amazingly restless, often looking through their doorway, climbing out only to turn around and go in again, coming and going more frequently than any other incubating woodpeckers that I have watched, with the exception of a nest of Acorn Woodpeckers with four or five attendants. Sometimes one of the pair in the garden would come to the doorway, find its mate inside, and fly away without replacing it, but far more often the bird on duty would leave before its partner arrived. Then, after an interval of several minutes, the same individual might return to resume incubation. All this contrasted sharply with the regular alternation of the two parents at the hillside nest.

In the 5 hours following the male's first departure in the morning (6:00 to 11:00 a.m.) he took four sessions ranging from 1 to 27 minutes and totalling 68 minutes. The female took nine sessions ranging from 5 to 36 minutes and totalling 146 minutes. The nest was left unattended for 12 periods ranging from 2 to 18 minutes and totalling 86 minutes. The parents were present only 71 per cent of the five hours, and much of their time in the nest was spent looking through the doorway. These figures hardly give an adequate notion of the woodpeckers' restlessness, for to simplify calculation, sessions interrupted for a minute or less were counted as continuous. Possibly the hot, dry, oppressive weather of this period was responsible for this erratic incubation, but the presence of ants, lice, or other insects in the nest might have caused the birds to sit restlessly. In the following days, short periods of observation showed that the woodpeckers came and went frequently. But by March 30 the parents were bringing food to the nest, proving that despite their inconstant incubation they had hatched at least one of their eggs.

By February 26, ten days after I noticed that the woodpeckers of the hillside pair were spending long periods in their nest, they were taking food to it. It will be recalled that some of the eggs of the Golden-fronted Woodpecker hatched only 11 days after the set was complete.

THE NESTLINGS

I have not seen nestlings of the Red-crowned Woodpecker until, at the age of about four weeks, they first show their heads in the doorway of their high, inaccessible nest. Both parents bring food to them, holding it visibly in the bill, which often bristles from apex to gape with an array of projecting parts of insects. Fruits of several kinds vary the nestlings' diet. Because I was uncertain of the number of young in a nest, I did not make an extended study of the rate of feeding. Short watches showed that the adults brought food to the nest at a rapid rate. To a nest with at least two feathered nestlings, the parents came nine times with laden bills in the first half-hour of the morning, but in the following half-hour only one more meal was added. At another nest, which seemed to contain a single young woodpecker almost ready to leave, nine meals were brought by the female and three by the male in the hour from 7:15 to 8:15 a.m. At least half of these 12 meals were pulled from the fruiting spikes of a guarumo tree, the boughs of which interlocked with those of the nest tree. Once the female came with a big orthopteron, which she placed in a crevice in the upper side of an ascending branch to peck at it. After continuing this for several minutes, she went off leaving the insect there. Soon the male found it and carried it down to the nestling. A nestling Red-crowned Woodpecker may receive in an hour about as many meals as a young Lineated or Golden-olive woodpecker, fed by regurgitation, receives in a day.

When the nestlings are small and weak and the parents must enter the nest to feed them, they may be seen carrying out billfuls of waste matter, but they appear not to clean the nest at all after the young birds can take their meals through the doorway. This is in accord with observations made at accessible nests of the Golden-fronted Woodpecker. But in those woodpeckers which use the nest cavity as a dormitory for the whole family, including the Golden-naped Woodpecker and the Olivaceous Piculet, much attention is given to sanitation throughout the nestling period, and when the young leave, the bottom of the cavity is clean.

After the nestlings are two weeks old they are brooded little by day, but the parents guard them, when they are not engaged in the quest of food, spending much of their time clinging to some trunk or limb in view of the nest. At this stage of nesting, I used to find the female of the hillside pair resting in the late afternoon in front of the hole, or in the top of the nest tree, or high in some neighboring tree, watching over her family while her mate was away foraging. Here she would linger, almost motionless, until he returned in the waning light and entered the chamber, to be greeted by the nestlings' weak cries. Then she would bestir herself, stretch her wings, and fly off to her own dormitory. Her spell of guarding appeared to be the equivalent of a turn at brooding, and when her mate returned she behaved just as though she had been relieved after a period in the nest.

At two nests, I first saw a nestling's head in the doorway, momentarily, 27 days after I first noticed the parents taking in food. Two or three days later, the young birds spent much time looking out of the hole, and one could already tell their sexes by the markings of their heads. Soon, in their eagerness for the next meal, they took turns in pushing their heads far out to look around. But on the arrival of a parent, the one in possession of the doorway drew back into the top of the chamber, and this facilitated the transfer of the food. If the nestlings did not cooperate in this fashion, the parents would have to lean far backward in order to pass the meals to them. In the evening after the last feeding, the adult male clung motionless to

some neighboring trunk or bough and did not enter the hole until the light grew dim. He stayed outside later than he did when sleeping alone, and doubtless he remained away from the nest as long as possible in order to avoid the importunities of his ever-hungry offspring.

At the nest of the hillside pair in 1936, one fledgling left two days before the other. The latter then slept alone in the nest, while its parents lodged in two other cavities in the same tree and the other fledgling roosted in the open. At the hillside nest the following year, the male slept with the two nestlings every night except their last in the nest. This was also true of another nest, which apparently contained only one nestling. From the nest of the hillside pair in 1937, the two fledglings departed 31 days after I first saw the parents bring food, but the nest in the garden in 1953 was not abandoned until 33 days after food was brought. This may be compared with the nestling period of 30 days at an accessible nest of the Golden-fronted Woodpecker. From a low nest the young would probably emerge sooner than from a high one.

THE YOUNG AFTER LEAVING THE NEST

After leaving the nest, the young woodpeckers make short journeys between trees, flying more slowly than their parents. They climb well over upright trunks, using their stubby tails for support in the manner of the adults. They peck much at the bark or wood on which they rest, without at first seeming to find anything edible, and they utter a long, rather sharp *krr-r-r-r* resembling that of their elders. Their parents feed and defend them, even driving away birds much larger than themselves, such as the Lineated Woodpecker, but in other respects they are surprisingly neglectful of them.

In both 1936 and 1937, I gave much attention to the hillside pair in the evenings immediately following the young birds' departure from the nest. As night approached, the parents retired into their holes, the male at times into the nest which the brood had just deserted, but they made no attempt to find shelters for their fledglings, or even to lead them to a secluded spot amid the foliage. On the contrary, each repulsed the fledgling that tried to enter the hole with it.

As to the four young woodpeckers themselves, there was a good deal of individual variation in their behavior as the day waned. One female fledgling, at the end of her first day in the open, tried to join the male parent in the nest chamber, only to be gently but firmly repulsed. The other fledgling, a male, appeared to make no effort to find a hole for himself even after he had been out of the nest for two days, but after his third day in the open he tried to enter the cavity where the adult male had retired and was also repulsed. The following year, the male fledgling likewise did not seem interested in shelter after he had been two days out of the nest, but at the end of the fourth day, I found him installed in a last year's hole of his male parent. His sib, a female, neglected an opportunity to sleep in a hole even after she had been flying about for four days, but two evenings later she also entered a cavity. In their first nights out of the nest, these young woodpeckers sometimes roosted in a crotch high up in a tree, but more often they slept clinging upright to a lofty and exposed dead branch, in a position utterly lacking in concealment.

Thus young Red-crowned Woodpeckers spontaneously seek a sleeping hole for themselves from one to six days after quitting the nest. In the hillside clearing where this family dwelt, there were so many dead trees, with so many old wood-

peckers' holes in them, that before they were ten days out of the nest the young birds had all found lodgings, although some holes were rather dilapidated. But in other localities with fewer dead trees or a shorter history of woodpecker occupation, it is probable that a longer period must elapse before the young birds are properly sheltered. Perhaps they must sometimes sleep in the open until they are strong enough to carve holes for themselves. Despite the difficulty young Red-crowns may have in finding accommodations, they refuse to "double-up" for the night; as with the adults, each insists on sleeping alone. Indeed, when they have been out of the nest for only a few days, siblings become antagonistic toward each other.

The Red-crowned Woodpeckers' strong aversion to sleeping two in a hole gave rise to a number of amusing vespertine incidents. On the evening of March 25, 1936, when the male fledgling had been in the open for three days and the female fledgling had been out of the nest only one day, I found the whole family resting in the clump of dead trees where the nest was situated. The older fledgling was restless, creeping over the dead trunks, flying from branch to branch, sometimes churring, much in the fashion of his parents. Climbing up to where the male parent rested, he began mildly to peck him, either playfully or in an effort to make him bestir himself and bring more food. But feeding had ceased for the day; and the parent, seeking repose, merely moved off to another branch.

The adult male was, as usual, the first to enter his dormitory for the night. Then the more active fledgling, the young male, which had slept under the stars for two nights, wished to join his parent inside. The latter tried to push the young woodpecker away, but he was not easily repulsed. The ensuing tussle lasted for several minutes. The parent did not peck, he merely pushed vigorously with his bill, but the fledgling pushed almost as hard in the opposite direction. I saw clearly that the parent grasped the fledgling's lower mandible in his bill. Finally, the parent was obliged to emerge from the hole in order to get rid of the obstinate young bird, which then flew across the clearing and vanished in the dusk. After the conclusion of this episode, the adult female inserted herself tail first into the end of the oblique stub where she slept. Now the adult male, instead of returning to the hole from which he had just driven the male fledgling, entered the nest hole, abandoned only that morning by the young female.

The second fledgling now tried to enter the hole which until that morning had been her nursery, but she was gently yet firmly stopped by the adult male. Without contesting the parental refusal, she flew away over the clearing, neglecting to take advantage of other holes that were available to her in the nest tree.

Two evenings later, I found that both of the young woodpeckers had retired unusually early, one into the former nest cavity, the other into the lower hole where the male parent had refused admittance to the male fledgling. Meanwhile, the male parent clung quietly in the treetop, apparently unaware that his offspring had stolen a march on him. When a little later he was ready to retire, he found both of his dormitories already occupied. Going to the nest hole, he confronted a fledgling head, bill open and threatening, blocking the doorway to him. After a moment's hesitation, the parent pushed through the round aperture and vanished into the cavity. For a fraction of a minute, it looked as though parent and offspring might peaceably occupy the same lodging. But soon the young bird appeared in the top of the cavity and slowly, resistingly emerged from the quarters it had so presumptuously claimed. It flew to a neighboring tree, where I lost sight of it. The other fledgling had better

fortune and was allowed to remain in the hole of which it had taken possession, for neither parent wanted it. Thus three woodpeckers, the two parents and a fledgling, slept in as many holes in the same trunk.

In the rainy night which followed, the wind blew hard and broke off the slender trunk at the level of the nest cavity, where the adult male was sleeping after having evicted the fledgling. Very little wood had been left in the walls of the chamber, and it was chiefly the strong, fibrous bark that had supported the top of the tree. By good fortune, the male escaped injury when the nest walls snapped in twain all around him. Both he and the other two members of his family, whose lower holes had not been directly affected by the mishap, were frightened out into the rain by the noise or movement of the breaking trunk. Now the male parent again took possession of the lower hole in the evening, leaving the fledgling that had slept there without a dormitory, while the adult female went off to the forest's edge to find a lodging. A few days later, the branch that contained the latter's dormitory also broke off.

Nine days after the top of his tree fell, the adult male had completed for himself a new hole in the remaining portion of the same trunk, working on the latter when he was not feeding his fledglings. In the first evening that I saw him installed in his new lodging, both his mate and the female fledgling came to visit him, but by vigorous movements of his head, he made them understand that their company would not be welcome. The adult female then examined the hole that he had just abandoned, a yard lower in the same trunk, and finding it satisfactory, she went in tail first. Now the female fledgling came to look in at her, but the adult female was no more willing than the adult male to have a guest, and she actually sallied forth to drive the fledgling away. After this second rebuff, the female fledgling remembered an old hole that she had found a few days earlier, in a neighboring guarumo tree, and here she settled down for the night. She had inherited the female parent's habit of inserting herself tail first into a hole. The young male was now sleeping beyond my field of vision.

In 1936, the young woodpeckers vanished from the parental domain about a month after leaving the nest, when they were about two months old. The following year, the adult female was unmistakably hostile toward her offspring only 12 days after their departure from the nest. She drove the young female from the tree where the latter was accustomed to sleep, and she actually evicted the male fledgling from his lodge to occupy it herself, although she had other holes at her disposal. The male parent remained on better terms with the young birds and was more constantly with them, but these, already unfriendly toward each other, disappeared from the vicinity less than three weeks after quitting the nest. Until their departure, they lodged in the dilapidated holes in which their parents had nested and slept in the preceding year.

Only once have I known two Red-crowned Woodpeckers past the nestling stage to sleep in the same hole. After the emergence of the brood from the nest in our garden in 1953, the adult male continued to roost in it. Two days after her departure, I watched a young female go to rest at nightfall in an exposed crotch high in a neighboring tree, and she was still in the same spot at the following dawn. After she had been in the open for a week, there came an afternoon of hard rain which continued until evening. As the wet day ended, I noticed the adult male in the old nest hole and the female fledgling outside, trying to join him. Every time she came

to the doorway he gave her a peck, whereupon she flew off, circled around, and returned to the doorway, to be greeted by another peck. After a few minutes of this, she managed to push in with her parent, only to be promptly driven out into the rain. Doubtless on a fair evening she would have been discouraged by so many rebuffs, but after her prolonged drenching she was apparently thoroughly miserable and in great need of a dry lodging. Once more she forced her way into her parent's quarters, and this time—to my great surprise—she stayed until it grew dark. Next morning the parent flew out first and the young bird rested inside for a while longer.

In the evening of the same day, a young female woodpecker flew to a horizontal branch close to the nest and rested. While she delayed here, a second young female came and entered. Next the adult male arrived and pushed in tail first. Soon he came out and flew away. Then the other young female went to the doorway but meekly withdrew in the face of the opposition of the one already within. Presently the male returned, again forced his way in tail foremost, came out, entered backward once more, and finally flew off out of sight. For the next month the young female had, as far as I saw, undisputed possession of the former nest hole in the burio tree, but she did not occupy it every night. I failed to find the lodgings of the other members of her family.

After the departure of the brood from a nest on the hill behind our house in 1949, none of the family returned to sleep in the hole. This complete abandonment of the nest cavity seems unusual, but in the present instance it was fortunate, for in less than a fortnight the tree fell.

Twelve days after leaving the nest, a young female of the brood of 1953 came to the neighboring feeding shelf and without clumsiness ate several billfuls of banana. Yet the parents continued for a long time to attend her and her sister. Seventeen days after their departure, one fledgling was helping herself to banana on the board when the adult female came and fed her. I have no further records of feeding by the female, but the adult male was seen to call and feed one of the young birds 36 days after she left the nest, when she was well over two months old. While still partly dependent on their parents, these young woodpeckers tried to drive birds of other kinds from the table, and they were more aggressive than adults of their kind usually are.

The male Red-crowned Woodpecker seems as a rule to attend the young woodpeckers and remain compatible with them, longer than does the adult female. This can hardly be because the latter is engaged with a second brood, for in this species the male devotes more time than the female to nest and eggs. It has already been mentioned that in the hillside pair the female became antagonistic to the young sooner than the male. In 1947 and 1948, as in 1953, Red-crowned Woodpeckers introduced their young to the feeding shelf, and in all these years it was chiefly, or only, the male who attended them. On May 1, 1947, I first noticed that a male was carrying banana from the table, probably to a distant nest that I could not find. This continued until May 22, when a young male followed the adult to the tree that held the table and was fed while he rested well above the board. A few days later, a young female as well as a young male came with the adult male and were given banana in the same fashion. On May 29, the two males ate side by side on the table, but when the young male was offered banana by his parent, he took it eagerly, with sharp calls. On June 1, the young male came alone and ate freely of the banana. By June 10, both young woodpeckers, male and female, were visiting the table and

eating alone, but if the adult male was present, they accepted additional billfuls from him.

For several months, these two young woodpeckers and the adult male continued to visit the feeding table, although it was apparently beyond the territory of the adults. This gave me an opportunity to follow the change from the juvenal to the adult plumage. On leaving the nest, Red-crowned Woodpeckers resemble their parents rather closely except on the head and neck, which in most species of woodpeckers bear the distinctive marks of sex. The fledgling male has a red patch on his crown but the back of his head and nape are pale yellow, whereas in the adult male the whole crown and nape are bright red. The fledgling female has the top of the head light grayish drab and her nape is pale yellow, instead of red as in the adult female. This was the condition of the young male and female when they began to visit the table with their father in late May; but by early August, when they were probably about four months old, each had acquired the colors of the adults of its sex. The napes of both had changed from yellow to red. In the young male the red of the nape was only slightly paler than his crown.

SEQUENCE OF BROODS

In 1936 the hillside pair, whose young of the first brood had left the nest on March 23 and 25, were incubating a second set of eggs in a new hole in the same burío tree by April 19. By May 4, this nest was no longer attended, and I do not know what befell the eggs or nestlings it contained. On May 9, these woodpeckers were incubating in a still newer hole at the very top of the same many-chambered trunk, but by May 20 the female was roosting in this cavity and the male slept in one that he had just made, a sure sign that the former was no longer used as a nest. After these two failures, I noticed no further attempt at breeding in that year.

The following year this same pair, after bringing forth two fledglings on March 29, were by May 2 incubating in a new hole in the trunk where they had nested in 1936, about 200 feet distant from their recent successful nest. By May 11, the latest nest was no longer attended, but on May 24 these birds were again incubating in a higher hole in the same decaying tree. On May 30, I found that the top of this tree had broken off, bringing down the nesting hole, which contained one unbroken egg that was infertile and no traces of others. Thus in both years the hillside pair reared two young in their first nesting in the drier part of the year, but they failed at two later nests after the onset of the rainy season.

Second broods sometimes fare better. On March 15, 1960, a well-feathered young male was looking out of the highest nest that I have seen, and a few days later he left. On April 18, I found that the parents were again feeding nestlings in the same high hole, while a young male of the first brood rested close by it, without exciting their antagonism. By April 30, a nestling, almost ready to fly, was in the doorway of this hole which had sheltered two broods. The male parent which in May of 1947 brought two young to my feeding shelf was in late June carrying away heaping billfuls of banana. Since the young of his first brood had become independent, this food was evidently for his second brood, which I could not find.

RELATIONS WITH OTHER BIRDS

In El General, the Golden-naped Woodpecker often nests in the same clearings as the Red-crowned Woodpecker. These two species of quite different appearance

are of about the same size, yet the Golden-nape dominates the Red-crown. When these two woodpeckers began to visit the feeding shelf at the same time, the Golden-napes often drove the Red-crowns away. After a while, the latter learned to avoid the former, leaving the board if a Golden-nape arrived while it was eating there, or if a Golden-nape happened to be there first, waiting until it finished its meal before approaching the table. Thus conflicts were avoided.

For some years, a family of Golden-naped Woodpeckers has been nesting and roosting in the shade trees of a small coffee plantation near our house. One evening in August, a male was about to enter the hole into which his three companions had already retired, when a Red-crowned Woodpecker churred in a neighboring tree. The male Golden-nape immediately flew toward the Red-crown, and two other Golden-napes left the hole to do the same. After chasing away the Red-crown, all three returned to their dormitory. Despite this antagonism, the hillside pair of Red-crowned Woodpeckers nested successfully for two years in sight of a nest of Golden-naped Woodpeckers.

In 1961, a pair of Red-crowns had a nest 10 feet above that of a pair of Golden-napes in the same trunk. Once I noticed a brief flurry of excitement between the two pairs, but mostly each pair kept to its own part of the dead tree, and the Red-crowns incubated with little disturbance from their neighbors, as far as I saw. After failing to raise a family here in April, while the Golden-napes were carving their nest cavity, the Red-crowns appeared to be incubating another set of eggs in May, while the Golden-napes were feeding nestlings. The latter successfully raised a brood of three, but the Red-crowns' nest again failed. Since their nest was inaccessible to me, I do not know what befell their eggs or young, or whether the Golden-napes were in any way responsible for their loss. In any case, these two species, which most systematists regard as congeneric, are more tolerant of each other than are Red-bellied and Golden-fronted woodpeckers which, in the narrow zone where their ranges overlap, hold mutually exclusive territories and cannot enter the same tree without conflict (Selander and Giller, 1959).

Early in the morning of March 14, 1951, I was in the pasture in front of our house when a male hawk dropped to the ground a short distance from me and promptly rose with a victim in its talons. This happened so suddenly that I did not see either bird clearly. Hoping to identify them, I followed the hawk, which had flown toward the neighboring woods. As I approached a small stream at the woodland's edge, the predator flew up without its prey, and soon I came upon a young male Red-crowned Woodpecker lying in the shallow water by the bank, his spread wings conspicuous with their black and white bars, his head bent beneath him and submerged. When I picked him up, his tongue was protruding and much water, slightly blood-stained, flowed from his open mouth. Although he seemed moribund, as the water drained out he began to gasp. I could find only one wound, in the side of his breast, and it appeared to be slight. After his plumage dried in the bright morning sunshine, his breathing became regular, he began to sit up and look around, and an hour later he flew from the porch, where I had taken him for treatment, apparently not much the worse for his narrow escape from death.

I did not have a good view of the hawk, which seemed to be a small migratory accipiter, possibly a Sharp-shin. Instances of the drowning of prey by this species and the related Cooper Hawk are given by Schmid (1947) and Davis (1948).

SUMMARY

On the Pacific side of southern Costa Rica, the Red-crowned Woodpecker inhabits clearings and plantations with scattered trees, from sea level up to at least 5000 feet. It remains paired throughout the year.

In addition to insects pecked from decaying wood, it eats a variety of fruits and arillate seeds and visits feeding shelves for bananas.

Its common note is a drawled rattle or churr, *krr-r-r-r*, which is often long-continued. Both sexes beat tattoos.

Throughout the year, adults sleep singly in holes in trees. The male is more active in carving these dormitories than is the female, which often lodges in very dilapidated ones abandoned by the male. Often the female enters her dormitory tail foremost. She usually retires later in the evening and emerges from her dormitory earlier in the morning than her mate. Frequent changes of lodgings are caused by the falling of the soft trees and limbs in which sleeping holes are carved and other, less obvious, influences; in a year, a male slept in at least nine different holes and his mate in at least eight. Sometimes the male entered his hole when a hard rain fell in the daytime.

The breeding season begins in February and continues until May or June. Nests are usually high and inaccessible, from 25 to 75 feet up. Often the female lays the eggs in her mate's dormitory, which is sounder than hers, but if necessary both members of the pair work alternately at carving a new hole for nesting. Although the number of young reared in a nest has not been known to exceed two, probably the set of eggs is larger than this.

The male incubates through the night, a natural consequence of the frequent use of his dormitory for nesting. By day, the two parents alternate in incubation, and at the changeover one leaves the hole before the other enters. At one nest, the diurnal sessions of both parents averaged about one hour, with extremes of 2 and 105 minutes. These woodpeckers jointly covered their eggs for 96 per cent of the day. Both members of another pair were much more restless, rarely sitting as long as half an hour. They attended their nest only 71 per cent of a five-hour observation period.

Both parents feed the nestlings at a fairly rapid rate, bringing the food visibly in their bills. They remove waste from the nest as long as they enter the hole to deliver food but neglect sanitation after the nestlings receive their meals through the doorway. The male attends the nestlings through the night until a day or two before their departure.

At two nests, the young flew 31 and 33 days after the parents were first seen to take in food.

After the young leave, the adult male may resume sleeping in the nest hole or he may lodge in some neighboring cavity, as does his mate. Fledglings are not led by their parents to a lodging, and at first they roost clinging to a tree in the open. But from one to six days after quitting the nest, they have been observed seeking holes in the evening. If a young one tries to enter a chamber with either of the parents, it is repulsed; if it enters a parent's lodging before the latter arrives, it is driven out. Only one fledgling has been known to sleep with a parent; at the end of an afternoon of continued hard rain, a young female, in the face of strong opposition from the adult male, stubbornly forced her way into the hole from which she had flown a week earlier. For one night, the two slept together; then the adult

moved elsewhere and left this hole to his offspring. She repulsed a sibling female that tried to join her in it.

One female became antagonistic to her offspring 12 days after they left the nest, but another female fed fledglings 17 days after they began to fly. The male is, however, the chief attendant of the fledglings; he has been known to feed them 36 days after they have left the nest. One fledgling helped herself to fruit only 12 days after she left the nest.

On leaving the nest, the young male's crown is red, the young female's grayish drab, and both have pale yellow napes. When the young are four months old, the napes of both sexes have changed from yellow to red and they resemble adults of the same sex.

Two broods may be reared in a year, sometimes in the same hole, but second broods, attended after the return of the rains, seem to fail more often than first broods, reared in the dry season.

Red-crowned Woodpeckers are sometimes chased by Golden-naped Woodpeckers, yet both may nest successfully in sight of each other. A small accipiter tried to drown a fledgling Red-crown.

GOLDEN-NAPED WOODPECKER

Tripsurus chrysauchen

The Golden-naped Woodpecker is one of the many noteworthy birds endemic in the region of heavier rainfall and dense, lofty forests which in southwestern Costa Rica and extreme western Panamá interrupts the savannas, thorny scrub, and low, open woodland typical of the Pacific coast of the North American continent, except at high latitudes. It is about the size of one of the smaller species of *Centurus*, with which this and related forms are sometimes united. But in addition to the morphological characters which have been used to separate these two genera, there are important differences in their life histories which, as far as present information goes, are constantly associated with these structural differences. Hence it appears advisable to keep these two genera distinct, unless it should prove that the behavioral differences are not consistently correlated with the morphological features which distinguish them.

This handsome woodpecker is slightly under seven inches in length. In the male, the forehead is bright yellow, the crown and occiput are intense poppy red or scarlet-vermilion, and the nape is yellow. This is succeeded, posteriorly, by an area of white which extends along the back as a wide medial band (sometimes mixed with black) then broadens to cover the whole rump and upper tail-coverts. A black area covers each side of the head, neck, and back and the corresponding wing. There is an inconspicuous light spot or short streak behind each eye, and the ends of the secondaries are prominently spotted with white. The tail is brownish black. The anterior under parts are yellowish gray; the abdomen is largely scarlet; and the sides, flanks, and under tail-coverts are broadly and irregularly barred with black and whitish. The female resembles the male except that there is no red on her head, but a black band across the crown separates the yellow of her forehead from that of her nape. In both sexes, the bill is black, the eyes are brown, and the legs and feet are dark gray.

In Costa Rica, Golden-naped Woodpeckers are found from sea level up to about 5000 feet. In the Térraba Valley, they are most often met about the edges of the clearings which for years have been steadily encroaching upon the heavy forests. They are adapting themselves to life among the shade trees of coffee plantations and to other areas where man has greatly altered the character of the vegetation. In the forest itself, they remain high in the trees, where they are seldom seen. They live throughout the year in pairs or in family groups, which are often composed of four, five, or occasionally as many as seven individuals. Each group resides permanently in the vicinity of the hole in which it lodges at all seasons. The flight of this woodpecker is swift and undulatory but rarely long continued. When not persecuted, it is tame and confiding in the presence of man.

I have sometimes seen a Golden-nape sunning itself by stretching lengthwise along an exposed, more or less horizontal branch, about half an inch thick, in a sunny treetop. Its red belly was in contact with the branch, its partly expanded wings drooped down on either side, its tail was spread, and its head was turned sideways. It maintained this posture for several minutes while it absorbed the sunshine. A Golden-nape scratches its head by raising a foot outside the corresponding

wing, which is folded against the body—not over the relaxed wing, as do many passerines. In this the Golden-nape agrees with a number of North American woodpeckers (Kilham, 1959*d*).

FOOD

Like other woodpeckers, the Golden-napes are constantly chiselling into decaying trunks and branches, where they uncover beetles and larvae. They capture insects on the wing, and on wet evenings when the winged brood of termites fills the air, they may rise above the treetops and twist and loop with admirable skill as they capture one after another of the fluttering insects. Sometimes they pursue their spectacular aerial flycatching in the evening twilight, just before they retire into their hole, as I have seen Crimson-bellied Black Woodpeckers do in South America.

Golden-napes also eat a variety of fruits, ranging from the berries of melastomes, succulent bananas, and well-ripened plantains to the dry, green, pistillate spikes of the *Cecropia* tree and the hard fruits of the pejibaye (*Guilielma utilis*). Although this native American palm is extensively planted throughout the tropics for its nourishing fruits, these when uncooked are harsh and severely sting the human mouth; yet they are eagerly sought by a variety of woodpeckers, finches, tanagers, wood rails, and other birds, as well as by squirrels, which astonish one by climbing over a trunk that bristles with close-set, long, exceedingly sharp, black spines.

Equally inexplicable to us is the Golden-nape's great fondness for the bright scarlet arils that enclose the small seeds of species of *Clusia*, for to the human palate they are decidedly bitter and unpleasant. Close by our house, one of these thick-leafed epiphytic trees (*C. rosea* or a closely similar species) grows upon a calabash tree. When, at some time between April and October, the whitish, globose fruits, about 2½ inches in diameter, spread out into stars with nine to 12 rays and expose the brilliant seeds that are packed into an equal number of cells, the woodpeckers can hardly wait for their expansion to begin. They hang inverted beneath a fruit that has just begun to split at the apex, sometimes seeming to hasten the separation of the thick, leathery valves by well-placed pecks, and with sharp bill and long tongue they extract the seeds through a narrow gap, while colorful honeycreepers of three kinds flit around, waiting for the woodpeckers to leave and sometimes trying to snatch the enticing seeds from their bills. After they have eaten as many clusia seeds as they desire, the Golden-napes cling in a neighboring tree until they are hungry again, when they return to the feast, to the great annoyance of the honeycreepers which almost constantly flit among the large, glossy leaves. While the fruits of the clusia are opening, the Golden-napes and the Blue Honeycreepers come infrequently to the neighboring feeding shelf; they leave the bananas, which taste so much better to us, to the tanagers, finches, and other birds whose bills are too short and thick to reach many of the scarlet seeds.

For nearly two years, I had been placing bananas or plantains daily on a board in a guava tree close by my house, and I had enticed a variety of other birds to visit it, before the Golden-naped Woodpeckers, which dwelt at the edge of the forest 50 yards away, took advantage of my bounty. A fortnight of wet and gloomy weather, which sends birds of many kinds from the dark, dripping woodland into adjoining clearings, had made food hard to find and brought to my feeding shelf such a multitude of birds of a dozen kinds as I had never seen there before and have rarely

seen since that memorable occasion. It was on the afternoon of October 27, 1944, that I noticed for the first time one of these woodpeckers, a female, standing on the board and eating banana. A male and another female clung to the branches close by but hesitated to come to the table, at least while I was in view. Although all the other visitors gathered on the board in multihued crowds of mingled species, while the Golden-nape ate, the others, from big Buff-throated Saltators and wintering Baltimore Orioles to little Blue Honeycreepers and Tennessee Warblers, waited warily at a slight distance, probably because the woodpecker was a stranger of whose temper they were uncertain. Little by little, they lost their distrust and began to eat beside her. Despite her formidable bill, they found her gentle; she pecked, mildly enough, at a fellow diner only if it came very near. Birds do not like to be closely pressed, and most of the other visitors, down to the smallest birds, were also careful to preserve a narrow clear space around themselves.

After her first visit to the table, the female Golden-nape became a constant attendant, and gradually the other members of her family formed the habit of eating there, too. Soon two males and a female were making frequent visits. By the beginning of December, three males and two females were regular visitors. They all slept together in the same hole in the top of a tall dead tree at the edge of the forest on the ridge behind the house, scarcely a minute's flight from the feeding shelf. Sometimes they would spend much of the day clinging, all five together, to the tall, pole-like trunk of a young flame-of-the-forest tree growing close by, descending to the board from time to time as they grew hungry. They approached the bananas by flying from branch to branch of the tree that held the table. One or possibly more of the males would bow deeply, at the same time churring loudly, as he clung to the boughs on his way to the food. After standing on the board and eating freely of the banana or plantain spread there, they flew back to the flame-of-the-forest tree, to cling idly until they had digested their latest meal and were ready for more. They soon became less shy, and allowed me to approach them more closely than many of the smaller passerine birds that attended the table. Sometimes in the evening they lingered close by the board until they were ready to fly up to their dormitory on the ridge. These daily visits of the woodpeckers continued until the end of February of the following year.

In the years that have sped by since that first visit in rainy October, Golden-napes have continued to attend my feeding shelf. They have taken fruit from it to their nests and have brought their fledglings, which waited on a branch above the board while billfuls of fruit were carried up to them. After a few days the young woodpeckers stood on the board while a parent fed them, and finally they proceeded to help themselves. The frequency of the woodpeckers' attendance, like that of other kinds of visitors, fluctuates greatly with the seasons and the abundance of other foods, such as *clusia* seeds. Once when I moved the shelf to a neighboring burio tree to avoid the domestic chickens which were stealing the bananas, the woodpeckers found the new situation most convenient. After eating, they could climb up the long, ascending branch that supported the board on one side. Here they would cling among the foliage until they grew hungry, then they would climb down, tail first, for another meal, repeating this again and again.

Golden-napes are also fond of citrus fruits and sometimes peck into oranges and tangerines, whether for the juice or for insect larvae I do not know. Sometimes, while a woodpecker is so engaged, a Blue Honeycreeper waits close by, and as soon as

the larger bird leaves it goes to the hole to sip the sweet juice. In the coastal lowlands near the Golfo Dulce, I have seen Golden-napes visit the large nectar cups beneath the umbellate inflorescences of *Marcgravia*, apparently drinking the nectar but possibly catching insects attracted by it, or more probably taking advantage of both these sources of nourishment, along with Scarlet-rumped Caciques, Green Honeycreepers, Baltimore Orioles, and Blue-crowned Woodnymph Hummingbirds.

VOICE AND MECHANICAL SOUNDS

The call of the Golden-naped Woodpecker is a resonant *churr* of a peculiar, pleasant quality, and it is often uttered with a deep bow. When the woodpecker is perturbed, its *churr* becomes lower and drier. Both sexes beat a rapid tattoo, but this is used rather sparingly.

NEST BUILDING

Although in the preceding accounts of woodpeckers we treated roosting habits before breeding, in this more social species the sleeping arrangements are so closely linked with the family life that it seems best to reverse this order and consider first how the families are produced.

For some years after I came to El General, most of the holes in which I found Golden-naped Woodpeckers nesting and sleeping were situated in tall, fire-killed trees that had been left standing in new clearings close by the forest. Less often the holes of these woodpeckers were in lofty trees, apparently killed by lightning, a short distance within the forest, in areas where it was more open. But I have never seen a Golden-nape's cavity in the midst of dense, unbroken woodland; if they occur in such situations, they are probably high in tall trees where they escape detection from the ground. All of the nests on which my first account (Skutch, 1948a) of this woodpecker was based were situated in trees of the original forest, usually those which the axeman had left standing when he made a clearing to be burned and planted with maize. Since 1955, however, a family of Golden-napes has lived in a small coffee grove near our house, where the dying limbs and dead trunks of planted trees, chiefly the *Inga* that shades the coffee bushes, have provided sites for holes. This coffee plantation is about 400 feet from an extensive tract of primary forest, and I have not found Golden-napes established much farther from it. In the present chapter, I have combined my observations on this one family over a period of seven years with those made on a number of families in the decade from 1935 to 1945 and reported in the paper mentioned previously, trying by this procedure to give a comprehensive picture of the life of this delightful woodpecker.

Golden-napes prefer to nest and sleep in holes well above the ground. With the exception of the cavities in the trees on the coffee plantation, most nest holes that I have seen were from 40 to 100 or more feet above the ground. Even in the smaller *Inga* and avocado trees in the plantation, these woodpeckers tend to choose high sites, and the lowest nest that I have found anywhere was 17½ feet up. A chamber in which I discovered Golden-napes sleeping but not nesting was only 12 feet 8 inches above the ground. I have no knowledge of lower holes occupied by them.

Since Golden-napes use holes throughout the year, they may carve them at any season. They start many more than they finish and use, and sometimes they seem to excavate such holes merely to occupy their leisure. At times when a new hole is not required, the male tends to be more active in carving than is the female, al-

though both work hard to finish a chamber which they actually need. Toward the end of June, 1936, the male of the first pair which I studied began a new hole (C) about 2 feet below the cavity (B) in which he and his mate had reared three fledglings in April and May, and which was still used as a dormitory by the four surviving members of the family. From time to time, I saw him work at this new hole in a desultory fashion, in the evening before he entered the upper hole to rest. On some days, he continued to work at this task for half an hour as the light faded, yet he accomplished little. For many months, I never happened to find him engaged in enlarging the hole at other times of day. And he could not have worked very hard, for by the beginning of October, after more than three months of intermittent activity, it was still too shallow for him to enter. By mid-October, the cavity was large enough to contain a woodpecker, and one evening I saw the female inside the hole, with her head in the doorway. But apparently there was no room to spare. Despite her interest in this new cavity, she did not actually work on it—at least, not in my presence—until four months after this. Once I found the young male taking a few pecks at the excavation, but he accomplished scarcely anything. At the end of October, I found the adult male working at the new hole in the forenoon.

Still, this chamber deepened so slowly that by the middle of the following February, when the female at last began to perform her share of the labor, the birds still pecked away from the outside. Now that another nesting season was approaching, they intensified their effort, working at all hours of the day and rapidly enlarging the new cavity. By March 11, it had become deep enough for the female to sleep in it, but apparently she was cramped, for on the next evening she rejoined her mate and remaining offspring in the higher hole (B). Possibly because they were disturbed by a pair of Masked Tityras, which had taken possession of hole B, the woodpeckers abandoned hole C and rapidly carved another hole (E) much lower in the same trunk. Here they laid eggs and hatched nestlings, only to have them destroyed by some predator that enlarged the orifice of the chamber. Thereupon, the pair of woodpeckers returned to hole C, worked hard during the day to deepen it, and slept in it by night. By mid-April this hole, which had been started nearly ten months earlier, was at last completed, and the female laid eggs in it.

Even if the hole in which they have been lodging for many months is still fairly sound, the Golden-napes always seem to carve a new one for nesting. Hence February and March, when the breeding season is approaching, is the time when one is most likely to find them actively engaged in carving a chamber. At this time the two sexes share the work rather equally, taking turns which rarely continue much over half an hour. Once, in the late afternoon, a female remained for nearly an hour in the hole that she was carving, but during the last quarter-hour she rested with her head in the doorway far more than she worked. After chiselling for a while, each partner throws out the wood that it has loosened, many billfuls in succession. Once I counted 48 billfuls, but this was unusual. At first, the woodpecker reaches in from the front to collect the debris from the bottom of the cavity, but when the hole becomes so deep that only the end of the bird's tail projects through the doorway as it gathers up the loose particles, the Golden-nape changes its mode of procedure and goes entirely inside, merely sticking its head out to drop a billful. I have never seen a woodpecker carry away the material that it loosens while carving, as barbets do. If the wood is hard, it is removed in fine particles.

While one Golden-nape is at work, its mate seldom waits close by but wanders off to forage at a distance. After the toiler has tired, it may stick its head through the doorway and, with a resonant *churr*, call for the other to come and take over the task. Or the resting partner may call the worker out, and then enter for its spell of carving.

If the new hole is still unfinished as the time for laying draws near, the male may work hard at it before he has had his first food of the day. Before sunrise on April 1, I saw a male Golden-nape leave the old cavity where he slept with his mate and drop right down to resume work on their unfinished hole lower in the same tree. By the time the female left the dormitory, he had thrown out nine billfuls of wood particles. After emerging from the dormitory, the female rested a good while in a neighboring tree, then flew off, evidently to forage. On her return, she at last went to the new hole and her mate left. On an empty stomach, he had worked for about half an hour and thrown out 35 billfuls of wood particles, most of which he had apparently pecked loose in this interval. The female again flew off without working.

When we watch a woodpecker digging into a trunk to whose surface it clings, it is easy to see that it puts its whole body into the blows that it delivers. But as it works more deeply into the wood, it encounters problems which we rarely consider. How does it deliver an effective blow against the side of a narrow cavity without striking the back of its head against the opposite side? What posture does it assume to loosen the wood at the bottom of the deepening shaft? One morning I watched a Golden-nape working at a cavity still so shallow that only the foreparts of his body were inside at the farthest point of each stroke. Many of these strokes were forward thrusts of his whole body, in the direction of its long axis, and the power for them evidently came from his legs. These strokes were directed against the rear wall opposite the doorway; when the woodpecker turned his attention to the bottom of the depression, his neck appeared to take a larger share in each stroke. Beyond this stage, when the greater part of the toiling woodpecker was in the hole, I could not follow his procedure. Possibly some day an observer with Sielmann's genius for watching and photographing what happens inside a woodpecker's hole will enlighten us on this subject.

Not only do both sexes share the labor of carving a hole for nesting, they likewise do so when a new dormitory is urgently needed. Soon after the end of the nesting season, I watched a pair of Golden-napes whose hole was being rapidly filled with leaves by a Black-crowned Tityra, so reducing the free space that the family of five could no longer squeeze into it. In these circumstances, the woodpeckers worked at a new chamber even on rainy evenings, continuing to carve after the light had grown almost too dim to distinguish their colors. Sometimes an adolescent, or even a fledgling, does a little work at a hole which its parents are excavating. Often its participation is limited to a few pecks, but sometimes it continues longer.

The time required to excavate a chamber varies. The hole which a pair of Golden-napes carved when a tityra claimed their dormitory was begun a few days before June 15, 1939, on which date it was still so shallow that the woodpeckers worked from the outside of the cavity. By June 25, the cavity had become deep enough to accommodate four members of the family of five, but the fifth woodpecker, evidently finding it too crowded, preferred to sleep in a neighboring old hole made by a larger woodpecker. Two weeks is a conservative estimate of the time devoted to the excavation of this chamber. In the following year, I found on April 4 a pair

of Golden-napes working from the outside on a new hole. By April 9 they worked inside the cavity, and two days later the chamber was large enough for both birds to sleep in it. But as late as April 23, the woodpeckers still enlarged the cavity a little from time to time. On February 28, 1958, I found a pair of Golden-napes working from the outside on a cavity which had already been driven a few inches inward but had hardly been deepened downward. On March 5 they were still carving from the outside, but by March 12 they were wholly within the cavity while they worked. They began to sleep in this hole in the interval March 19-24. In this *Inga* tree with moderately hard wood, the preparation of the nest cavity had taken almost a month. In the following year, the new nest chamber in this same tree was large enough to accommodate three roosting woodpeckers after about three weeks of work. I have already mentioned a hole which was completed ten months after it was started.

The chamber which serves a family of Golden-napes for nesting and sleeping is deep and capacious. A cavity in a trunk which fell while the woodpeckers were incubating was in hard, sound, dead wood; if the trunk had been as solid at the base as it was at the top where the hole was, it would not have toppled over. This cavity extended one foot below the doorway, and its diameter over most of its length was $4\frac{3}{4}$ inches. The bottom was neatly rounded and, as usual in woodpecker nests, devoid of a soft lining. The round orifice was $1\frac{3}{4}$ inches in diameter.

THE EGGS

Exceptionally, as in 1960 when showers fell frequently in the first quarter of the year, Golden-napes may lay their eggs in the middle of March, but in El General I have found only one pair incubating before the last week of March. At one nest, four eggs were laid on successive days. The third was deposited between 6:15 and 7:20 a.m. or in the hour following sunrise. The fourth egg was laid between 7:15 and 8:20 a.m. of the following day. In a set of three eggs, also laid on consecutive days, the second egg was laid between 6:15 and 7:26 a.m., probably toward the end of this interval. The third egg was laid between 7:57 and 8:54 a.m. Of the four nests into which I have looked, two contained sets of four eggs and two held sets of three eggs. Possibly sets of four are not infrequent in high, inaccessible holes, but I have never known a pair of Golden-napes to rear more than three fledglings. The eggs are pure white, and the yolk shines through the fine, translucent shell.

From the lengths of the incubation and nestling periods and the dates of the emergence of the fledglings, I have calculated the approximate dates when eggs were laid in 20 inaccessible nests, and in three other nests this was learned by direct observation. In these 23 nests in El General, 2000 to 3500 feet above sea level, eggs were laid as follows: March, 8; April, 9; May, 3; June, 3. Two of the sets laid in June were definitely known to be second broods following successful first broods, but the third late nesting was apparently by a pair whose earlier attempts to rear young had failed. In this latest of all the nests that I have seen, incubation was still in progress on June 27, 1939.

INCUBATION

After the completion of their new chamber, both parents sleep in it, and they may do so for two or three weeks before the first egg is laid, but often this interval is shorter. In the period of laying, the woodpeckers not only sleep in the chamber but they spend considerable time in it by day. This is a wise precaution, since at

this season woodpeckers' holes are coveted by many birds which breed in cavities but cannot make them. Since hatching may be spread over two days, it appears that the earlier eggs of a set are not only guarded but are actually incubated before the last are laid.

Throughout the period of incubation, the adults continue to sleep in the nest cavity. Either may leave first in the morning, but if the female emerges first, she usually returns promptly. One morning at nest 1, the female came out before the male and climbed to the top of the dead trunk, where she remained clinging until, after 7 minutes, he flew away for his first meal of the day, whereupon she promptly entered the nest to take charge of the eggs. At another nest, the female, which flew out first in the morning, returned to the eggs after only 5 minutes.

Throughout the day, the two incubate alternately, but they are restless and sit for shorter intervals than the other woodpeckers that I have studied, with the exception of Acorn Woodpeckers at nests with four or five attendants, and one nest of the Red-crowned Woodpecker. In 38 hours of watching at five nests of the Golden-nape, the longest session that I timed continued for only 51 minutes (table 7). Despite the frequency with which they replace each other, the incubating Golden-nape often fails to wait for its partner to relieve it and goes off leaving the eggs unattended. After a brief excursion, the same bird may return to resume incubation. I have known a Golden-nape to take three sessions separated by two short recesses, before its mate came to take charge. More often, however, a single session by one partner is followed by a session of the other. If the incubating bird does not stay in the hole until its mate comes, one or the other member of the pair usually arrives after a few minutes. With the exception of the abnormal nest 11B, which we shall consider later, I have not known an interval of neglect to exceed 16 minutes, and usually it is less than 5 minutes. Thus, while incubation is in progress, there is far more activity at a Golden-napes' nest than at that of other, less volatile, woodpeckers.

Only at nest 2 were the eggs attended constantly throughout my watch, but unfortunately this nest fell after I had studied it for only 4 hours. Nest 1 was occupied for 90 per cent of 10 hours of observation, on the morning of one day and in the afternoon of another. The male took 12 sessions which totalled 232 minutes, the female took 10 sessions which totalled 255 minutes, and the nest was unattended for 11 intervals that totalled 53 minutes. I watched nest 13 from 5:15 to 11:49 a.m. on April 21, 1956, and from 11:52 a.m. to 6:05 p.m. on the following day. The female left the nest first on April 21, at 5:30 a.m. and she was the last to retire on April 22, at 6:00 p.m. Thus the active day of this pair of woodpeckers at this season

Table 7

Incubation by Golden-naped Woodpeckers

Nest no.	Hours watched	Male's sessions in minutes		Female's sessions in minutes		Intervals of neglect in minutes		Total time on eggs (per cent)
		Range	Average	Range	Average	Range	Average	
1	10	4-38	19.3	4-44	25.5	2-16	4.8	90
2	4	11-51	31.4	15-24	19.0	—	—	100
13	12.5	5-39	17.0	2-51	13.4	1-7	3.4	89
18B	6	5-32	12.0	1-40	12.6	4-14	6.9	76
11B*	6	1-30	10.4	—	—	1-32	8.5	55

* An abnormal nest.

was 12½ hours (750 minutes) in length. Disregarding parts of sessions which had begun before I started or ended my watch in the middle of the day, the male took 21 sessions which totalled 356 minutes; moreover he left 2 minutes after the female in the morning and returned 4 minutes earlier in the evening, so that in all he was in the nest for 362 minutes of the active day. The female took 22 sessions which totalled 294 minutes. The nest was unoccupied for 25 intervals which totalled 84 minutes.

Even while in the chamber, however, these woodpeckers did not incubate constantly, but again and again they climbed up to the doorway to look out, sometimes lingering for several minutes in this position. In the course of a turn in the nest which lasted 19 minutes, the female came out three times to stretch her wings and preen her feathers while she clung in front of the doorway, then returned to her eggs. Since she was constantly present and her periods outside the hole were short, for computation I counted this as a single session of 19 minutes. Likewise, I did not consider a brief spell of looking through the doorway as interrupting a session, for to have done so would have made the record too complex. These woodpeckers incubated most constantly toward the end of a brilliantly sunny morning. They were most restless, and alternated most frequently in the hole, early in the morning and in the early part of a cloudy afternoon, when rain threatened to fall. They were more active when the light was subdued than while the sun shone with full brilliance.

In my 12½ hours of watching at nest 13, a woodpecker left the hole before its relief arrived on 25 occasions, but, as is evident from table 7, in 7 minutes or less, on the average, this bird or its mate came to incubate. On 19 occasions, the woodpecker in charge of the nest stayed until its mate arrived to replace it. Whenever this occurred, the partner that had been incubating emerged through the doorway before the other went in. I did not once see the two birds stay inside together at the changeover. At nest 18B, however, the newcomer sometimes went in before the incubating partner left, a mode of changing over which scarcely ever occurs among those woodpeckers which sleep singly. Nest 18B was close to the site of nest 13, four years later, and it may well have belonged to the same two individuals, which seemed to have occupied the coffee plantation continuously throughout this interval.

At nests 1 and 2, the new arrival more frequently entered the chamber without giving its incubating mate time to emerge. Sometimes the newcomer climbed out again to make way for the other's departure, but more often they passed inside the cavity. At nest 2, soon after sunrise, the female entered the nest where her mate was incubating, stayed with him for 7 minutes, then came out leaving him sitting, as evidently he refused to relinquish the eggs to her. Later in the morning, the same thing happened again, but this time the female remained within only 2 minutes. Of the other species of woodpeckers that I have watched during the period of incubation, only in piculets have I found the members of a pair staying in the nest together by day or night.

Between the male and female Golden-naped Woodpeckers, a closer companionship exists than between mated individuals of most other woodpeckers. Not only do they sleep together in the nest and sometimes remain in it together for short intervals even while the sun is overhead, but the member of the pair which happens to be off duty spends much time near the nest, often pecking over the nest tree itself. This perhaps distracts the incubating partner, causing it to look out and perhaps to leave the eggs sooner than it might have done if it had been left alone. At times,

when the incubating woodpecker has come forth to join the other, after a few minutes they fly together to the hole and both enter. Then one stays to warm the eggs, and the other soon departs.

ABNORMAL NESTS

After I had seen, at my first nests of the Golden-naped Woodpeckers, the harmonious relations which usually exist between the members of a mated pair, I was not prepared to find, in 1945, a male that treated his partner with such hostility as I have never known in any other bird of whatever kind. In the second week of April, the Golden-napes which had been visiting my feeding shelf began to incubate in a new hole (nest 11B) just within the forest on the ridge behind our house. At first, they alternated on the eggs and slept together in the nest by night, in proper Golden-nape fashion. But before the eggs hatched a most curious, and in my whole experience with woodpeckers entirely unprecedented, domestic situation arose. The male Golden-nape alone took charge of the nest and eggs by night, while the female slept by herself in one or another of the old, dilapidated holes high above him in the top of the dead tree. This, of course, is normal behavior in other species of woodpeckers, but what follows was altogether unique. By day, whenever the female approached the nest chamber, the male sallied forth to chase her away! He was trying to carry on incubation all alone, but he would have warmed the eggs more constantly if he had not so often left the nest to drive away his erstwhile collaborator. The female apparently still desired to incubate, and once she did actually enter the hole for a few minutes in the male's absence, remaining until he returned, but in the face of repeated rebuffs, she abandoned the attempt.

After a few days, there appeared to have been a partial reconciliation between the two. The male now permitted the female to peck over the dead trunk near the nest, but although she sometimes looked in through the doorway, she no longer tried to incubate. The male successfully hatched at least one of the eggs, for by April 20 he was carrying food into the nest. The quarrel had now been so far composed that the female again entered the hole for short intervals by day, but she still slept in the old hole at the top of the tree and paid little attention to the nestlings, leaving to the male almost the whole burden of their care. I awaited their emergence from the nest, to learn how many he would be successful in rearing, but before the nestlings were many days old, some mishap befell them, and the parents no longer entered the hole.

This pair now, at the end of April, began a new hole in a neighboring dead trunk, working alternately in the usual manner. After it was large enough, the male slept in it, but the female still roosted in the very old hole at the top of the original trunk. However, this newest hole apparently never contained an egg, for about May 3 the pair returned to the hole from which the nestlings had been lost. They slept together in it, and by day each occupied it briefly, the male more than the female. But after incubation of the new set of eggs was well under way, the male again kept them warm during the day, with little or no help from his mate. Unhappily, at this point the nest was apparently again raided, for the woodpeckers abandoned this tree and I could not find where they went.

As an alternative to the view that the male Golden-nape became hostile to his mate, we might consider the possibility that he lost his mate and another female tried to attach herself to him, much against his will. But considering the low

proportion of females in the Golden-nape population, I think it unlikely that a new female should have arrived so promptly, or tried so hard to pair with an unresponsive male. And when we recall that during the second nesting, too, incubation did not proceed in the normal fashion but that the male covered the eggs with little or no help, we see that even assuming the loss of the first female, we are still faced with our original difficulty of explaining the lack of harmony in a mated pair.

While the male of this abnormal pair was incubating alone, I spent a total of about 6 hours watching the nest, timing 18 of his sessions and 17 of his absences (see table 7). He kept the eggs covered only 55 per cent of the time. During some of my watches, he devoted a considerable amount of his energy to driving the female from the vicinity of the nest, but even after he ceased active hostility and tolerated her presence, his attendance did not increase. Compared with male Golden-naped Woodpeckers incubating normally in alternation with their mates, the sessions of this peculiar male were on the average only about one third to three quarters as long, but his absences were also very much shorter (see table 7). It should be kept in mind that at this nest the male's absences were equal to the intervals of neglect, whereas at all the other nests they were equal to the intervals of neglect plus the female's sessions. This peculiar male spent a greater proportion of the day in the nest than the males of nests 1, 13, and 18B, but not as much as the male of nest 2.

The only other pair of which the male slept alone during the incubation period was that which occupied the lowest nest of all that I have seen, only 17½ feet up in a dying avocado tree. Aside from sleeping apart while they had eggs, this pair seemed normal in every way. Apparently the female did not pass the night with her mate because the nest was unusually shallow, only about 8 inches deep, and instead of being rounded at the bottom it was long and narrow. It had been carved rather hastily in wood that seemed too hard for the woodpeckers. While the male attended the eggs through the night, the female occupied a hole higher in the same tree, where the two had roosted together before incubation began. In the morning, the female would emerge first and, without going to forage, replace the male on the eggs, to stay until he returned from foraging. Once in the evening the female joined her mate in the nest, but after staying for about ten minutes she came out and climbed up to the higher hole to sleep alone. Evidently they had found the cavity too small for both to sleep there comfortably.

Soon after the nestlings hatched, they vanished from this shallow hole. Again the pair slept together in an older hole until they had carved a new one in the same tree. When this hole was large enough, the male slept alone in it, continuing to do so after the new set of eggs had been laid. One evening after incubation began, the female tried to join her mate in the nest but was repulsed with pecks. Without resisting, she climbed up the trunk and entered the hole where she had slept during the first nesting. This was the only breach of perfect amity that I witnessed in this pair.

Years earlier, I had found a pair of Black-cheeked Woodpeckers sleeping apart during the incubation period, apparently because the cavity in which the male attended the eggs during the night was too small for both adults. The fact that, when the pair do not sleep together in the nest, it is the male which stays with the eggs through the night, suggests that when both occupy the nest, as they normally do, the male actually incubates the eggs while his mate roosts beside him.

Length of incubation.—At one nest the fourth and last egg was laid between 7:15

and 8:20 a.m. on April 3. At 3:30 p.m. on April 13 there was one nestling; at 7:00 a.m. on April 14 there were two; at 5:30 p.m. on the same day there were three. One egg failed to hatch. Unfortunately, I could not reach and mark these eggs as they were laid, and I do not know whether this unhatched egg was the last or an earlier one. Either the third or fourth egg did hatch. If the fourth egg hatched, the incubation period was between 11 days and 11 days and 10 hours; if the third egg hatched, this period was between 12 days and 12 days and 11 hours. We have assumed here that the eggs hatched in the order in which they were laid, as I have nearly always found to be true in sets marked in open nests.

At a later nest, the last egg of a set of 3 was laid between 7:57 and 8:54 a.m. on April 12. At 1:00 p.m. on April 23, the first nestling was just pushing off the cap of its shell. A second nestling hatched during the following night, and the third between 6:00 and 7:05 a.m. on April 24, after an incubation period of 11 days and 22 hours \pm 1 hour.

THE NESTLINGS

Development.—Newly hatched Golden-napes have pink skin with no trace of down. Their eyes are represented by dark protuberances on the sides of the head. Each nestling has a prominent white eggtooth on the end of its upper mandible. Whether there is a smaller shield at the tip of the lower mandible, as in certain other woodpeckers, I could not tell by examining the young with a mirror. The young seem to lie much of the time with their heads inward and their thin necks crossing, much as I have seen in very young toucanets. When I visited their nest soon after they hatched, they sometimes stretched up their necks all together, uttering a sharp, buzzy squeak, or a loud, sizzling sound, while they held their pink mouths open for food.

When the nestlings are six days old, feather rudiments are visible as dark spots on the wings and shoulders, while those of the rectrices already project slightly from the skin. The white projections at the basal corners of the lower mandible are becoming prominent, and the eggtooth at the tip of the upper mandible is disappearing. At nine days, the pinfeathers are pushing out on the back and wings; the eyelids can be opened slightly but seem to be kept closed most of the time. At 12 days, the eyes can be opened to almost full extent; the upper mandible has caught up with the lower in length; and the white projections at the corners of the mouth are very prominent. The bare skin is still pinkish or flesh color.

When the nestlings are 15 days old, the feathers on the back and wings are just beginning to protrude from the tips of their sheaths, but the pinfeathers on the head are still inconspicuous. The nestlings now have wide-open eyes and they can cling upright to the vertical wall of their chamber. At 18 days, they sometimes take their food while the parent clings outside the nest hole and passes it through the doorway, but the parents still often enter the cavity to feed the nestlings. At 19 days, the most advanced nestlings are fairly well covered with feathers on the dorsal surface, including the crown, so that the sexes may be distinguished, but the face is still nearly naked. At 21 days, the white knobs at the corners of the mouth are disappearing. At 26 days, the more retarded young woodpeckers are clad in plumage. At four weeks of age, or a little less, the nestlings' heads are first seen in the doorway. The white projections at the base of the bill are now no longer evident, but since the nestlings actively grasp their food, these guide marks are no longer

needed to help their parents feed them. The young do not leave the nest until they are 33 to 36 days of age.

Brooding.—While the nestlings are very young, the parents brood them with about the same constancy as they incubated the eggs. On June 25, a day or two after the nestlings hatched in inaccessible nest 18B, I watched from 7:01 to 11:07 a.m. In this interval, the male brooded for 12 periods, ranging from 1 to 26 minutes and averaging 9.9 minutes. The female brooded for ten periods, ranging from 2 to 22 minutes and averaging 10.3 minutes. The ten intervals when both parents were absent ranged from 1 to 5 minutes and averaged 2.4 minutes. These nestlings were brooded for 90.2 per cent of the 5 hours, and when a parent was not in the nest, one was often clinging close by it.

Six days later, these same nestlings, now about a week old, were brooded less constantly. From 7:01 to 11:04 a.m. on July 1, the male was in the hole for 11 periods, ranging from 2 to 13 minutes and averaging 6.5 minutes. The female brooded for nine periods, ranging from 2 to 25 minutes and averaging 11.3 minutes. The nestlings were alone for seven intervals, ranging from 2 to 24 minutes and averaging 9.8 minutes. They were brooded 71.6 per cent of the 5 hours.

By July 9, when these nestlings were about 15 days old, diurnal brooding had practically ceased. From 7:04 to 11:04 a.m. on this day, the male remained in the nest for appreciable periods only three times, for 5, 20, and then 6 minutes. During much of his last spell in the nest, he looked through the doorway instead of staying down in contact with the nestlings. The female remained in the nest only once, for 5 minutes. Accordingly, the nestlings were accompanied by a parent for a total of only 36 minutes and were brooded somewhat less than this.

Both parents sleep with the nestlings as long as the young birds remain in the nest, but probably they do not brood them by night after they are well feathered.

Feeding.—When the nestlings hatch, the parents at first bring them particles so small that they are difficult to detect in the adults' bills. The portions brought to the nest soon grow larger, leaving no doubt that the young are nourished with food carried in the bill and mouth rather than by regurgitation. The nestlings are given substantial amounts of both animal and vegetable foods, but the latter forms the bulk of their nourishment after they are older. The parents are skillful foragers and often return to the nest with the first installment of their nestlings' breakfast 2 or 3 minutes after they first leave it in the early morning. At this time, the rate of bringing food is often surprisingly rapid. Parents with three young about 33 days old brought them 28 meals in the first half-hour of feeding. This was unusual activity, but older nestlings are often fed ten or more times in the first half-hour after their parents leave the nest. In this interval, the parents seem to choose the most readily available food, such as fragments of pejibaye fruits from neighboring palms, pieces of the green fruiting spikes of *Cecropia*, banana from a neighboring feeding shelf, or shining, little, blackish berries of *Miconia* lined up in a row in their bills. After they have taken the edge off their nestlings' hunger, they turn to the more time-consuming quest of insects, and the rate of feeding falls.

Table 8 gives some rates of feeding at nests with young of various ages. The frequency of feeding rises rapidly at first and then increases more slowly during the second half of the nestling period. The number of meals brought in a single hour is often much greater than this table suggests. When the three young in nest 17 were about 33 days old, they were fed 33 times in the first hour of the morning.

Table 8
Feeding of Nestling Golden-naped Woodpeckers

Nest no.	Number of young	Age in days ¹	Hour (a.m.)	Feedings			Rate per nestling per hour
				Male	Female	Total	
18B	2?	1	7:00-11:00	8	7	15 ²	
18B	2?	7	7:01-11:01	13	9	22	
18B	2?	15	7:04-11:04	26	13	39	
18B	2	28	7:05-11:05	32	14	46	5.8
18B	2	29	7:00-11:00	24	18	42	5.3
18B ³	2	34	7:00-11:00	32	27	59	7.4
18B ³	2	34	5:48- 7:00	14	6	20	16.7
13	2	31	5:42- 9:42	30	27	57	7.1
17	3	32	5:56- 9:56	28	50	78	6.5
17	3	33	5:52- 7:52	20	24	44	7.3
Totals			35.2 hours	227	195	422	

¹ Approximate.

² This is a minimum; possibly at times a parent brought a meal too small to be seen in its bill.

³ Together, these two lines give a continuous record from 5:48 to 11:00 a.m. From 9:34 to 10:59 a fledgling was out of the nest but in view of the observer. At 10:59 she re-entered.

When the two nestlings in nest 18B were about 34 days old, they received 26 meals between 8:00 and 9:00 a.m. At nest 13, two nestlings about 31 days old were fed 19 times between 6:42 and 7:42 a.m. The slowest feeding that I have recorded for feathered nestlings is seven times an hour for two individuals and 11 times an hour for three.

When the adults find an opening clusia pod, they may carry billful after billful of the highly prized seeds to the nest in rapid succession. One day I saw both parents bring this enticing food 19 times in 27 minutes, and another time they brought 12 billfuls in 13 minutes, which seems to be about as rapidly as they could extract the seeds from the pods and deliver them. I have seen the parents so stuff their young with clusia seeds that they refused to take more, with the result that the parent which brought the food ate it. As a female flies toward the nest with her bill overflowing with these red seeds, it is easy to mistake her for the red-crowned male. When both parents cling in front of the nest together, each with a billful of this brilliant food, they make a most colorful sight.

Sometimes a parent brings an insect too large for the nestlings to swallow. When this occurs, the adult carries the insect to a small hole in a branch and pecks at it until it is reduced to a convenient size, much as I have seen Acorn Woodpeckers prepare food for their young. One large insect was presented three times to the nestlings, with treatment in a niche in the intervals, before it was finally devoured. The male nearly always brings food more often than the female, sometimes more than twice as frequently; the only observation periods in which the female brought more meals than her mate were the two at nest 17 (table 8). But the female brought the nestlings chiefly fruit, which is easily gathered, whereas the male delivered a larger proportion of insects, which are harder to find. From this I judged that the male was working about as hard for his family as the female was. Some of these insects were of kinds which seemed to have been plucked from foliage or bark rather than extracted from wood.

As I saw when I looked into the nest with a mirror, very young nestlings raise their open mouths for food, much in the manner of passerine nestlings. Doubtless,

the prominent white projections at the corners of the gape direct the parents to the mouths of the young birds in the dimly lighted chamber. When, from the age of about four weeks onward, the nestlings spend much time awaiting their meals in the doorway, the white knobs have become inconspicuous, and the young woodpeckers take their food in a very different manner. As a parent alights before the doorway, the nestling, which perhaps has been thrusting its head far out to look around for the approach of a meal, draws back into the doorway or sometimes withdraws to the inside of the cavity. This helps the parent to deliver the food, for otherwise the adult bird would have to lean far backward in an uncomfortable position. The parent inclines its head sideward, so that one eye is directed upward and the other downward. With a forward thrust of its open mouth, the nestling seizes the food and easily pulls it out of the parent's bill, the commissure of which is turned almost at right angles to that of its own bill. After receiving its meal, the nestling, if very hungry, may continue to thrust its head forward as it closes its bill, giving the impression that it is viciously trying to bite its parent. Indeed, if the adult is not careful, the young bird may pull a feather from its breast. To avoid this, the parent usually leaves as soon as the nestling has extracted the last particle from its bill. Sometimes the young woodpecker sticks its slender white tongue far out toward its departing parent.

When a nestling woodpecker of any species gains possession of the doorway of its chamber, it often seems to stay there for a long while, intercepting all the food that its parents bring and depriving its nest mates of their share. My lowest nest held one female and two males, which I could distinguish by the different amounts of yellow on their foreheads. This provided an opportunity to learn how far the attempt to monopolize the food supply could be carried. On one occasion, the light-fronted young male received seven meals in uninterrupted succession, and the dark-fronted male and the female each received an unbroken series of four meals. Otherwise, as far as I saw in 6 hours of watching, a nestling received only three or fewer consecutive meals. Since 122 meals were delivered to them in these 6 hours, it is evident that none of these young woodpeckers had succeeded in establishing a monopoly. The nestlings replaced each other in the coveted position in the doorway far more frequently than it appears when one watches a hole whose occupants cannot be distinguished individually.

Sanitation.—At both of the nests which I examined frequently with a mirror, the parents left the empty shells in the chamber for two or more days, but finally they removed the shells and also an unhatched egg. Thus their procedure differs from that of passerines, which promptly remove empty shells but may permit an unhatched egg to remain in the nest for a number of days, or even until the nestlings leave.

As long as the nest chamber is occupied, the parent Golden-napes continue to remove waste from it. Their method of cleaning the nest is quite different from that of passerines, which as a rule carry off or swallow one fecal sac after feeding the nestlings. The Golden-napes often allow the nestlings' droppings to accumulate in the hole and then remove them in a spell of concentrated house-cleaning. Once I saw a female take food into the nest, then emerge with a billful of excreta which she carried to the top of a neighboring tree, where with vigorous sideward shakes of her head she threw away the waste matter. Then she promptly returned to the nest and removed another billful, which she disposed of in the same manner. She cor-

tinued this until she had carried out nine heaping mouthfuls of refuse, when I judged that the chamber was clean.

At this nest, both parents attended to sanitation. But at four nests of the pair of Golden-napes in the coffee plantation, I have seen only the male remove waste. Sometimes he made special trips to carry out a number of billfuls in succession, but at other times he removed the excreta more gradually, carrying out a billful after taking in a meal. This refuse was sometimes thrown from the doorway, but far more often it was carried to a somewhat distant tree before it was dropped.

Defense.—In 1957, 1959, and 1962, I often climbed a long ladder to examine the nest in the coffee plantation by means of a light and mirror. Whenever I made these visits, the male, if in sight, would look on from a very safe distance, or else he would fly away as though indifferent to what was happening to his offspring. The female, on the contrary, would become greatly excited. She would cling, protesting, only a short way above my reach, and she often darted past my head. From the time her eggs were laid until the nestlings grew so large that I discontinued my visits so as not to drive them prematurely from the chamber, she repeatedly struck the top or back of my head, my shoulder, or my arm, but too lightly to hurt me. She never touched me while my eyes were turned toward her, but only when I looked another way. Hence I could not see just how she touched me, but often she seemed to brush me with a wing. She attacked me in this ineffectual fashion even when I looked into the nest soon after the last young had flown.

In 1960, the nests of this pair were too high to be reached. But while the first of them held nestlings, I climbed as close to it as I could, to see how the parents would respond. Both were then in sight. The male soon flew off, but the female climbed and flew above my head, protesting with *churr*'s. She did not, as in earlier years, strike me or even dart at me, but this was evidently because I was still about 6 feet below her nest. Probably, as I had found earlier with the Golden-fronted Woodpecker, the demonstrativeness of the parents when their nest is disturbed varies from individual to individual, so that in some pairs the male, in others the female, makes the greater display. The fact that the female of the pair which has nested for seven years in the coffee plantation has always more spiritedly protested my intrusion, whereas the male has consistently taken charge of sanitation, strengthens my belief that this pair has been throughout this period composed of the same individuals. In the species as a whole, the removal of excreta is, as we have seen, not confined to one sex.

When a squirrel climbed toward a nest of this pair, a parent darted at it until it left the tree. This happened several times, and sometimes the male put the squirrel to flight. Once, while the parents were absent, a squirrel went to the doorway, then ran rapidly down the trunk as though frightened. When it returned to the doorway a little later, it behaved in similar fashion. Perhaps the nestlings made a noise which alarmed the rodent.

Although, in defense of their young, Golden-napes drive away squirrels and sometimes even strike a man, when birds of other kinds molest their nests they show less spirit. When a Fiery-billed Araçari removed an egg from a hole that was evidently shallower than most, the woodpeckers flew around with excited cries but did not attack the toucan. In the accounts of the Masked and Black-crowned tityras, I told how these birds fill chambers still used by the Golden-napes with leaves and other materials, without opposition from the woodpeckers. The latter do nothing

more violent than throw out some of the leaves, and soon growing tired even of this, proceed to carve a new hole nearby, relinquishing the old one to the tityras. But I have not known tityras to claim a woodpeckers' chamber while it held eggs or nestlings.

Leaving the nest.—From the age of about four weeks, the young woodpeckers, now well feathered, spend much of the day looking, one at a time, through their high doorway. About a week after they first view the outside world, they venture forth into it. Their earliest excursions beyond the nest may be short. At nest 1, I first saw a young woodpecker outside the nest hole at 10:00 a.m. on May 10. It was clinging to the trunk near the doorway, and another nestling was looking out of the opening. After a while, the fledgling grew tired of clinging in the open and climbed back into the nest.

While I watched nest 18B on July 27, 1960, the young woodpecker in the doorway would from time to time stretch far outward and move its foreparts rapidly up and down, in a sort of deep bow. It also looked around much, and sometimes it appeared to pluck something from the bark beside or above the orifice. Several times it seemed on the point of leaving, but always in the end it drew back into the safety of its chamber. But on the following morning, at 9:34 a.m., the young female suddenly climbed out and clung beside the doorway. She tried to re-enter, but her brother blocked the way. Then she began to climb restlessly over the branches of the nest tree, pecking much, and taking short flights from limb to limb. Twenty-five minutes after her emergence, she had reached the dead top of the tree, well above the nest, where she rested a while close to the male parent. Soon she began to work downward again. Presently she entered an old hole with a wide opening, 4 or 5 feet below the nest.

After resting for 11 minutes in this cranny, the fledgling emerged and resumed her exploration of the many-branched nest tree. At 10:59, while the adult female clung in front of the doorway, the young female came to the nest, which she entered as soon as her parent moved aside, an hour and 25 minutes after leaving it. I believe that this was the female fledgling's first excursion beyond the chamber in which she was hatched. As far as I could see, her parents did nothing to bring her out or to lead her back into the hole. They appeared not to care whether she was outside or inside the cavity. After her departure, the first four meals which the parents brought went to the young male, which remained in the chamber, looking forth much of the time. The fifth meal was taken to the young female in the treetop. While the fledgling female was outside the nest hole, I saw her receive food only twice, whereas the young male in the nest was given 14 meals.

I do not know whether the young female made another excursion from her nest on the afternoon of this same day, but she was in the nest cavity when the older members of her family entered for the night. Next morning, the adults left the chamber between 5:48 and 5:53 a.m., but the young birds stayed inside while the parents fed them. Both fledglings at times rested in the doorway and stretched their necks far out. At 7:28, the female fledgling spontaneously flew out of the nest hole. Failing to alight on a branch of the nest tree in front of her, she continued on to a neighboring tree, where I soon lost sight of her. But after an hour and 20 minutes in the open, she followed the male parent as he flew to the nest with food. The young male inside refused the food, whereupon the young female entered the nest hole and received the meal. She remained in the nest or its doorway for the next 72 minutes.

At 10:00 she flew out and stayed until 10:35, when she flew directly to the doorway and entered in the absence of the parents. This time she stayed in only 21 minutes, leaving at 10:56. I then left but when I returned at 12:25 p.m. the young female was again in the nest. In the course of the forenoon, she had left and returned to the chamber three times. On the following morning, the second after her initial venture beyond the nest, she left along with the adult birds before sunrise and she apparently stayed out of the nest until it began to rain in the afternoon.

The behavior of the male nestling of this brood was quite different. Through the morning of July 29, when the restless fledgling female was going in and out, he remained in the nest or its doorway. Several times he tried to climb out on the trunk beside the nest hole, but each time he lost courage. On the following morning, he finally left the nest between 6:30 and 7:18 a.m., when I found him in a neighboring mango tree. He failed to return to the nest when it rained that afternoon, and he stayed out through the following night, which is most unusual for a Golden-nape. On the next night, however, he slept in the chamber with the rest of his family.

Nestling period.—From one accessible nest, a single nestling left when 34 days old; from another, three young left at the age of 33 and 34 days. From six inaccessible nests, 15 young left from 34 to 37 days after I first noticed the parents taking in food. The nestling period is, then, from 33 to 37 days.

In the Golden-naped Woodpecker, the nestling period is three times as long as the incubation period. Aside from woodpeckers, in no other bird treated in these Life Histories is there such great disparity between the lengths of these two developmental stages, and in a number of antbirds, ovenbirds, and manakins, the nestling period is shorter than the incubation period. In birds whose nests are highly vulnerable, both of these periods tend to be short, whereas in those whose nests are fairly safe, they tend to be long. We see this clearly in the American flycatchers; those species that build pensile nests that are difficult for predators to reach (for example, the Royal Flycatcher) have long incubation and nestling periods. That woodpeckers' holes are in general fairly immune from predation is attested by their prolonged occupancy by the nestlings, which remain in these secure chambers for many days after they are well feathered and can presumably fly. Why, then, is the incubation period of woodpeckers so short?

I believe that the explanation is to be found in the conditions in which the nestlings are reared. Woodpeckers have large broods, and perhaps in consequence of the difficulty of distributing the food equally in the dimly lighted chamber, the younger nestlings often succumb from malnutrition. Hence the nestling that is hatched first has considerable advantage over the succeeding nestlings. Although the order in which the eggs are laid seems to be primarily responsible for determining the order in which they hatch, the disparity arising from this cause might be either increased or diminished by diverse speeds of embryonic development. Selection for increased rate of development has, I believe, kept the incubation period of these nonpasserine hole-nesters as short as that of many small passerines with open nests—shorter, indeed, than that of a considerable proportion of them.

BEHAVIOR OF PARENTS WHICH LOST NESTLINGS

A few days after the eggs hatched in the lowest nest of the Golden-napes that I have seen, the nestlings mysteriously vanished. The parents promptly started to carve a new hole in the same trunk, only 3 feet from the empty nest. Abandoning

this undertaking, they carved a higher hole, where by May 21, somewhat over three weeks after their loss, they were again incubating. They hatched three eggs in early June, but within ten days they again lost their brood. Nevertheless, the adults continued to behave, in certain ways, as though they still had nestlings. One of them would come with a billful of food, enter the nest, look through the doorway still holding the billful, go down inside once more, and finally come up where it could be seen to swallow what it held. Sometimes the parent would go down into the hole three times in succession before it ate the food that it had brought. This strange behavior continued for at least six days after the loss of the nestlings. On the sixth morning, I spent 2¾ hours watching the nest. In this interval, the male brought food three times, the female twice. The male spent periods of 2, 5, 8, and 6 minutes, a total of 21 minutes, in the hole, and he entered several other times but did not stay. Once he emerged with a billful of whitish wood particles that he had evidently loosened while inside, and he carried them out of sight, as though cleaning a nest with young, for during nest construction the particles are dropped from the doorway. Both parents spent much time pecking idly over the tree that contained the empty nest. It was already late in June, and after hatching two sets of eggs and losing both broods, this pair did not attempt to breed again that year.

SEX RATIO

In the Golden-naped Woodpecker, it is easier to learn the number of young of each sex that come successfully through the nestling period than in the case of most birds. Young males are easily distinguished from young females by their red crowns, and the fledglings can be counted as they return to the nest in the evening or leave it in the morning. In 12 nests that I have had under observation, 29 young were fledged, of which 18 were males and 11 females. Six of these nests belonged to the pair which for seven years has lived in our coffee plantation, and in these nests five males and eight females were reared. The other six nests, situated in various parts of El General, produced 13 males and only three females. Although Golden-napes sometimes lay four eggs, I have not known them to rear more than three young in a nest. The average size of the 12 broods was 2.4.

THE FLEDGLINGS

Appearance.—When they leave the nest, the young Golden-napes rather closely resemble the parent of the same sex. The most obvious difference between adults and fledglings is in the markings of the head. Many young males have a more or less broad dusky band across the forehead, and there is little yellow between this and the red of the crown. On some, however, the forehead is largely yellowish, but on none that I have seen is the yellow of the forehead as broad and bright as on the adult male. One male fledgling had a narrow black band across his crown, behind his prominent red crown patch, and since there was scarcely any yellow on his forehead, this bright patch was margined almost all around with black. Females recently emerged from the nest are most readily distinguished from the female parent by the narrower and slightly duller band of yellow on the forehead. But as the weeks pass, the young woodpeckers become increasingly difficult to distinguish from their parents; three months after they begin to fly, it is hardly possible to tell which are old and which are young.

The return to the nest for sleeping.—After they begin to fly among the trees,

young Golden-napes, with rare exceptions, return each evening to sleep with their parents in the nest cavity. As we have learned, some fledglings may enter and leave the chamber a number of times before they go beyond sight of it, whereas others when they first emerge fly farther off and remain away longer. These differences in the experience of the young woodpeckers, in conjunction with variations in the site of the nest and the vagaries of the weather, cause great differences in the time and manner of the fledglings' return in the evening after their first excursions through the surrounding trees with their parents. They stay out longer on clear than on rainy afternoons, and they require more guidance when their nest is in a tall, branchless, isolated trunk than when it is in a many-branched tree which facilitates their approach. On the whole, Golden-naped Woodpeckers just out of the nest regain their high doorway with far less adult guidance than is required by fledgling wrens, which forsake the nest at a far earlier age.

On the evening of June 17, 1940, I watched three male fledglings return to nest 7, which that same morning I had found unoccupied for the first time since the young had hatched. This nest was situated about 100 feet up in a tall, barkless tree at the forest's edge. At about 4:50 p.m., the parents and their young came out of the woodland and alighted near the top of the towering trunk. After a few minutes, the adult male flew down and clung beside the doorway of the nest, while the adult female went inside. Thereupon, two of the fledglings flew down and entered the hole without much difficulty, although they were still slightly shaky in their movements. After the young were safely within, the female came out again and flew up to cling to the stub of a branch at the very top of the tree. The male rested on another stub, and the third fledgling stayed with the parents in the open.

After a while, one of the young woodpeckers which had been in the hole came out. The female at once noticed his departure and immediately flew down to enter the nest. The newly departed fledgling promptly followed her inside once more. Her move suggested to the third fledgling that it was time to go to rest. He made his way by short flights down the trunk, clinging to the upright surface to rest between drops, and entered at once. The adult female then emerged and continued to repose in the open. She retired for the night at 5:49 p.m., 45 minutes after the first two young woodpeckers had entered the hole. The adult male joined his family in the chamber four minutes later.

Apparently, the parents did not call their offspring to the nest. At least, they uttered no call loud enough to reach me where I stood on the opposite ridge, about 200 feet away. The young woodpeckers have a strong tendency to follow and imitate their parents; when the adults go into the nest, the young follow without being urged. This was shown clearly when the fledgling which had just come out of the hole promptly followed the female parent inside once more, and her move was the signal for the entry of the third fledgling.

The tendency of the young woodpeckers to follow their parents, and of these to show their fledglings the doorway to the nest, was also evident at nest 17, a low hole in a dead limb of a spreading *Inga* tree. On May 18, 1959, at 4:45 p.m., after the afternoon shower had stopped, I found all five members of the family clinging to the branches of the nest tree. This family group included two young males which had flown out of the nest on the preceding day and a young female which had, I believe, emerged for the first time on the morning of this day. From time to time, a parent flew off and brought a morsel to a fledgling. At 5:17, the adult male

dropped down to cling in front of the nest chamber, whereupon the light-fronted young male came down and entered. The male parent did not go in. A minute later a drizzle began, but it soon stopped. At 5:43, the adult male again went to the doorway, silently as before. Immediately, the young female flew down and clung to the trunk a few feet above the nest, from which point she somewhat tediously hitched down, tail foremost, to the doorway and entered. At 5:47, the adult male once more went to the nest, again without calling, and at about the same time the dark-fronted young male flew down and climbed over the trunk near the entrance, pursuing his parent for food. Meanwhile, the adult female passed food to the young female through the doorway. Then the adult male entered the hole and the dark-fronted fledgling followed him in. The adult promptly came out. At 5:50 I departed, leaving three young in the chamber and the parents in the branches of the nest tree. Perhaps, each time that the male parent flew down to show a fledgling the doorway, he noticed signs that it wished to return, but if so, these signs were not evident to me, for I could not keep such close watch on all the woodpeckers.

Very different was the course of events on the evening of the day when the single fledgling emerged from nest 14 in the coffee plantation. Of the three nestlings that hatched in this nest, two died, probably because of an invasion by small black ants, and only one female was fledged. At 5:50 p.m., I found her looking out of the much higher hole where her parents had nested in the preceding year. Its doorway had been greatly enlarged, and a Masked Tityra had been building a nest in it. The parents of this fledgling found it difficult to settle down for the night. The male went into the hole from which the fledgling had emerged earlier in the day, but he did not remain. Presently each parent entered a different hole in a dying avocado tree nearby. The fledgling now left the high cavity and followed them to this tree, quite spontaneously, it seemed. On her arrival, the male promptly left his hole, as though to avoid the young bird. Instead of entering the cavity which he had vacated, the fledgling clung for some minutes below that from which the adult female looked out, then as the light was growing dim the young bird entered the latter cavity with neither invitation nor opposition from the parent bird. The female thereupon pushed past the fledgling and left the hole. Soon, however, she re-entered it and rested for many minutes with her head framed in the doorway. At last, in the dusk, she descended below the orifice. Thus the adult female and the fledgling slept together in what appeared to be a very old and possibly shallow chamber, while the adult male roosted at a distance, I knew not where. This family was unsettled, probably because it lacked an adequate dormitory, and for some days after this episode I could not find where its three members slept.

At nest 1, the fledglings, after their first days afield, returned to their nest earlier than I have found with other families. They sometimes retired soon after 3:00 p.m., even if no rain fell, as it often did on those afternoons in May. But they had no fixed hour for entering the chamber, and one of the three young males would at times stay out long after the other fledglings had gone to rest. If there was no shower, their homecoming seemed to depend on how soon they grew tired of clambering over the trees. Late in the afternoon of his second day out of the nest, one of the young Golden-napes, which had retired earlier, was frightened from the chamber by a visit from a pair of Fiery-billed Araçaris. He flew to a neighboring trunk, while his excited parents darted back and forth above the nest. After the intruders had departed and the turmoil had died away, the adult male entered the

hole, where the other young woodpeckers had remained through all the hubbub, and turning around to look out, he uttered a peculiar churring call, quite distinct from anything that I had ever heard from him or his mate. This brought the young fugitive home in an instant. But ten days later, when the parents entered the hole at 4:00 p.m. and called their fledglings to come to rest, the young birds, whose voices I heard coming from the neighboring forest, ignored the summons. These parents were ever watchful and attentive to their young. Sometimes one of the young birds, going alone to the doorway, would hesitate to enter, pushing his head in only to withdraw it again, repeating this over and over, afraid to go in alone, or else displaying a surprising degree of caution. If a parent was nearby when this occurred, it would hurry to the hole and enter, whereupon the young woodpecker would promptly follow.

After their early return to the nest, the fledgling woodpeckers were fed inside the hole, exactly as though they were helpless nestlings which had never flown. After delivering food through the doorway, the parent needed to be quick in getting out of the way of the bill that received it, for the young bird would often peck or bite at its elder. Once the adult male was not sufficiently alert, and the fledgling he had just fed plucked a downy feather from his breast. It stuck to the young woodpecker's bill, and cost him considerable shaking of his head and rubbing of his bill against the sides of the doorway, before he could rid himself of the light encumbrance. If the fledglings were very hungry, they would peep loudly in a high-pitched voice whenever food was brought to them. This feeding of the fledglings after their return to the nest does not occur in all families of this species. Some young birds from the first go to rest later, and they receive no more food after retiring. All seem to be slow to outgrow their nestling habits, and the adults must continue to clean out the hole for a number of days after the young have fledged.

When the light began to grow dim, the parents would join the fledglings in the hole for the night; the adult male usually entered first. Often the parents' entry was greeted by a chorus of high-pitched cries. Sometimes the parents of older nestlings, or of fledglings, remain outside, clinging to the trunk near the doorway, until an hour unusually late for woodpeckers, as though wishing to escape the young birds' importunings for yet more food. I have even known a female Golden-nape with three young fledglings to go to rest in a separate hole in the same trunk, apparently to enjoy a more tranquil night.

The morning departure from the nest.—For a view of the fledglings' departure from the nest which they have re-entered to roost, let us turn again to nest 7, where the young retired on the evening of June 17, 1940. On June 18, the adult female began to look through the doorway at 5:25 a.m., and 6 minutes later she came out and clung to the top of the dead tree. At 5:36, her mate left the hole. Soon after he emerged, both parents flew off into the neighboring forest. At 5:51, the adult male brought food to a fledgling which was looking through the doorway. A minute later, a young woodpecker came out and promptly flew off to the forest in search of his parents. Soon afterward, a second fledgling came through the doorway, but apparently afraid of falling, he clung to the trunk beside the entrance and soon returned to the safety of the interior. He and the remaining fledgling lingered a long while in the hole, looking forth as though trying to gather courage to fly out, but in the end both drew back inside. Finally, at 6:20, one of the fledglings flew

forth to search for his parents. Two minutes later, the third and last followed. Doubtless growing hunger prompted them to quit the sheltering chamber.

Some fledglings receive a number of meals before they follow their parents into the open. At daybreak on June 10, 1956, I watched nest 13, from which one male and one female fledgling had first emerged two and three days earlier. At 5:48 on this dark and drizzly morning, the adult male left the hole, and 5 minutes later his mate followed. Soon each returned with food for the fledglings. Before these ventured forth, at 6:09 and 6:20, the adult male and female had brought five and two meals to the nest, respectively. In a later year, these woodpeckers fed three young females, which had fledged on the preceding day, 12 times in the 20 minutes that they lingered in the dormitory after their parents' departure. Other fledglings, however, are not given food before they leave the hole in the morning, even in the first days after they begin to fly, but they may be fed after their return to the nest in the evening.

The delay of the fledglings in the nest after the parents have departed in the morning rapidly decreases; a week after they have begun to fly, the young rarely remain in the nest as much as a quarter of an hour after their parents' departure. Often the whole family sallies forth within 5 or 10 minutes. A laggard young fledgling is sometimes brought out to receive food by a call from one of the parents. Soon there is no fixed order of emergence, and a young woodpecker may precede a parent.

Taking shelter from rain.—The capacious chamber in a dead trunk or limb is more than a nest and a dormitory; it provides the family shelter from rain. Adult Golden-napes differ greatly in their concern to keep their fledglings dry. Of those which I have studied, my first pair was the most careful in this respect, possibly because they dwelt at a somewhat higher altitude (3000 feet), where rains are cooler. If a light rain fell in the afternoon, the fledglings entered the nest, while their parents flew through the drizzle bringing them food. A heavier downpour, however, might send the whole family into the chamber. If the rain stopped early, the parents and even the young might come out for a while before retiring for the night; if it continued to rain hard and without interruption, all would stay within the cavity from about 4:00 p.m. until the next morning, the fledglings going to sleep hungry. Rains before noon were rare in this region, but once I saw the adult male lead a young male into the hole to escape a light shower than began at 7:00 a.m. Then the adult flew across to the forest edge to join the rest of his family. But the young woodpecker, preferring companionship to dryness, soon came forth to seek the others.

In sharp contrast to this parental solicitude has been the behavior of the pair of Golden-napes in the coffee plantation. Early in the afternoon of the day when two young males first left nest 17 of this pair, a shower fell for nearly half an hour. For about 5 minutes the rain was hard. Neither parents nor fledglings entered the hole to keep dry, but they clung to upright trees or to the lower side of slightly leaning trunks. On the next day, the young female of this brood followed the two young males into the open. At about 3:20 p.m. a light drizzle began to fall. When I reached the woodpeckers' nest a few minutes later, I found the adult female inside the cavity. As the rain grew harder, her mate quickly joined her. A minute later, the female flew out into the downpour. Only the adult male took shelter from the

deluge. One fledgling endured the rain while clinging with uplifted bill to the end of a stub at the top of the nest tree. The rest of the family remained out of sight.

On the following day, it suddenly began to rain hard at about 2:00 p.m. Hurrying to the coffee grove, I found the adult female looking out of the nest. After a few minutes, she emerged into the hard rain and clung to the lower side of the slightly inclined trunk at a point a few feet above the doorway, where she remained upright and motionless. After her exit her mate, which had been inside, took possession of the doorway, where he stayed until the rain abated. After his departure, the hole was empty; the fledglings had not sought protection with him. Soon they flew into the top of the nest tree from a neighboring leafier tree, where apparently they had remained through the shower. The parents now brought them food. When the rain increased again, no woodpecker sought to avoid it in the nest. A few days later, the same thing happened, the male parent alone entering the chamber to keep dry. Possibly certain members of the family crept into some of the old holes in neighboring trees, but all that I saw indicated that they took a wetting while clinging to a trunk. The adult female looked quite bedraggled, and a young male tried to dry his damp face by wiping it against a wet branch.

The following year, these parents were no more careful to keep their second-brood fledglings dry. On the day that the young male first left the nest, rain fell early in the afternoon. Soon after it began, a grown female entered the hole. Then, as the shower increased, the chamber was entered by the adult male and another grown female, whether the other member of the pair or an adolescent of the first brood, I could not tell. The female fledgling, which had first emerged from the nest two days earlier, followed them into the hole. But the male fledgling, less able to find his way back, was left out in the downpour. Indeed, he did not even return to the nest for the night, which was most unexpected. However, he came to no harm, and the following evening he joined his parents and the four young females in the nest.

Length of parental care.—As soon as they leave the nest, the fledglings begin to peck the trunks and branches over which they restlessly climb. Three days after her first emergence, I watched a young female of this second brood peck into a decaying palm trunk and remove something which she swallowed. But despite this early beginning, it is a long time before the young woodpeckers find enough to satisfy their hunger. As in the Red-crowned Woodpecker, the male Golden-nape gives more food to the fledglings, and attends them longer, than does the female. The male parent of the two young, a male and a female reared in the coffee plantation in July of 1960, soon led them to the tree in which our feeding shelf is situated and carried billfuls of banana up to them. Twenty-seven days after the young female left the nest, I saw the adult male give her food nine times in a few minutes, chiefly pieces of pejibaye.

Now the clusia by the house, which flowered late this year, began to expose the scarlet seeds that so strongly attract the woodpeckers, and 47 days after the young female left the nest, I watched the adult male give her such seeds. She took the food with the same thin, high-pitched cries that she had voiced on such occasions when she was younger. After passing a few billfuls of seeds to the young female, the parent gave her a peck to send her away and continued to eat by himself. Soon the young bird returned, begging, and he gave her more seeds, and then another peck. This happened many times. It seemed that the parent was undecided whether he should or should not continue to feed this full-grown young bird. Presently the

young male arrived and also received a few billfuls of seeds, followed by a peck. While the woodpecker fed his offspring, the Blue Honeycreepers, which flitted impatiently around them, tried several times to intercept the coveted food, but they were always unsuccessful, as far as I saw.

I last saw the adult female of this family feed the young when they were 81 days old. The male gave many billfuls to both fledglings when they were 92 days old, and two days later I last saw him feed the young female a few times. The young woodpeckers could now cling inverted beneath the clusia pods and extract seeds, thereby demonstrating that they had developed considerable proficiency in foraging.

FAMILY LIFE AFTER THE BREEDING SEASON

Tenancy of dormitories.—By the time the young have become wholly self-supporting and no longer receive food from their parents, they are difficult to distinguish from the adults. These immatures, as we may now call them, do not disperse but continue for many months to accompany their parents and to sleep in the same hole with them. The family may lodge until the following breeding season in the chamber in which its younger members were reared, or it may occupy a series of other holes; there is great variation in this respect. In 1957, the pair in the coffee plantation abandoned their nest cavity (number 14) after the emergence of the single fledgling, apparently because of an invasion of small ants, but such an early change in domicile is most unusual. In the following year, this pair had a sounder nest chamber (number 16), in which they continued to lodge with their two offspring from the time the latter emerged in May until the following February, when the doorway of this hole was enlarged by some animal, causing its abandonment.

In 1936 and 1937, my first pair of Golden-napes also roosted in their nest cavity for a long while. Three males were reared in this hole in April and May. One vanished soon after he began to fly, but the two surviving immatures continued to sleep in the nest chamber with their parents. From May through September, I noticed no interruption of their tenancy of this hole. In October they were unsettled, and some members of the family slept in this cavity while others lodged in a neighboring older hole with a gap in the outer wall near the bottom, where the parents had roosted before the last nesting season. About this time, one of the males, apparently a young one, vanished, but from early November onward the three survivors slept regularly in the hole where the parents had nested in the preceding April and May. Toward the end of February, a female Masked Tityra began to build a nest in this cavity, causing the woodpeckers to sleep elsewhere on certain nights. Nevertheless, the family of three lodged in it on many nights until the middle of March, when the last of the young males departed and the parents moved into the new hole which they had been carving. Thus, with temporary interruptions, one chamber had served as the family home for a full year.

Probably the Golden-napes generally lodge in their nest cavity, if it remains sound and they can retain possession of it, until the approach of the following breeding season. But there are many mishaps, one of the most frequent of which is the falling of the dead tree or limb in which the hole is situated, a disaster which may occur at any time but is most likely to happen in the rainy season. Often, too, the Golden-napes lose their dormitory to birds which nest in holes but cannot make them, especially the tityras, which have a long breeding season. In June of 1939,

I found a Black-crowned Tityra filling with leaves a cavity in which a pair of Golden-napes slept with three fledglings, which had emerged only two weeks earlier. Although the woodpeckers threw out some of the tityra's litter, they made no real attempt to dispossess her. Instead, they promptly proceeded to carve a new hole in the same trunk, and as soon as it was large enough, the whole family slept in it.

In addition to these obvious causes of change in domicile, there are others more obscure. Possibly infestation by lice or other small pests, in addition to ants, sometimes leads the Golden-napes to change their dormitory temporarily or permanently. When they have no single adequate lodging, the family may divide up in various ways. Thus, in October of 1936, when my first family was unsettled, two would sometimes occupy the newer chamber and two the older one, whereas on other nights the division would be three and one, and sometimes all four would sleep together. Moreover, they had difficulty in deciding just where each would spend the night; often a woodpecker would enter one of the holes only to crawl out and climb over the trunk to the other. This restlessness continued to the end of the month, and I could not ascertain its cause. It appeared not to be that the several members of the family were incompatible, for I never noticed any sign of discord.

In August and September of 1956, the Golden-napes in the coffee plantation had three holes close together in a vertical row in a dead upright branch of an *Inga* tree. One evening, I found the red-crowned head of a male framed in the upper and middle doorways, while a black-crowned female was looking out of the lower one. Although these holes were not high, the woodpeckers were almost indifferent to my presence below them. It required a good deal of shaking of the tree to bring them out, but finally they emerged, revealing that another female was inside one of the cavities. After I retired a few paces, the four woodpeckers returned to their chambers, but now they arranged themselves differently, with two males and a female in one hole and a solitary female in another, while one cavity remained empty. On subsequent evenings, the family divided up among their three bedrooms in the most diverse combinations: sometimes two males in one and two females in another, sometimes two females and a male in one and a lone male in another, sometimes a male and a female in each of two holes, and so forth. Occasionally, as the light faded, a woodpecker would move from one chamber to another.

When I studied the sleeping habits of Banded-backed Wrens in the Guatemalan highlands, I found similar differences among families. For reasons which were usually obscure, some changed their dormitory far more frequently than others.

Opposition to fellow lodgers.—Although, as a rule, the parents dwell in harmony with their offspring until the following breeding season, sometimes a male becomes antagonistic to his companions, as I have never known a female to do. In two different years, the male of the pair in the coffee plantation tried to keep other members of his family out of the dormitory. Probably it was always the same male, and in 1957 it was clear that the unfriendly one was the adult. In this year the pair, after one female left their first nest in May, tried in June to rear a second brood, only to lose their nestlings, probably because of an invasion of ants. The young female of the first brood slept with them in the nest while they were engaged with the second brood.

After the loss of this brood in July, each member of the family slept for some nights in a separate hole, doubtless because they now had no single dormitory adequate for the three of them. A month after the loss of the nestlings, a male and

a female had settled in a neighboring hole, but when the second female, evidently their offspring, tried to join them in the evening, she was repulsed with pecks by the male and she finally went to rest in an old cavity. The same thing happened on the following evening. Soon after this, the mated pair installed themselves in a hole which they had just carved in a dead avocado tree, but still the male refused admittance to the female fledgling. One evening, I found a female within and the male resting nearby. He made no hostile move when the second female entered in his presence, but after a while he went to the doorway, pushed his foreparts inside, and evidently pecked or bit the young female until she emerged and flew to another hole.

On the following evening, the male was the first to enter the new hole. When a female, apparently his mate, tried to enter with him, he repulsed her. She managed to push halfway in before she abandoned the attempt and flew off to another cavity, leaving the male to sleep alone. A few evenings later, all three entered the new hole, seemingly without friction. Nevertheless, two days after this, the male repulsed the second female from the doorway, pulling a downy feather from her neck. On yet other evenings, he emerged from the cavity and chased her from tree to tree until she flew away, after which he returned to sleep with the other female. Strangely enough, these three woodpeckers would often climb amicably over the same tree until the time for retiring arrived and antagonism sprang up when the young female tried to join her parents for the night. These disagreements continued from the middle of August until the end of September, when the second female vanished, leaving the mated pair alone until the following nesting season.

In 1958, the pair of woodpeckers in the coffee plantation reared one male and one female fledgling and the family remained together, with no serious friction that I noticed, until March of 1959. In this year, the pair brought forth two males and a female. These young woodpeckers continued for some months to reside with their parents in the nest chamber and also later in a neighboring newly carved hole. In late October, three members of the family vanished, leaving one male and one female to sleep in the new cavity. In November, the other three returned, but now the harmony of this family was broken by one of the males, which attempted to keep other members of his family, of both sexes, out of their dormitory. He seemed, however, to be on friendly terms with one other male. One evening, he entered the dormitory first and with vigorous pecks tried vainly to repulse both of the females and one male. On another evening, two of the males grasped each other's bills and shoved in opposite directions. The male outside the hole went off, but soon he returned and pushed inward so vigorously that the male inside could not keep him out. Sometimes a female gained admission by means of a very rapid and unexpected approach, which seemed to catch the surly male off guard. On some evenings, there was chasing among the surrounding trees before the woodpeckers retired.

It is evident that these woodpeckers did not put all their strength into the pecks that they directed at each other, for a blow that can loosen fragments from solid wood would certainly have wounded or killed a small bird. It was obvious, too, that these scuffles did not continue inside the chamber, for next morning all five woodpeckers would emerge with unruffled plumage. After the male disappeared in December, the remaining four members of the family lived together harmoniously, with occasional unexplained absences of one of them, for the next two months.

We have already noticed how a male Golden-nape drove his mate away from the nest where he was incubating without assistance. It is apparent that Golden-naped Woodpeckers are not perfectly and consistently compatible, but from time to time they may become aggressive. It seems to be always the males, which in woodpeckers are the more zealous home-makers, that suffer these outbreaks of truculence, but once I saw a female give a few pecks to another female which, clinging beside her to the outside of a trunk, was trying to force her way into their dormitory against the opposition of a belligerent male. The males reveal these aggressive tendencies inconsistently, for one evening they try to drive away their companions and the next evening they may appear perfectly amicable.

Arising and retiring.—In the last quarter of the year, some families of Golden-napes are most irregular in their time of departure in the morning, lingering in their dormitory for from half an hour to more than an hour after the early birds have become active, and an interval of half an hour sometimes separates the exits of two members of the family on the same morning. The woodpeckers do not awake, or at least they do not reveal themselves in their doorway, until the early risers of the feathered community have been flying about for many minutes; then, while waiting to come out, one Golden-nape may gaze through the aperture, or they may take turns in occupying this position. On cool mornings, I have seen Golden-napes return, after a tentative excursion to the outer side of their trunk, to enjoy the snugness of their chamber for a few minutes longer. They appear not to wake up with a ravenous appetite, and often they are in no hurry to feed. Even after delaying in the cavity for a long time after earlier birds have been up and about, on emerging they may cling to their own or to a neighboring trunk, preening, stretching their wings, and yawning, for a good while before they fly off to hunt food. So, too, in the afternoon they often satisfy their hunger long before it grows dark, and they wait idly either near their hole or in it until they are ready to sleep.

At this season, the members of a family have no definite order for entering their dormitory in the evening or for leaving in the morning. But my records for the first family which I studied show that one of the males retired first on 17 evenings, whereas the female retired first on only five evenings. In the morning, however, the female left first 16 times and one of the males left first only nine times. The female of a pair in the lowland forest near the Golfo Dulce, on the contrary, rather consistently entered the dormitory before her mate on a number of evenings in November and December. In the pair of Red-crowned Woodpeckers which occupied the same clearing as my first pair of Golden-napes, the male, as we learned, was nearly always the first to retire in the evening and the last to leave his hole in the morning.

Dispersal of the family.—From time to time, a member of a family permanently vanishes between breeding seasons, but I have never been able to learn whether it has gone elsewhere or died. Frequently, however, the young fledged in May or June continue to lodge with their parents until the following March or April. Five times I have known young of the preceding year to remain with their parents to within two weeks of the beginning of incubation. Usually they continue to roost in the old dormitory, while the parents move to the newly carved chamber in which they will breed, but one young male slept with his parents in the new nest at least until they began to lay. My observations on this point are, briefly, as follows:

Nest 1B. One of the young males hatched in 1936 slept in the old nest cavity until March 13, 1937. His mother slept in the neighboring new hole on March 11. By March 19, both parents had moved to another newly carved chamber, lower in the same trunk, in which the female laid about March 27.

Nest 11. A family, evidently consisting of parents, two immature males and one young female, was found lodging in a very high hole on February 9, 1945. Lower in the same dead tree a new hole was begun about this time, and by March 16 the mated pair slept in it. Two of the young continued to roost in the old hole until at least April 3. Incubation began in the new chamber about April 8.

Nest 14. This nest belonged to the family of which in September of 1956 I found two males and two females sleeping in three holes in a vertical row, as already described. By March 16, 1957, this family, now reduced to two males and a female, roosted in another hole that had been started in January if not earlier, lower in the same tree. On the night of April 4-5, these three birds still slept in it. On April 8, I managed to reach this cavity and found four fresh eggs. Only the mated pair now slept in it. Accordingly, the young male had remained with his parents until laying began.

Nest 17. In 1959, the nest cavity of the pair in the coffee plantation was begun about February 25. On the night of March 16-17, a male and two females roosted in it. When I climbed a ladder to examine this hole on the following day, both females came closer to me, and protested more vehemently, than did the male. The young female slept here on the night of March 24-25, but not the following night. The first egg was laid March 31.

Nest 18. On February 19, 1960, the pair in the coffee plantation was found sleeping in the hole in which they eventually nested. I did not find their offspring of the preceding year occupying this hole, but they continued to roost in the family's former dormitory, about 50 feet away. A young male and female lodged here until February 29. Then the male vanished, but the female slept here alone until March 6. By March 15, the parents were incubating in the neighboring tree.

I do not know what causes the young of the preceding year to forsake their parents' territory as the adults begin to breed again. Sometimes I have noticed rather mild chasing at this time, especially in the evening as the woodpeckers are about to retire, but I could not tell which bird took the offensive. At nest 17, the male was the first to enter the new hole on the evening of March 24. When a female came to join him inside, he pushed his head out and repulsed her gently but firmly. After a few seconds, she withdrew to a neighboring tree. Soon a female, probably the other one, entered the hole without hindrance from the male. This female continued to look through the doorway and did not oppose the entry of the second female a few minutes later. The three slept together that night. On the following evening, one female joined the male in the hole without opposition, but the second female failed to appear. My interpretation is that on March 24 the male repulsed the young female from the nest but freely admitted his mate. When the latter occupied the doorway, she did not deny admission to the young female.

All that I have seen suggests that the breeding male is chiefly interested in sending off the yearlings as he resumes nesting. But, as already recounted, in the midst of the nonbreeding season strenuous efforts to exclude certain members of the family from the dormitory may fail to cause their departure from the parents' territory. Apparently, at the beginning of the nesting season the yearlings feel an urge to leave the parental domain, and at most mild persuasion is necessary to make them go. I doubt that yearlings which have lived with their parents until March or even early April will breed in that same year. Since they have still to find a mate and territory and to carve a hole, if they do indeed nest they must begin much later than older individuals. Probably Golden-napes first breed in the second year after they hatched. But I have found none lodging alone in April, May, and June, when breeding is at its height.

Records have been given of five family groups that remained intact from one breeding season to the next, although in most instances there was a loss of certain members. Another family passed beyond my ken after the fall of the isolated dead tree in which it lodged. In only one instance have I noticed the disintegration of a family of Golden-napes between breeding seasons. In a hole about 25 feet up in a dead trunk standing in a field of maize, a pair reared two male fledglings and one female, which emerged from the nest in May of 1942. Two months later, I found this family sleeping in a hole newly carved lower in the same trunk, its doorway only 12 feet 8 inches above the ground—the lowest Golden-nape's hole that I have ever seen. The young female had already vanished and only the two young males remained with the parents. By early September, the four were sleeping in still another hole, freshly carved a yard above the last. I could discover no cause for these frequent changes in domicile.

Toward the end of the year, this family of Golden-napes began mysteriously to dwindle away. By early December, it was reduced to two males and a female; by January of 1943, it consisted of a male and a female, which usually slept in separate holes in the same trunk. From this, I inferred that the survivors were an adult female and her offspring; had the two been a mated pair, they probably would have slept together. One evening the female, frightened from the lowest hole by my approach, tried to enter the male's higher chamber but was refused admittance. After delaying 5 minutes before the forbidden doorway, she climbed backward down to her own. But a week later, the two roosted together in the male's hole; he was present first and allowed the supposed parent to enter without protest. By early February, the female had vanished, and for well over a month the male Golden-nape was the sole occupant of the trunk with many chambers—in addition to those we have had occasion to mention, there were a number of older ones. By the last of March he, too, had disappeared. Only a lone Fiery-billed Araçari arrived in the dusk and, after calling many times without response, winged swiftly away from the deserted tree.

THE SECOND BROOD AND YOUNG HELPERS

I know of six instances when a pair of Golden-napes definitely did not attempt to rear a second brood after a successful first nesting, and of two instances in which they did attempt to raise two broods. These latter two records involve the pair in the coffee plantation which, in first nestings, brought forth from the nest a female fledgling on May 23, 1957, and three female fledglings which left the nest on the exceptionally early date of May 3, 1960. It may be that in 1957 they renested because they had reared only a single fledgling (the only time that I have known this to happen), and that in 1960 they renested because their first brood took wing a week or two earlier than usual.

In 1957, the second nesting of the pair in the coffee plantation took place in an old hole not far from the first nest, which had become infested with ants. The young female of the first brood slept with her parents while they incubated the eggs and brooded the nestlings, which had hatched by June 25. On the morning of June 28, the male left first and returned with food while the two females delayed in the chamber. On his arrival, the young female emerged and tried to take it from him, but he refused her and carried it in to the nestlings. I watched in vain for the young female to bring nourishment or otherwise attend the young. Since she was still at an

age when some Golden-napes receive at least a few meals from their parents, probably she required all the food that she could find to satisfy her own hunger.

The nestlings of this second brood died in the middle of July, apparently because of an invasion of ants. When a female woodpecker arrived in the evening to enter this hole, it paused a good while in front of the doorway, hesitating to go in, and then began to pluck from its legs and body small objects which were probably ants. Finally she entered, but soon she retreated and went to rest in another hole. After the failure of this nesting, the male repulsed the young female from the dormitories occupied by himself and his mate, as has already been told.

In 1960, when the pair in the coffee plantation brought forth three female fledglings on May 3, they were incubating their second set of eggs in a neighboring hole, 40 feet up in a dead branch of a living *Inga* tree, by June 14. The three young females slept in this chamber with their parents. One evening the male mildly opposed the entry of one, but on other evenings I noticed no antagonism to them. Sometimes, after the four females entered, the male came out and clung near the nest for a few minutes before he retired for the night.

Because of the exciting possibilities of this nest with five grown occupants, I watched it while it contained eggs and nestlings more than any other (see tables 7 and 8, nest 18B). I found no evidence that the immature females helped their parents to incubate, but they did take a definite, although ineffective, interest in the nestlings. This interest was already evident on June 24, when I first noticed the parents carrying in food. In the middle of the morning, a young female went repeatedly to the doorway and looked in, but she was repelled by the adult female, which was brooding. The immature seemed to be afraid of her parent, but later, while the adult male was brooding, she entered the nest with him, unopposed, as far as I could see. The male remained within but he looked much through the doorway, and he tried to wipe from his bill a stubbornly adherent downy feather, which might have come from his daughter. Finally, he crawled out to free his bill of the feather, then flew away. After 6 minutes in the hole, the young female dropped an empty shell through the doorway—which I have never seen a parent do—then left.

A quarter of an hour later, this or another young female entered the nest, again while the adult male was brooding, without taking in any food that was visible to me. From this point onward, my record became confused. The young woodpecker stayed inside while the parents brought food and replaced each other in the nest; again the male came to the doorway to rid his bill of a small downy feather. As far as the record shows, the young female remained in the nest for 2 hours and 43 minutes, from 10:44 a.m. until 1:27 p.m. When it is recalled that I have never seen a parent incubate or brood for more than 51 minutes continuously by day, it seems incredible that the young bird's first contact with a nestling should have excited such a strong impulse to attend it. Certainly it is not impossible that she slipped out of the hole while I was making an entry in my notebook, or that I confused the adult and the young females. But the parents' behavior in this long interval showed plainly that they were troubled by something, and the most probable cause of their perturbation was the immature's continued presence in the nest, possibly covering the nestlings so that they could not be fed. The male went in and out in quick succession; he did not, as usual, fly off to forage when his mate arrived, or if he did go, he returned very promptly, without bringing food. For 2 hours, I did not detect anything in a

parent's bill. In this interval, the other two young females arrived and were chased by the adult female. As I was preparing to go at 1:27 p.m., two females left the nest.

During my four-hour watch on the following day, I saw a young female, with spread wings and sharp notes, approach the adult male and try to take the food that he was bringing to the nestlings. Apparently she received the billful, but she did not carry it into the nest. Later, an immature forced her way slowly into the chamber against the pecks of the adult female. For several seconds, one of her wings projected stiffly through the doorway after the rest of her body had passed through. After the young female disappeared inside, the adult emerged and called excitedly. The young woodpecker stayed within for only 3 minutes.

On July 9, when diurnal brooding had all but ceased, a female came with a small object in her bill at a time when the 15-day-old nestlings were evidently not hungry, as they had just refused a large billful brought by the male. Several times the female went in and out still holding the object, and finally she swallowed it. I believe that she was an immature, now about 102 days old.

After this I was absent from the farm for a fortnight, and I did not watch the nest again until July 22, when the two nestlings were feathered and took their food through the doorway, so that the parents did not need to enter to feed them. From this date until the nestlings' departure on July 28 and 30, the young females brought an occasional morsel to them, as I repeatedly saw. At least two of these immatures, now about four months old, were so engaged, and probably all three did so. Sometimes as they approached the nest in the daytime, the adult female chased them mildly, but more often she made no hostile move. The young helpers came with food only two, three, or, at most, four times in the 4 hours of the morning when I watched. They always carried very small particles, far less than the parents usually brought, and they did not know how to deliver them. They feared the rapid grasping thrust which these older nestlings used to take food from their parents' bills, for they had not learned to incline their heads to the side to facilitate the transfer of the meal, as the adults always did. Accordingly, when they were greeted by a nestling's snapping bill at the doorway, they slid rapidly to the side in a movement of avoidance. Sometimes they carried the particle away, but more often they advanced to the doorway and retreated a number of times, until at last, mustering courage, they pushed past the importunate nestling. As they did so, their heads were drawn down and in, as if to shield the face. If they fed the nestlings at all, they did so inside the chamber, where I could not see. After from 1 to 3, and rarely as much as 7, minutes in the cavity, the young female would emerge with empty bill.

In bringing small particles and taking them inside, instead of delivering large billfuls at the doorway, these helpers behaved as though they were attending newly hatched nestlings instead of feathered young almost ready to fly. They certainly did not bring enough to influence the parents' rate of feeding, as given in table 8. These young females were not much older than the young of the next brood when I last saw their parents feed them, and probably they could not find enough food to spare large amounts for the nestlings. In the early morning, when I watched the five grown woodpeckers leave the nest in which all had slept, I often saw the adult male, who at this period almost always became active first, return to the hole with food before all the females had left. On a number of these occasions, he gave his billful to a female, apparently a young bird, and she seemed to eat it rather than pass it on to a nestling.

On the day the last of these nestlings emerged, I watched the family sunning and preening in the dead top of their nest tree. A grown female seemed to try to preen the head and neck of the female fledgling, but the latter did not relish this and moved away.

After this brood began to fly, the whole family slept in the nest chamber, which accordingly sheltered the two parents, three females of the first brood hatched late in March, and a male and a female of the second brood hatched late in June. These seven formed the largest family of woodpeckers of any kind that I have found sleeping in the same cavity. On the morning of August 1, the adult male as usual left first, then four grown females, then the fledgling female, and finally the fledgling male, which had first flown only two days earlier. All left within 3 minutes, and the fledglings were not, as sometimes happens, fed before they left the hole.

Two weeks later, the stub which contained the nest of this second brood broke away from the tree, and the seven woodpeckers went to roost in the long-neglected hole in which the first brood had been reared. They lost no time in beginning to carve a new chamber in the remaining part of the dead branch that had held the fallen cavity. In fact, a few days later I found them working at two holes close together in this decaying branch. On the morning of August 18, I found a female throwing out chips, and apparently also carving, in one of these holes. After she had worked a good while, another female arrived, entered the other cavity, and started to enlarge it, throwing out chips and also pecking at the wall. I could see this clearly through the doorway, as the bird was near the top of the hole. I could not tell whether these females were an adult female and her female offspring or two young females, but there could be no doubt that at least one of the immatures, now nearly five months old, was excavating a hole.

One and then another stopped work and flew away, but presently two females arrived and resumed work on the two holes. Whether they were the same individuals that had been carving a short while before, I could not tell. After some minutes, the adult male replaced the female in the lower hole and worked there, while the other female continued to carve in the hole just above him. Presently the male came to the doorway and with hardly a pause threw out about 30 billfuls of chips. While the woodpeckers worked in this lower hole, particles of wood sifted out from the bottom through a large gap in the side of the limb. Evidently they were wasting their time in carving a chamber that would not be habitable.

Three mornings later, I found a grown female in the upper of these two holes and the male fledgling in the lower one. He seemed to be working on the inside of the cavity, for he threw a few billfuls of chips through the doorway. After a while, the female left the upper hole, and then the fledgling emerged from the lower one and climbed to the top of the stub. Now the adult male entered the upper cavity and started to work. When the fledgling came to the doorway, his parent pushed him away. Soon, however, the male fledgling returned and entered with the adult male, which this time offered no opposition, as far as I saw. Whereupon, the adult left and the young male remained in the hole. I could not see what he did in the bottom of the chamber, and I could not hear him pecking, but I likewise had failed to hear, above the roar of the neighboring river, the adults hammering in these holes. From time to time, however, the fledgling came to the orifice and ejected fragments of wood. All the other members of the family now flew away, yet he stuck to his task. Finally he emerged, churred much in the manner of the adults, and flew off in search

of his parents. He had been in the holes intermittently for nearly half an hour and had removed at least ten billfuls of chips, although each billful contained a smaller amount than the adults usually remove.

This young male engaged in nest carving when he was about 57 days old, and only three weeks after he left the nest. From time to time over the years, I had seen fledgling or immature Golden-napes take a few pecks at a hole which their parents were carving, but I had not previously witnessed such sustained activity by one so young. As we have noticed earlier, this young male received food from the adult male until he was at least 92 days of age.

About the middle of October, this family of woodpeckers began an orgy of hole carving. The site of this activity was an upright dead branch of a large avocado tree, about 100 feet from their nest tree, where they often rested before retiring in the evening. Here they soon had a dozen holes of various depths, all facing in almost the same direction in a roughly vertical series. I found the woodpeckers at work only from the middle of the afternoon until they went to rest, sometimes in a light rain. They never worked in the mornings, which were often sunny. Sometimes a male and two females carved simultaneously at different holes, and once I found three females working at the same time. I could no longer distinguish the young birds from their parents, but it was evident that at least two immature females engaged in carving holes of the type used for nesting and sleeping. If all of these cavities had been carried to the normal depth, a number of neighboring ones would have become confluent, making one long hollow with several entrances. Soon the dead limb broke across at one of the holes; the fallen part contained three more. The woodpeckers continued to enlarge the remaining holes until about the middle of November, when their preoccupation with this activity waned.

Meanwhile, the seven Golden-napes continued to sleep in the holes which they had carved in August in the neighboring *Inga* tree where the second brood was reared. Sometimes they divided up between two, or even among three, cavities that were close together, but through November and most of December, I always found the seven in the same chamber, and I noticed no antagonism among them. At the end of December, a male slept alone in one of the numerous holes in the avocado tree, leaving a male and five females to share the preferred chamber in the *Inga*. Early in January of 1961, the male which slept alone carved a new hole in a small, dead avocado tree nearby, and in the middle of the month a female began to roost in an old, dilapidated cavity in the same tree. Here they soon had trouble with the Tawny-winged *Dendrocincla* which, during three years, roosted and nested in this tree. Driven away by her, the female Golden-nape rejoined the other five woodpeckers in the *Inga*. I found the six sleeping there for the last time on January 23.

In the last week of January, a male and female vanished, leaving one male and four females in the little coffee plantation. On February 1, they all slept together in their old dormitory in the *Inga* tree. A few days later, two more females disappeared. Thereafter, each of the three remaining woodpeckers, two females and a male, usually slept in a separate hole in the same or neighboring trees. When a male came to the hole which a female had already entered for the night, she left. When one of the females tried to join the other in an old hole, the latter emerged and there was mild chasing; they finally entered separate holes. But a few evenings later, one female, after clinging to a trunk until it was nearly dark, suddenly flew down and pushed into the hole where the other was roosting. Angry notes and sounds of

knocking issued from the cavity, but in less than a minute it became quiet, and both females remained in it. Two evenings later, a female tried to join the male in his dormitory but was repulsed from his doorway with the loss of several feathers.

During the last ten days of February and throughout March, I found only one male and one female roosting in the coffee grove, always separately, and on some nights only the male could be found. I do not know why these woodpeckers did not continue to roost as a family group until the following nesting season. Possibly the unusual size of the family and the resulting crowding exacerbated unsocial tendencies that have already been discussed. In any case, in this year, for the first time in six years, the Golden-napes did not nest in the plantation near our house, but a pair was found raising a family in a neighboring coffee plantation beyond a stream and a patch of second-growth woods. In early April, after the last male vanished from the plantation where the seven had lived, there were no resident Golden-napes until the following year.

RELATIONS WITH BIRDS OF OTHER KINDS

The first Golden-naped Woodpecker that I ever saw was a female, which on the evening of December 21, 1935, flew out of the forest and alighted on the top of a very tall, bare trunk that stood, stark and gaunt, near the center of a new clearing. Here she crept around for a few minutes, uttering a nervous little *churr*. Presently she backed down the trunk and slipped into an old, weathered woodpecker hole. Once within, she lingered many minutes with her head framed in the doorway, her light forehead conspicuous in the dark circle, and at intervals she bowed emphatically. As the sky darkened and the neighboring birds became silent for the night, she descended into the cavity, where I could no longer see her.

Next morning, I came by the light of a thin crescent moon to watch. A pair of Lineated Woodpeckers were completing a nest cavity slightly lower in the same trunk, but the male had not yet begun to pass the night in it. While the Golden-naped Woodpecker still looked through her doorway in the dim early light, one of the larger woodpeckers arrived and cautiously inspected the new cavity from the outside. Then it drummed a loud tattoo against the resounding dead trunk. This brought its mate flying out of the neighboring forest. The new arrival also made a careful inspection of the nest chamber from the outside. Then one member of the pair climbed up toward the higher hole in which the smaller woodpecker had slept. The latter at first drew back into her hole to make herself less conspicuous, but as the big bird came steadily nearer, she slipped out and fled to another dead tree standing a short distance down the slope. Not satisfied with this retreat, the Lineated Woodpecker pursued the smaller bird from branch to branch. The small woodpecker nimbly dodged the large one, and in her brief moments of respite repeated her low *churr*. The Lineated Woodpecker would not let her rest until it had driven her quite out of the clearing into the neighboring forest, where she began to make her breakfast upon the fruit of a small tree with glossy foliage. But as I approached, she fled and was lost to me in the depths of the forest.

Again, two days later, the Lineated Woodpeckers drove the Golden-naped Woodpecker from her hole as soon as they had finished their early morning inspection of their own. After the male, in the last nights of December, began to sleep in the new hole, the Golden-nape no longer occupied hers so close above it. Probably the bigger woodpecker, which objected so strongly to her presence, would not permit

her to enter her hole at nightfall. Perhaps the Lined Woodpeckers were unnecessarily concerned; but it should be noted that Fiery-billed Araçaris, Masked Tityras, Gray-breasted Martins, and other birds were looking covetously upon their laboriously carved chamber, and they needed to exercise constant vigilance lest it be stolen from them before they reared their brood in it—as indeed it was taken as soon as that brood departed.

I have not again seen a Golden-naped Woodpecker chased by a Lined Woodpecker. But whenever one of these larger woodpeckers comes near a tree in which Golden-napes sleep or nest, they fly around excitedly, churring in protest, yet hesitating to approach the intruder, especially when it raises its yellow-lined wings in a defensive attitude. I have not known a Lined Woodpecker to harm the Golden-napes, which may rear a brood in a clearing where the former nest and roost.

Of the relations between Golden-naped and Red-crowned woodpeckers, enough has been said in the chapter on the latter. Although the Golden-nape is only slightly larger than the Red-crown, it chases this species, which I have never seen offer resistance. Yet their antagonism is not serious, and the two kinds of woodpeckers may rear their broods within sight of each other in the same clearing.

Likewise, details of the relations of the Masked and Black-crowned tityras with Golden-naped Woodpeckers have been given in earlier chapters. Over a great area in Central and South America, holes carved high in fairly sound wood by species of *Tripsurus* are favorite nest sites of tityras, which may claim cavities of the previous year that the woodpeckers are about to abandon, newly carved holes in which they are preparing to lay, or, later in the season, chambers in which the parent woodpeckers sleep with their fledged young. They do not, in my experience, try to capture chambers that hold the woodpeckers' eggs or nestlings. Whatever the condition of the cavity which the tityra covets, she usually gains possession of it by the simple expedient of persistently filling it with leaves, fine twigs, and similar materials. As they retire in the evening, the woodpeckers may throw from their dormitory some or all of this litter, but soon growing tired of this trouble, they proceed to carve a new hole nearby, leaving the tityra to occupy the one she has chosen. I have seen no fighting between tityras and woodpeckers as the hole changes ownership. But, as she was beginning to incubate her second brood, an exceptionally quarrelsome Masked Tityra took the offensive against the Golden-napes which still lodged in the dead tree where both species had reared first broods without any friction that I noticed. On a few evenings, her spirited onslaughts greatly discomfited the woodpeckers as they approached their dormitory, but soon she left her neighbors in peace.

Fiery-billed Araçaris, which nest and roost in holes carved by Lined and Pale-billed woodpeckers, are frequent neighbors of the Golden-napes. The approach of these toucans to a Golden-napes' nest greatly perturbs the woodpeckers, and they carefully avoid the huge-billed intruders. Although the doorway of a Golden-napes' chamber is too narrow and too solid to admit an araçari—a circumstance which doubtless increases its attractiveness to tityras—I once saw a Fiery-billed Araçari push in its long beak and remove a Golden-nape's egg from a hole that had been hastily carved and was evidently shallower than usual. Nevertheless, the woodpeckers hatched part of their set in this cavity, a yard away from a hole in which the araçaris were nesting, only to lose their nestlings to the same predator that took the araçaris' eggs. On the following day, the male woodpecker several times carried food

into the desolated nest and came out still holding it, much as I have seen parent birds of a number of other kinds do in similar circumstances.

Although Fiery-billed Araçaris are, like other toucans, inveterate nest robbers, they appear seldom to despoil nests situated close to their own, in this resembling some of the hawks. At least, I have often known Gray-breasted Martins, tityras, and woodpeckers, including Golden-napes, to rear their broods in safety near an araçaris' nest, sometimes in the same trunk. When araçaris begin to roost in a tree where Golden-napes lodge, the latter are at first thrown into great confusion by the arrival of the larger birds in the evening. But finally they return to their chamber only a few feet from that into which the toucans have retired. The woodpeckers normally go to rest earlier than the araçaris, and they learn to remain in their hole when their great-billed neighbors, coming to their own dormitory, alight with a loud thud against the trunk which contains the holes of both species. The Golden-napes seem to be aware that in their chamber they are safe from most predatory creatures.

SUMMARY

The Golden-naped Woodpecker is endemic in the region of high rainfall and heavy forest on the Pacific side of southern Costa Rica and western Panamá. Here it is found from sea level up to about 5000 feet, chiefly at the edge of the forest and in neighboring clearings with scattered dead or dying trees. It lives throughout the year in pairs or family groups, which often contain four or five individuals and rarely as many as seven. Each family resides permanently in the vicinity of the hole in which all its members sleep together.

The woodpecker's diet is highly varied. Not only does it extract insects from wood but it skillfully catches them in the air. It eats a variety of fruits and visits feeding shelves for bananas, but scarcely anything attracts it so strongly as the arillate seeds of *Clusia*.

Its call is a resonant *churr*, and it beats tattoos.

The holes in which Golden-naped Woodpeckers nest and roost are usually high, up to 100 feet or more, but rarely they may nest as low as 17 feet and sometimes they sleep as low as 13 feet. If needed, new holes are made at any time of the year, but chiefly they are carved in February and March, as the nesting season approaches. Then the two sexes work alternately at the cavity, taking turns which rarely continue for more than half an hour. At times when a new chamber is not needed, the male may work alone in a leisurely manner. The time devoted to carving a hole is most variable, ranging from about two weeks to ten months.

In El General, laying begins in mid- or, more often, late March. The Golden-nape's set consists of three or four pure white eggs, laid soon after sunrise on consecutive days.

Both parents may begin to sleep in the new chamber as much as two or three weeks before laying begins, and they continue to do so throughout the period of incubation and rearing the young. By day, the sexes incubate alternately, replacing each other frequently and often leaving the eggs alone for short intervals. The longest diurnal session observed in 38 hours at five nests was 51 minutes. Both parents are sometimes in the nest together at the changeover. One abnormal male chased away the female whenever she approached the nest. He incubated alone, covering the eggs about 55 per cent of the daytime. In the normal nests attended

by both parents, the eggs were incubated for from 75 to 100 per cent of the day. The incubation period is 12 days.

The nestlings are hatched blind and perfectly naked. Their eyes open at 9 to 12 days, and at 19 to 26 days they are covered with plumage. At first, the parents brood about as constantly as they incubated, but diurnal brooding has almost ceased when the nestlings are 15 days old. The young are fed with food carried in the bill, at a rapid rate, which for feathered nestlings varies from 7 to 33 times per hour for a brood of two or three. Older nestlings alternate frequently in the favored position in the doorway, where they are fed. As long as the nest is occupied, the parents continue to remove waste, often a number of billfuls in succession. In some pairs, both sexes clean the nest, but in one pair only the male was seen to do so. The members of a pair also differ greatly in their zeal in defending the nest.

At the age of 33 to 37 days, the young spontaneously leave the nest. A fledgling's first excursions from the nest may be brief, and without parental guidance it may enter and leave the nest hole a number of times in the course of a day. Other fledglings, however, promptly go farther from the nest and remain out much longer. Each fledgling resembles its parent of the same sex.

Although four eggs may be laid, no Golden-nape's nest has been known to produce more than three young. Twelve broods totalled 29 fledglings, of which 18 were males and 11 were females. If six nests of the same pair in successive years are omitted, the other six nests produced 13 males and only 3 females.

After their first day among the trees, fledglings are led by their parents to sleep in the chamber where they were reared. Usually the adults show them the doorway, and they require little urging to go in. After their return, they may be fed in the nest by their parents, and more food may be brought to them in the morning before their departure, but families differ in this particular.

Some parents lead their young to the nest when it rains, but others leave their fledglings exposed to a downpour while they take shelter themselves.

Although fledglings seem to find a little food when they first emerge from the nest, they may be fed by their parents for the next two months, or until they are about 94 days old. The male parent feeds the young more frequently and continues to feed them longer than does the female.

Even after the young have become independent, they continue to lodge with their parents. Some families occupy the same dormitory almost continuously from one breeding season to the next, but others frequently change their domicile. Sometimes the members of a family lodge in two or three neighboring holes, different individuals sleeping together on different nights.

In the nonbreeding season, an exceptional male may try to exclude other members of his family, of both sexes, from the dormitory. A male which on one evening strenuously opposes the entry of another individual may on the following evening show no hostility. Often the woodpecker whose entry to the nest is opposed forces its way in despite pecks, but sometimes it goes elsewhere.

After the young have been out of the nest for a few weeks, the several members of the family enter the dormitory in the evening, and leave in the morning, in no fixed order. Golden-napes retire early, and in the morning they may linger in their chamber long after other birds have become active. Even after emerging, they are often in no hurry to eat.

Often the young of the preceding year roost with their parents to within two

weeks of the beginning of incubation. Sometimes they accompany their parents to the newly carved nest cavity, and exceptionally they sleep there until laying begins. The male appears to be more interested than the female in sending off the yearlings, which at this season need little urging to depart. It is doubtful whether yearlings that remain with their parents until the latter are about to lay will breed before the following year, when they are about two years old.

Second broods are exceptional and appear to be undertaken only when the first brood is reared unusually early, or when it consists of a single fledgling. Young of the first brood sleep in the nest with their parents and the eggs or young of the second brood. Two or three immatures brought a little food to their parents' next brood, sometimes in the face of mild opposition from the adult female. But these young helpers brought very small particles even to feathered nestlings, and they did not deliver the food with the sideward inclination of the head which the adults use to facilitate its transfer. Hence they avoided the grasping thrust with which older nestlings take food, and they delivered the food they brought, if at all, inside the chamber instead of at the doorway as the parents now did.

Immatures, and even fledglings, may on occasion help their parents carve a hole for sleeping. One young male removed loose particles from an unfinished cavity, and apparently also chiselled at it, when he was only 57 days old.

Golden-napes are chased by Lineated Woodpeckers and in turn they chase Red-crowned Woodpeckers, yet all three species may nest successfully in sight of each other in the same clearing. When Masked and Black-crowned tityras carry nest material into the chambers where Golden-napes sleep and perhaps are preparing to lay, the woodpeckers may throw out some or all of the litter, but soon tiring of this housecleaning, they carve a new hole nearby. The Golden-napes have not been seen to attack the tityras, and these rarely threaten the woodpeckers. Golden-napes fear Fiery-billed Araçaris, which occasionally take their eggs; yet both species sleep, and sometimes rear broods, in the same tree.

BLACK-CHEEKED WOODPECKER

Tripsurus pucherani

The Black-cheeked Woodpecker is slightly over seven inches in length. The male has a yellow forehead, a red crown, hindhead, and hindneck. A broad black band, enclosing a white postocular spot, extends from in front of his eyes over his ear-coverts and down the sides of his neck to join the black of his shoulders, back, and wings. The back and shoulders are barred with white, and there are conspicuous white marks on his wings. His rump and upper tail-coverts are white; his tail is black. His lores, malar region, and upper throat are brownish white. His more posterior under parts are yellowish olive and dull wax yellowish, with a bright red patch on the abdomen and black bars on the lower breast, sides, flanks, and under tail-coverts. The female differs from the male in having the red of her head restricted to the nape and hindneck, while her crown is mostly black, becoming whitish anteriorly. In both sexes, the bill, eyes, legs, and feet are dark.

This woodpecker ranges through the Caribbean rain forests from southern México to Colombia, thence down the Pacific coast of South America to southwestern Ecuador. In Central America, it extends from sea level up to about 4000 feet, but it is most abundant in the lowlands. It inhabits the forest and its edges, clearings with scattered trees, orchards, cacao plantations, and similar situations. Its call is a loud, full-voiced *krrrr*, not quite so mellow as that of the Golden-naped Woodpecker. Once I watched a Black-cheeked Woodpecker drill a hole into a cacao pod, probably to reach the sweetish white pulp in which the seeds were embedded.

NESTING

Although I passed large parts of five nesting seasons on the Caribbean side of Central America, where the Black-cheeked Woodpecker dwells, I learned little of its habits and saw only one nesting pair, in contrast to the nine nests of the Golden-naped Woodpecker that I found in my first four seasons in El General. On April 18, 1941, I discovered a pair of Black-cheeked Woodpeckers in a cornfield beside the forest, on a steep hillside above the Río Pejivalle in eastern Costa Rica, at an altitude of about 2200 feet. These woodpeckers were evidently preparing to breed in a hole that appeared new, 40 feet up in a tall, barkless, branchless trunk standing above the maize. The male was in the cavity when I first noticed it at ten o'clock in the morning, but it was unoccupied when I returned late in the same day. I waited three quarters of an hour before the pair of woodpeckers flew up together and both entered the chamber. The female promptly emerged, leaving her mate inside. She clung to a neighboring dead trunk until, at 5:32 p.m., she returned to the hole to sleep with her partner. Thus, my very first observations on the roosting habits of this species showed that they resemble those of the Golden-naped and Crimson-bellied Black woodpeckers, which I had already studied, rather than those of the Golden-fronted and Red-crowned woodpeckers.

On the following day, the Black-cheeked Woodpeckers, especially the male, spent much time in their hole, alternately, and from time to time they threw out a few billfuls of wood particles. They seemed to be guarding the finished or nearly finished chamber rather than incubating. At daybreak on April 22, I watched the woodpeckers

emerge from this cavity. The female flew out at 5:17 a.m., but her mate stayed in the hole 12 minutes longer. Later in the morning, I saw him eat an egg, which apparently he had removed from his own nest. Possibly it had been broken by a Masked Tityra which I found a few days later carrying nest material into the woodpeckers' chamber.

Without trying to drive away the pair of tityras, the woodpeckers now transferred their attention to another hole, only 20 feet up in the same trunk. This hole was present when I discovered the pair ten days earlier. At that time it appeared newly carved. Now the woodpeckers proceeded to enlarge it. By May 5, however, they were excavating a third cavity, midway between the first two. The male and female carved alternately, as in other woodpeckers. Later in the morning, they entered the hole in which they formerly slept, and the male threw out two dry leaves that the tityra had carried in. Then the female spent many minutes inside. The tityras were absent at this time.

By May 12, the woodpeckers were carving a fourth hole, a yard above their second cavity, or about 23 feet up. I do not know why these woodpeckers started so many holes, but possibly as they dug more deeply into the wood they found it too hard for them, and they were searching for a spot where advancing decay had made it soft enough for them to finish their chamber. By May 14, this fourth hole was large enough for a woodpecker to enter, and on the morning of May 19, the female stayed inside the cavity for many minutes. After her emergence, her mate entered and threw out an egg which, I surmised, she had just laid. It appeared small for a Black-cheeked Woodpecker's egg, and when I examined its smashed remains on the ground, I could detect no yolk. In the chapters on the Acorn Woodpecker and the Olivaceous Piculet, examples of the removal of eggs from the birds' own nests are also given. Possibly, woodpeckers eject from their nests eggs which are small or otherwise visibly abnormal.

That evening, the male was in the newest hole when I arrived at 5:38 p.m. When his mate came to the doorway at 6:00, he did not make way for her to enter, so she went to the second hole and there she passed the night, a yard below him. The female tityra was now incubating in their first and highest hole, whose doorway was so narrow that she wriggled through it with an effort.

Incubation began in the fourth hole about the end of May, and by June 13 both parents were taking in food for the nestlings. The male still slept in this chamber, while his mate continued to lodge alone in the second hole. In view of the difficulty which these woodpeckers had in completing a cavity after their first had been taken by the tityra, it seemed likely that they now slept apart because their nest chamber was too small to hold both of them in comfort.

While studying the Golden-naped Woodpecker some years earlier, I had wondered which of the two parents, both of which sleep in the nest with the eggs, actually incubates through the night. The fact that in the early morning the male often goes off first to forage while his mate remains in charge of the eggs, as well as analogy with other species of woodpeckers in which the male sleeps alone in the nest, suggested that the male Golden-nape covers the eggs through the night while his mate sleeps beside him. These observations on the Black-cheeked Woodpecker support this view, which was still further strengthened when, some years later, I found a male Golden-nape carrying on incubation alone, by day as well as by night.

A few days after the Black-cheeked Woodpeckers' eggs hatched, my sojourn by the Río Pejivalle came to an end, and I did not learn whether the parents lead their fledglings to sleep with them in the nest cavity or in some other hole, as the closely related Golden-naped Woodpeckers do. I present here these fragmentary observations on the Black-cheeked Woodpecker, because I have found almost nothing about its habits in print. I hope that, before long, I or some other birdwatcher will be able to provide more complete information on its life history.

SUPPLEMENTARY OBSERVATIONS ON THE CRIMSON-BELLIED BLACK WOODPECKER

In the eastern foothills of the Andes of Ecuador and Perú, and on the western side of the immense Amazonian plain, one of the most abundant members of the family is the handsome Crimson-bellied Black Woodpecker (*Tripsurus cruentatus*). This small woodpecker is clad largely in black. The rump and upper tail-coverts are white, and there is a large patch of deep crimson on its lower breast and belly. In the male the forehead is black, the fore part of the crown is red, and the hind part of the crown is also black. He has a band of pale yellow which extends from the lores along the sides of his head and which joins a patch of bright yellow on his hindhead. The female differs from the male in having the crown wholly black. I found this woodpecker far noisier than its Central American congeners and almost as vociferous as the Acorn Woodpecker, which it somewhat resembles in language as in sociability.

One evening while I dwelt at Puyo, 3000 feet above sea level in eastern Ecuador, five of these active woodpeckers gave me a magnificent exhibition of aerial fly-catching, in their strong flight and intricate maneuvers rivalling the Tropical Kingbirds which were engaged in the same occupation at the same time. They continued this activity until the sunset glow had faded from the snowy, smoke-plumed summit of Sangay, far off in the south. Then, when it was nearly dark, the woodpeckers retired, all five together, into a hole high up in a dead palm trunk, standing pole-like in a hillside pasture. They were evidently a family consisting of parents and three young, sleeping in exactly the same fashion as their northern cousins, the Golden-naped Woodpeckers.

A year later, I watched four of these woodpeckers retire to sleep in a cavity only 10 feet above the ground. This hole was in a low stub in a pasture, at Caballo-Cocha near the Amazon in Perú. Like the birds at Puyo, they did not enter the cavity until it was nearly dark. I watched the woodpeckers at Puyo in August, and those at Caballo-Cocha in October; the presence of family groups in these months suggested that the woodpeckers had nested earlier in the year.

But at Satipo, considerably farther to the south in the Andean foothills of Perú (in the Department of Junín), early in September, I found a male and a female Crimson-bellied Black Woodpecker sleeping in the same hole, in a lofty branch of a tree growing near the Agricultural School. They seemed to be preparing to breed, for they were engaged in carving a new hole in a neighboring limb of the same tree. Meanwhile, a female Black-crowned Tityra was carrying leaves into the old hole where the woodpeckers slept. The Tityra and her mate looked on quietly and made no protest while one of the woodpeckers threw some of her material from their dormitory. From Central America to Perú and Brazil, woodpeckers of the genus *Tripsurus* must contend with Masked and Black-crowned tityras, which use their holes for nesting and fill them up with leaves, to the great annoyance of the owners.

And over all this vast territory, the competition for nest sites goes on, apparently, with silent persistence and never a fight, never even the vengeful tearing out of a feather by the chief protagonists. So mild-tempered are these tropical birds!

SUMMARY

On the Caribbean side of Central America, the Black-cheeked Woodpecker inhabits the forest, its edges, and clearings with scattered trees, from sea level up to about 4000 feet.

In April, a mated male and female slept together in a hole high in a dead trunk, where they seemed to be preparing to breed. When a Masked Tityra claimed their chamber and carried in nest material, they made no protest but proceeded to carve another. They worked at three other holes in the same trunk before they began to incubate in the last of them. This new nest chamber was evidently smaller than the first, for now only the male slept in it with the eggs and nestlings, while the female lodged in another cavity a yard below him. By day, both attended the nestlings.

The male ate an egg, which apparently he had removed from the first hole. Later, he threw from the fourth hole an egg which lacked a yolk.

In eastern Ecuador and Perú, five Crimson-bellied Black Woodpeckers lodged in one hole and four slept in another. They retired late in the evening, after spectacular aerial flycatching. Farther south in Perú, a male and a female slept together in a high hole. While this pair carved a new chamber near their dormitory, a Black-crowned Tityra carried leaves into the latter. The woodpeckers did not attack the tityras, nor did the latter threaten the woodpeckers when, in their presence, one of them threw out some of their material.

ACORN WOODPECKER

Balanosphyra formicivora

Woodpeckers present the rare combination of great structural specialization with great flexibility in behavior. Their highly modified heads, feet, and tails fit them for activities which are denied to most birds, yet often with admirable efficiency they perform feats, such as aerial flycatching, that one would never expect of them. This versatility makes them most entertaining to watch. And of all the woodpeckers I know, the most interesting are the Acorn Woodpeckers, so strikingly attired, so sociable, so loquacious, so restlessly active.

About eight inches in length, the Acorn Woodpecker is clad in black and white in a bold and arresting pattern. The nasal tufts, chin, and upper throat are black. This dark patch is framed in a broad zone of white which crosses the forehead, narrows on the lores, widens on the sides of the neck, and merges into pale yellow on the foreneck. The orbital and auricular regions, hindneck, back, and much of the wings are glossy blue-black. The rump and upper tail-coverts are white, and there is a conspicuous white area in the middle of each expanded wing. The tail is wholly black. Below the pale yellow throat, the chest is, in the northern forms, crossed by a black band, which in races inhabiting Central America is narrow or lacking. The more posterior under parts are white, more or less heavily streaked with black. In the adult male the whole crown and hindhead are red, whereas in the female the crown is black and only the hindhead is red. The bill is black; the iris varies from white to yellow and brown in color; and the feet are dark.

The Acorn Woodpecker ranges from southwestern Oregon, southern Arizona, and central Texas to western Panamá. Its distribution closely follows that of the oak trees with which it appears everywhere to be closely associated. In the more northerly portions of its range, where oaks flourish at low altitudes, it goes down to sea level, but in southerly regions, where these trees are usually restricted to higher altitudes, the Acorn Woodpecker is likewise restricted. In British Honduras, where pine forests with associated oaks reach the lowlands, the Acorn Woodpecker does so, too. In Guatemala, it occurs principally in the mixed woods of pine, oaks, and other broad-leaved trees between 5000 and 9000 feet above sea level, although in the Department of Altavera Paz it has been recorded considerably lower (Griscom, 1932:224). In Costa Rica, I have found it at points ranging from 3000 feet in El General to about 10,000 feet on El Cerro de la Muerte and Volcán Irazú.

In this country, not only is the Acorn Woodpecker closely restricted to the oaks but it appears to be extremely sedentary. About two miles from my home in the valley of El General at 2500 feet, and only a few hundred feet higher, is a stand of oaks where for years I have found these conspicuous woodpeckers on practically every visit; yet on my farm, which lacks oak trees, I have never seen a single Acorn Woodpecker in 20 years. My experience in other parts of El General has been similar: the Acorn Woodpeckers scarcely ever descend below the 3000-foot contour along the northern side of the basin, which marks approximately the lower limit of the oaks that become increasingly abundant as one ascends the Cordillera de Talamanca. On the very wet northern slopes of the Cordillera Central, there were no oaks about my residence at 5500 feet, and I found no Acorn Woodpeckers there.

But about 500 feet higher, great oak trees, and with them the woodpeckers, became abundant.

Acorn Woodpeckers prefer open stands of oaks, pines, and other trees, or else the woodland's edge, to the interior of heavy, unbroken forests. Throughout the year, they live in parties of three to six or possibly more, which are apparently family groups, in which great concord seems to prevail. Once I watched three clinging to the high limb of a pine tree. The woodpecker on the inside wished to move nearer the end of the bough, but another, farther from the trunk, blocked its path. Instead of trying to make its companion move away, the first bird descended to the side of the branch and sidled outward along it until it had passed the other. The flight of these woodpeckers is swift and strong, with little or none of the typical picarian undulation. The contrasting black and white areas on their wings and back show conspicuously when the bird is in flight.

FOOD AND ITS STORAGE

Acorn Woodpeckers are expert flycatchers. Sometimes one takes its stand at the very top of a tall pine or other tree, from which it darts out over the surrounding treetops, doubling and looping with consummate skill, then returning to the same high lookout to watch for other insects. Often they make long aerial sallies in the evening twilight, when many insects are flying.

The fruit of the oak enters prominently into the economy of these woodpeckers. On the Sierra de Tecpán in western Guatemala in mid-August of 1933, I first saw them gathering acorns, which were still far from ripe. As the crop matured, they gave increasing attention to it. Each of the three kinds of birds which chiefly feasted on acorns at this season had a different way of dealing with the fruits. Band-tailed Pigeons settled in the tops of the oak trees, plucked the acorns from their cups, and swallowed them whole. Steller Jays carried acorns to a convenient branch and there held them beneath their feet while with strong blows of their heads they pecked the nuts to pieces. Acorn Woodpeckers secured their acorns in crevices in the bark on the upper side of horizontal branches or in clefts in the ends of broken-off trunks or limbs while they hammered at them with their powerful bills. Often, instead of gathering the acorns singly, a woodpecker broke off a twig to which as many as three acorns were attached. The twig, grasped in his bill, served as a convenient handle for carrying the fruits to the thick branch or end of a stub, where they were broken off one by one and fitted into a cavity for further treatment.

In California, and at least as far south as Veracruz in México, the Acorn Woodpecker carves little round holes in the trunks of dead trees, the bark of living trees, telephone poles, or even the wooden walls of buildings. Each is just large enough to hold an acorn, which is driven in firmly by a blow of the bill (Sumichrast, 1869; Ritter, 1938). In Central America, I have looked in vain for this method of storage. Some observers, not finding the array of whole acorns neatly fitted into special niches that they had seen in the United States, have concluded that Central American forms of the species fail to store acorns. But this is wrong. In Guatemala I repeatedly saw Acorn Woodpeckers spend much time in autumn storing the abundant mast, but not in special receptacles. When a woodpecker had eaten as much of an acorn as it desired, it frequently took the remaining fragments and pushed them beneath the loose bark of a dead tree, or into a natural crevice in the wood, or even into the



Fig. 28. Acorns stored in thick bark of *Pinus caribaea* by Acorn Woodpeckers, in northwestern Honduras at about 1300 feet above sea level. This mode of storage seems to be exceptional in Central America. Photograph from Professor Gerardo Budowsky.

luxuriant growth of lichens on the boughs. Often whole acorns were tucked away in the same manner as the fragments. Although a number of northern woodpeckers store food (see General Summary, p. 549), the Acorn Woodpecker is, as far as I know, the only member of the family that does so in the tropics.

Although I have not myself seen acorns stored in specially made holes in Central America, recently Professor Gerardo Budowsky showed me a photograph taken in northwestern Honduras of a pine tree, in the thick bark of which woodpeckers had drilled many small holes, each just large enough to receive a neatly fitting acorn. The birds that did this could hardly have been other than Acorn Woodpeckers.

Acorn Woodpeckers also hammer on pine cones, as Hairy Woodpeckers more frequently do, either to extract the seeds or to obtain the larvae sometimes present in them.

VOICE

The loud, bass, indescribably queer notes of the Acorn Woodpeckers are in keeping with their harlequin attire. *Rack-up rack-up* they shout, bowing deeply up and

down atop some lofty stub or else *r-r-r-rack-up*, *r-r-r-rack-up*, with a long, deep roll. Others have seemed to me to say *rub-a-dub* or *rub-a-dub-dub*. If the woodpecker calls while clinging upright above a horizontal branch, its deep bow brings its head to the level of its feet. Probably because it has such a well-developed voice, the Acorn Woodpecker seems to beat tattoos with its bill less often than many other woodpeckers, at least in Central America. I have no record of drumming by them, but then I have not watched them as the breeding season approaches.

ROOSTING

Like other members of the family, Acorn Woodpeckers sleep in holes which they carve in trees. These holes have the same form as their nest holes. Several individuals may lodge together, as in *Tripsurus* and *Picumnus*, although solitary sleeping seems to be more usual in the family as a whole. Often Acorn Woodpeckers retire very late in the evening, after most other diurnal birds have gone to roost. However, they are not consistent in this, and sometimes they seek their dormitory early, as seems to be the more usual practice in the woodpecker family. In the morning, they often linger in their snug chambers long after other birds have become active, as is typical of woodpeckers. But in this, too, they are not consistent.

In late November of 1933, I found an Acorn Woodpeckers' dormitory high in the dead trunk of a branchless, decapitated pine tree that stood in a maize field on the Sierra de Tecpán. The pole-like trunk was penetrated by four woodpeckers' holes. These were of various ages, as revealed by the lighter or darker color of the wood surrounding the entrance; in addition, the birds were carving a fifth hole when I found them. They slept in one of the newer cavities. Sometimes a woodpecker would enter this hole in the middle of the day and remain for many minutes entirely within it, or else with its body inside and its parti-colored head framed in the round orifice, looking out, while its companions sought acorns, darted high into the air to catch some passing insect, hammered away at the new hole in the same trunk, or threw out loosened chips with vigorous sideward jerks of their heads. More than once, two woodpeckers clung side by side below the entrance of this hole, with their wings half spread, revealing the black and white pattern, and communicated in their queer voices. When a Red-shafted Flicker alighted on their pine trunk, they drove him away, and they would not even permit him and his mate to remain on another dead tree 100 feet distant.

The number of woodpeckers that slept in this dormitory was not always the same, and the hour at which they went to rest and emerged in the morning varied greatly from day to day. On the evening of November 22, I arrived at 5:00 and found no woodpecker in sight, but I heard their voices in the pine woods down the slope. I waited until daylight was fading away and the earliest stars became luminous points in the darkening, half-overclouded sky. Still no woodpecker appeared, and I had started to walk away when I heard a deep, rolling voice close at hand. As I stood motionless with my eyes on the naked pine trunk, a lone Acorn Woodpecker flew from the pines across the road and alighted below the entrance of the dormitory. Here it clung for a minute, violently bobbing its head back and forth and calling *r-r-r-rack-up*, *r-r-r-rack-up*. Then it climbed into the hole and remained alone for the night.

Three weeks later, I revisited the pine stub about which the woodpeckers' activities centered and in which they slept. The new hole had progressed very slowly and was

still so shallow that the birds, while clinging in front of the entrance, could reach the loosened chips on the bottom and throw them out. In the evening, long before dark, a red, white, and black head was framed in the round orifice of the sleeping hole. The bird continued to look out for perhaps 10 minutes, then at length flew out and rested on the top of the decapitated trunk. As soon as this bird had left, a second head took possession of the doorway. Presently, still another woodpecker flew out of the woods across the road and alighted in front of the hole. The bird that had been blocking the entrance made way, and it climbed in. Not expecting that the woodpeckers would go to bed so early, I had not taken a suitable position for watching them. I feared that they would not stay for the night if they saw me standing so conspicuously in front of their dormitory, and accordingly I started to move to a more secluded spot. But I succeeded only in causing the bird that was watching to fly from the hole, and at intervals of a few minutes two more followed. Although I waited in an inconspicuous position until darkness fell over the mountain, they did not return. Most probably, if I had not disturbed them, three or four woodpeckers would have remained to sleep together.

A few days later, I watched this same sleeping hole at dawn. While the light was still dim, the appearance of something white in the dark circle of the entrance caused me to focus my field glasses on the hole. A woodpecker had awakened and was looking out of the opening. While he remained peering forth, almost motionless, the bird world gradually became active. Soon I heard the calls of some other Acorn Woodpeckers, which must have slept in the pine trees on the other side of the road. About 5 minutes later, the bird which I was watching finally crawled through the entrance, after looking out for over half an hour. He alighted on the short stub of a broken-off branch, just below the sleeping hole, and called loudly. The moment he emerged, a similar head replaced his in the entrance. In a minute, the first woodpecker flew back to the hole again, and the other head withdrew into the interior. He hung perfectly motionless just below the doorway, and soon the first rays of the rising sun began to strike him there, and to warm him on this frosty morning.

When the woodpecker had clung motionless in the sunshine for a good 10 minutes, he at last bestirred himself, flew over into the top of the tall dead pine beneath which I rested, and called. The second woodpecker reappeared in the orifice, spent about a minute looking out, then flew forth to join the first. It was then a few minutes past seven, an hour after daybreak. I continued my watch, but no other woodpecker appeared in the entrance of the dormitory. These two birds joined the rest of the flock, which had slept at a distance, and the whole party went off to forage among the pines.

Another dormitory on the Sierra de Tecpán was situated in the short, thick stub of a dead branch of a pine tree, at least 80 feet above the ground. As usual with woodpecker holes, the entrance was on the lower side of the ascending stub, facing downward. In the frosty December nights, three birds slept there. They sometimes retired very late, after dusk had descended. In the morning, they emerged much earlier than the woodpeckers in the cornfield, but each in turn delayed with its head in the doorway, gazing out upon the treetops, sometimes for many minutes, before flying out to join its companions at their breakfast of acorns.

Early in March of 1937, I found the dormitory of five Acorn Woodpeckers above the Río Buena Vista in southern Costa Rica, at an altitude of a little over 3000 feet. This sleeping hole was about 70 feet up in the top of a massive, branchless,

fire-gnawed trunk that stood among other dead trees in a hillside pasture at the forest's edge. In this milder region, where frost was unknown, the woodpeckers consistently stayed out very late. In the waning light, they made long aerial sallies to snatch up the insects which fly at this hour, chased each other, and called with animation. Sometimes the whole family circled over the dusky hillside in close formation, with a strong, direct flight more suggestive of pigeons or parrots than of woodpeckers. As the twilight deepened, they clung motionless in the tops of the blasted trees.

One evening, when they had been resting together in the same high treetop, four woodpeckers suddenly flew down in a cluster, as though moved by a single impulse, to their dormitory in a neighboring trunk, uttering their queer notes as they went. All tried to push simultaneously through the doorway, which was wide enough to accommodate just one at a time. After they had entered, necessarily in single file, the fifth woodpecker flew down and went into another hole a little above them. Finding itself alone, it promptly came out and climbed down to join its four comrades for the night. On a later evening, all five flew in a bunch to their doorway and passed through it, one by one, as rapidly as they could. Other woodpeckers that I have watched are more independent and less subject to group behavior than are Acorn Woodpeckers.

After this family began to nest, a single woodpecker slept with the eggs, in this contrasting with Golden-naped Woodpeckers and piculets, in which both parents, and sometimes one or more young of an earlier brood, pass the night with the eggs and nestlings. The other four members of the family apparently still slept together in another hole, but they now remained out so late that my eyes could hardly follow their black figures shooting swiftly through the dusk, and I did not find their dormitory.

INCUBATION

By May 3, the five woodpeckers on the hillside above the Río Buena Vista were incubating in a hole a foot or so above that in which they had been sleeping. This hole was over 70 feet above the ground. I now assured myself, by long watching, that this group consisted of four males and a female, and that at least four of them, including the female, took turns in the nest. Although I did not succeed in keeping the individuals separate until all five of them had entered the nest, it seemed likely that all participated in incubation, for the behavior of all was much the same.

With so many birds taking turns at incubation, it was not surprising that their sessions on the nest were short. I spent a total of nearly 12 hours timing their shifts in the nest, chiefly before 8:30 on different mornings, but once from 10:00 to 11:00, and twice in the last hour of the day. In all this time, the longest session that I recorded was only 17 minutes. These woodpeckers sat only exceptionally for over 10 minutes at a stretch, and frequently one bird was relieved by another after it had been in the nest for only a minute or two. Sometimes, indeed, it scarcely had time to settle down on the eggs before another came to take its place. On May 4, from 5:50 to 7:55 a.m., I recorded the following sessions and intervals (in italics) when the nest was neglected: 4, 9, 3, 4, 2, 6, 5, 3, 10, 3, 5, 5, 1, 12, 5, $\frac{1}{2}$, $\frac{1}{2}$, 9, 2, 12, 2, 3, 2, and 17 minutes. On May 8, from 6:09 to 8:31 a.m., they shifted about as follows: 2, 5, 7, 10, 2, 1, 6, 1, 5, 9, 6, 1, 7, 1, 6, 9, 4, 2, 4, 10, 2, 3, 5, 2, 5, 6, 9, 1, 6, and 5 minutes. Later in the morning they were just as impatient to enter

and leave, as this record, made between 10:03 and 11:11 a.m. on May 5, shows: 4, 5, 4, 3, 8, 3, 4, 4, 4, 4, 3, 4, 2, 13, and 3 minutes. In the late afternoon the schedule was much the same. I made the following record on May 4, from 5:08 to 6:08 p.m.: 4, 7, 4, 9, 7, 2, 3, 5, 1, 5, 4, 1, 2, 1, 1, and 4 minutes.

The woodpecker that wished to take a turn on the eggs flew up to cling beside the doorway and await the sitting bird's departure, which usually was prompt. Sometimes the newcomer stuck its head through the doorway to peer in, but nearly always it then withdrew and stood aside until the other had time to fly out. Two woodpeckers were seldom in the hole together. Rarely a woodpecker that had been incubating for only a few minutes refused to leave when another came to replace it, and in this case the new arrival flew away, or else it remained clinging quietly to the trunk; it never disputed the possession of the nest. But nearly always the eggs were turned over to the newcomer. Once I saw three changeovers in little more than a minute. On another occasion, while one woodpecker was in the act of replacing another in the nest, a third flew up and the first two made way for him.

It not infrequently happened that two, three, or all four woodpeckers flew to the hole simultaneously, as though moved by a common impulse. They alighted around the orifice, as close together as they could cling, and often they spread their black wings against the trunk, displaying the white area in the center of each. Soon, one woodpecker entered, whereupon the others flew away or climbed to the top of the trunk. I never saw them quarrel on these or any other occasions.

Sometimes a woodpecker alighted beside the doorway, as though to take its turn on the eggs, thereby causing the departure of the bird which had been inside, but then the newcomer flew off again, perhaps in pursuit of an insect that just then flew by, but usually for some less obvious reason, and the nest was left unoccupied. Sometimes, too, a woodpecker went to the entrance, only to hurry off again before the incubating partner had time to come all the way out. In this case, the bird that had been sitting might back down into the hole again and continue to incubate. Or it might even come out, cling beside the doorway for a few moments, and then return to resume incubation. It sometimes happened that even when two or three woodpeckers came simultaneously to the nest all flew away again, including the one they came to replace, and the eggs were left uncovered. But it was never long before another member of the group came to take charge of them.

These woodpeckers were restless sitters, and after incubating for 9 or 10 minutes, sometimes even less, one often looked through the doorway for the arrival of relief and called; if one of its partners did not soon come, it would fly off in search of them. Frequently, after sitting for only a few minutes, the woodpecker would dart out to join its companions, for no apparent reason. Any excitement, accompanied by loud calling, among the woodpeckers outside, was almost certain to bring forth the member of the family that happened to be in charge of the nest. Another cause for leaving the eggs uncovered was that the latest arrival, after the one it had come to replace had flown off, would enter the lower hole in which all five formerly slept, instead of going into the nest. Usually after a minute or two it discovered its mistake and climbed up to the hole with the eggs. In the evening twilight, the nest was neglected while the entire family indulged in the flycatching and vigorous group flights that I have already described, and at dawn there was a shorter interval of neglect.

With these several reasons for neglecting their nest, the five Acorn Woodpeckers

kept their eggs less constantly covered than did other woodpeckers in which a single pair attends the nest. In 11½ hours, the five woodpeckers were in the hole a total of 549 minutes and they left it unattended for 141 minutes, or about one-fifth of the time. They kept the eggs most constantly incubated between 5:50 and 7:55 a.m. on May 4, when they sat a total of 114 minutes and left the hole unoccupied only 11 minutes. They were most neglectful from 6:21 to 8:13 a.m. on May 9, when they jointly occupied the nest only 80 minutes and left it alone for 32 minutes. One hundred and eight sessions by all the cooperating woodpeckers ranged from less than 1 to 17 minutes and averaged 5.1 minutes.

The single woodpecker that attended the eggs through the night entered far too late in the evening, and flew out much too early in the morning, for me to distinguish the color of its crown and learn its sex. Probably it was a male, as in other species of woodpeckers in which a single parent spends the night with the eggs and nestlings. Although I could not find where the other four attendants now slept, apparently they all lodged together, for once at daybreak I saw all fly toward the nest in close formation, as though all had left the same place at the same time.

By the middle of May, some mishap had befallen this nest. Although a woodpecker sometimes entered the hole, it always emerged promptly, and it was evident that the birds were neither incubating nor feeding nestlings. By the end of the month, this group was incubating in a hole a few feet below their former nest. The woodpeckers exchanged places on the eggs as frequently as before. This nest was no more fortunate than its predecessor, and by June 10 the birds had ceased to attend it. However, one of them sometimes entered the hole, and I saw a male, after staying within for a few minutes, fly out with an egg in his bill. He deposited it in a crevice in the broken-off end of a high branch of a neighboring tree and left it there. Woodpeckers not infrequently carry eggs from their nests; in addition to the Acorn Woodpecker, I have seen the Black-cheeked Woodpecker and the Olicaceous Piculet do so.

These Acorn Woodpeckers were zealous in territorial defense. They were not, like Golden-naped Woodpeckers, indulgent of the presence of Masked Tityras in the vicinity of their nest but chased them away as soon as they came near. I never saw a tityra resist them.

On August 22, 1955, we found another nest in which incubation was apparently in progress. This hole, which seemed to have been recently carved, was about 35 feet up in a massive charred trunk in a pasture, not far from a woodland which contained oak trees. Although it was past the middle of the day and rain was approaching, my companion, Robert M. Laughlin, stayed for over an hour to watch it. He reported that at least two males and one female were attending it. The longest interval that a woodpecker remained in the nest was 11 minutes. When I returned four days later to make more extended observations, the nest appeared to be abandoned. A party of Fiery-billed Araçaris that flew from the charred trunk as I arrived might have been responsible for its destruction.

THE NESTLINGS

On May 25, 1937, I found, in the hills east of the Río Chirripó in El General, a nest situated about 60 feet up in a towering, barkless tree in a new clearing in the forest. It contained feathered nestlings which looked through their high doorway, uttering from time to time a dry *churr* that resembled the call of certain species of

Centurus and *Tripsurus* more closely than did any note that I have heard from an adult Acorn Woodpecker. This nest was a long distance from my residence and very unfavorably situated for observation, but by watching on two mornings I was convinced that at least two males and two females were feeding the nestlings. Possibly there were additional attendants, for at times I had six grown woodpeckers simultaneously in view.

A large proportion of the food given to these nestlings consisted of insects that were caught in the air. Often they were seized at the end of a long outward or upward dart by the woodpecker. Then they were carried to the upper side of a horizontal branch, or even to a crevice in the side of an erect, decaying trunk, where they were prepared for the nestlings. The insects' wings were pulled off, and apparently their bodies were pecked and billed to soften them. Sometimes the woodpeckers prepared the food while clinging to the side of a low, decaying stub quite close to me, for they were almost fearless of their watcher. At other times they prepared it high up in the dead tree that held the nest. Then, with half-closed wings, they fell almost vertically 40 or 50 feet in the most spectacular fashion, skillfully checking their descent when they reached the level of the doorway. The nestlings' meals were passed to them while the attendant clung in front of the hole, without entering.

Near this nest I saw, on May 27, a young Acorn Woodpecker which flew with ease but still received food from others. He closely resembled the adult males, but the red of his crown was not so bright. He seemed too much older than the nestlings I was watching to belong to the same brood. Probably two families were established in this extensive clearing, for I noticed that all the woodpeckers did not live in such amity as those that attended the same nest; on the contrary, one sometimes chased another. To judge by the rate of development of other species of woodpeckers of about the same size, this young Acorn Woodpecker had hatched from an egg laid early in April. The breeding season of this woodpecker in El General accordingly extends at least from early April until late August. It continues later than that of the other woodpeckers of the region and is at a period when no acorns seem to be available for feeding the nestlings. In California, the Acorn Woodpecker may rear three broods in a year, sometimes in the same nest (Leach, 1925).

THE RELATIONSHIP OF THE ATTENDANTS OF A SINGLE NEST

The attendance of a single nest by a plurality of birds is widespread in the Acorn Woodpecker. According to Leach (1925), a whole colony participates in the excavation of the nest cavity, sometimes taking over three months to complete the task. Likewise, incubation appeared to be carried on by more than two individuals; changeovers in the hole were frequent, and the woodpeckers stayed with the eggs from 5 to 15 minutes at a stretch. This is in close agreement with my observations on incubation in Costa Rica, with the difference that the woodpeckers studied by Leach never left the eggs before the arrival of relief, whereas mine frequently did. At several nests, Leach made sure that at least four or five birds were bringing food to the nestlings, with the probability that the number of attendants was greater than this, for in each case a larger number of individuals seemed to be interested in the nest. Unfortunately, he was unable to distinguish the sexes of these woodpeckers, nor could he learn the number of eggs or young in the nests which they attended.

What is the relationship of the several woodpeckers that attend the same nest?

The presence of four males and one female at my first nest suggested polyandry. At my second nest in the same region, however, at least two males and two females were feeding an unknown number of nestlings, and this suggested that two pairs were nesting communally, as in the anis (*Crotophaga*). But it is improbable that both pronounced polyandry and communal nesting should prevail in the same population. Unfortunately, the three Costa Rican nests that I have seen were all inaccessible, and no information on the number of eggs laid by the Acorn Woodpecker in this country is available. In western United States, where the domestic arrangements of the Acorn Woodpecker appear to be quite similar, the size of the set is given in various standard reference books as four or five, or four to six. This is not an exceptionally large set for a woodpecker in the temperate zone and hardly even for one in the tropics. If two or more females often laid in the same nest, one would expect frequent reports of larger sets and a greater range in their size. Bent (1939: 214) stated that sometimes the Acorn Woodpecker's nest contains ten eggs, but an occasional set of double the normal size is on rare occasions found in the nest of a number of birds which do not breed communally.

I think it most improbable that Acorn Woodpeckers nest communally like anis, and I doubt that they are polyandrous. The other possibility is that a mated pair is assisted at the nest by immature or innubile helpers, as in White-tipped Brown Jays and other birds (Skutch, 1961). The situation in the Acorn Woodpecker appears to represent a further development of that found in the Golden-naped Woodpecker on the rare occasions when they rear a second brood; the young of the first brood sleep in the nest with the parents, eggs, and nestlings, sometimes bringing food to the latter. Obviously, further observations on the family life of the Acorn Woodpeckers are needed.

SUMMARY

Throughout its range from southwestern Oregon to western Panamá, the local distribution of the Acorn Woodpecker seems to be determined by the presence of oak trees. In northern Central America, it occurs from near sea level in the pine-oak woods of British Honduras to 9000 feet in Guatemala, but it is found chiefly above 5000 feet. In Costa Rica, it ranges from about 3000 to 10,000 feet. It prefers open groves and the woodland's edge to the interior of dense forests. Throughout the year, it lives in groups of three to six or more, which are quite sedentary, seldom straying far from stands of oaks.

Insects caught on the wing form an important part of the Acorn Woodpeckers' diet. Expert flycatchers, they are especially active in the pursuit of flying insects in the evening twilight. When acorns ripen, these woodpeckers often pluck a twig bearing one or more and carry it to a convenient branch or stub, where they place an acorn in a cranny and peck it to pieces with the bill. In Central America, whole acorns and pieces thereof are hidden away in crevices in bark and wood or amid tufts of lichens, but acorns are usually not stored in little holes made specially to contain them, as in the northern parts of the Acorn Woodpecker's range.

Acorn Woodpeckers are loquacious, often calling loudly *rack-up rack-up*, *r-r-r-rack-up*, and similar notes in a strong, deep voice. When several rest close together, they communicate in lower tones.

From one to five individuals have been found sleeping in high holes carved by themselves. Unlike other woodpeckers, they frequently retire very late, when it is

nearly dark. Exceptionally, they go to roost early. They may remain within the cavity until sunrise, especially on frosty mornings.

In Costa Rica, the breeding season extends at least from early April to late August. Three nests ranged from about 35 to 70 feet up in dead trees and were inaccessible. At one nest, incubation was performed by certainly four and probably five individuals, only one of which was a female. Changeovers during incubation were frequent, and in nearly 12 hours of watching, the longest continuous session lasted only 17 minutes. The average length of 108 sessions was 5.1 minutes. A single woodpecker, of undetermined sex, occupied the nest by night. At another nest, at least two males and one female shared incubation.

At yet another nest, feathered nestlings were fed by at least two males and two females. The young birds were nourished largely on insects which were caught in the air by the adults and carefully prepared before being given to them.

Although the situation at some nests suggests polyandry and that at others communal nesting, available evidence points to the conclusion that a single breeding pair is assisted by unmated helpers. In its social habits, the Acorn Woodpecker seems to represent a further development of the situation exemplified by the Golden-naped Woodpecker. But definite conclusions cannot be reached without further studies.

OLIVACEOUS PICULET

Picumnus olivaceus

In the tropics of both the Eastern and Western hemispheres are found pigmy woodpeckers which are among the smallest of all birds. The dwarf woodpeckers of the New World are included in the genus *Picumnus*, which is represented in South America by about 25 species, but in Central America by only one, the Olivaceous Piculet. This diminutive woodpecker is about three and a half inches in length. In the male, the top of the head is dull black, finely streaked with orange on the crown and behind this minutely dotted with white. The remaining upper plumage is largely olive. The tail is dull black, with a broad longitudinal stripe of pale buffy yellow along its center. The sides of the head are buffy olive, with a row of whitish spots above the ear-coverts. The throat and upper breast are likewise buffy olive, and the more posterior under parts are buffy yellow with broad, poorly defined streaks of grayish brown or olive. The female differs from the male in the markings of her crown, which is without orange streaks and sparsely dotted with white like the hind-head. In both sexes, the bill is black; the eyes are brown; and the feet are dark.

The Olivaceous Piculet ranges from the Caribbean littoral of Guatemala southward through Central America to northern South America. Its distribution in Central America is curiously and inexplicably discontinuous, for in Honduras and Nicaragua it is recorded only from the eastern lowlands, whereas in Costa Rica it is unknown on the eastern side of the Cordillera and is present only on the Pacific slope south of the Gulf of Nicoya, where it is abundant, especially in the valley of El General. In this region, it is a common resident up to at least 3000 feet above sea level, and sparingly to 4500 feet and even higher. Strangely, this species, which in Central America is confined to the Tropical Zone, occurs chiefly in the Subtropical Zone in Venezuela, from about 3600 to 7500 feet above sea level (Phelps and Phelps, 1958:259).

In Central America, the Olivaceous Piculet inhabits light but often densely entangled second-growth vegetation rather than the high rain forest. Some writers (Carriker, 1910:594; Peters, 1929:438) have detected a preference by the piculet for tangles of vines, bushes, and small trees on low ground in the vicinity of water, but I have found it not uncommon far up on hillsides where the second-growth vegetation was lush. It is fond of shady pastures and plantations and has even nested in our garden. Occasionally it enters the primary forest, but I have never found it far from the edge. The piculets live in pairs or family groups at all seasons. Not as shy of man as are most of the larger Central American woodpeckers, they often permit a close approach.

FOOD

Although nearly all woodpeckers creep in an upright position over the trunks and thicker branches of trees, supporting themselves with their rigid, spiny-tipped tail feathers, the piculets, as far as I have seen, neither hunt nor rest on thick limbs or trunks, but climb over thin terminal twigs of bushes and low trees, or along slender dead vines, clinging with their feet but never propping themselves with their tail feathers, which lack acute and rigid tips. Often they perch upright on a twig like any finch or tanager.

Although their bills are so short and not especially sharp, the piculets, like the true woodpeckers they are, peck constantly in search of food, confining their attention to branchlets that are usually far thinner even than the birds themselves. Such slender twigs are almost never investigated by the larger woodpeckers, and the piculets have almost a monopoly on the edible things hidden within them. Only the curious little Plain Xenops, a brown ovenbird not much bigger than the piculets, competes with them for the insects that lurk within these thin dead twigs and vines. It is a curious fact that this passerine, so different from the piculet in lineage but so like it in manner of foraging, should resemble it also in voice and should sometimes nest in its abandoned holes.

Like many other woodpeckers large and small, piculets are fond of ants, and specialize on those which make their homes in the pith of slender dead branches. When the bird has with repeated strong, hammer-like blows perforated the wood and the ants run out of their retreat, it eagerly picks them off and devours them and then busily extracts the white larvae and pupae, interrupting this activity from time to time to snatch up additional adults which have sallied forth from their desolated home and might otherwise escape. The immature stages of ants are the principal food of nestling piculets, almost their sole nourishment until they are feathered. In addition to ants, piculets remove insects of other sorts from the dead twigs and vines in which they live, and occasionally they even uncover some edible morsel in the heart of a green leafy shoot. They also at times peck into the petioles of great leaves, such as those of the guarumo (*Cecropia*) and chumico (*Pourouma*), that have lodged among branches or vine tangles after becoming detached from the parent tree. The tiny birds know in some mysterious fashion just where they must perforate the dead petiole in order to extract the grub hidden in its core.

In streamside woodlands in the upper Magdalena Valley of Colombia, the Olivaceous Piculet is somewhat more versatile in its mode of foraging. According to Miller (1947:363), it performs "like nuthatches, titmice, or woodpeckers, often in rapid succession, as occasion demands." It can progress head downward over a trunk. Probably the more arid environment of this region has caused the piculet to adopt nuthatch-like modes of hunting which it has little occasion to employ in humid southern Costa Rica.

VOICE

In the piculet, the typical woodpecker churr has been reduced to a fine, rapid twitter or trill, which is at times somewhat insect-like and shrill, but at its best is clear, soft, and melodious in a small way. Another utterance of the piculet is a clear, sharp monosyllable. I have never found this little woodpecker beating a tattoo on resonant dead wood, in the manner of its larger relatives.

NEST BUILDING

For a long while after I became acquainted with the piculet, I wondered whether a bill so short and relatively thick could be an efficient tool for carving a nest cavity, and it seemed more likely that the bird laid its eggs in a hole which it found already made. But I misjudged the piculet, which in spite of its small size is every inch a woodpecker, and excavates its own nest chamber in the best tradition of its family. Yet there are limitations in the uses to which so diminutive a tool can be put. Just

as the piculet finds its food in twiglets too thin to be worthy of the notice of its larger relatives, so it must carve its holes into wood softer than many of the woodpeckers would deign to use. And since the stubs of trees with very soft wood, or those far advanced in decay, are likely to topple over if high, as a rule the piculet contents itself with a nest near the ground.

In the valley of El General, a favorite site for the piculet's nest is a dead, decorticated stub of the burío (*Heliocarpus*), a tree whose wood is almost as soft as that of the more widely known balsa. The burío is far more common in the upper portions of the Tropical Zone, where it springs up quickly and abundantly in abandoned clearings. Decaying fence posts are also frequently used for the nest if the fence is near sheltering thickets. Thirteen nests that I have seen varied in height from 35 inches to 30 feet above the ground. Six were less than 5 feet up, and only one was above 15 feet.

On April 21, 1937, I found that a pair of piculets had begun a hole in a low stump of a burío tree in a weedy clearing at the forest's edge. The entrance of this new hole was only 8 inches above that of an older one which in the preceding October and November had been used as a dormitory. Although when first discovered the fresh excavation scarcely extended below the round orifice that would be the doorway, the task of carving out the soft wood went so swiftly that after two working days it was deep enough to contain the male and female piculets together. When it had reached this stage, I set up a blind and watched the little woodpeckers at work. Although this hole was used as a dormitory, its construction was probably similar to that of a nest.

At 6:40 a.m. on April 24, the female piculet arrived and entered the hole, and a minute later her mate followed her in. While together in the cavity, they communicated in very low, dry trills, such as I also heard from a pair with eggs while they lingered together in the nest in the early morning. Presently the male stuck his head through the doorway with his bill full of wood chips, which he was slow in dropping. Probably pushed by his mate from below, he flew out after this; then she threw out many billfuls of flaky wood particles, bringing them up in rapid succession, and merely sticking her head through the orifice in order to drop them. For the next half-hour she continued alternately to chisel and to throw out the particles she had loosened. The carving proceeded rapidly, and after a few minutes of tapping inside the hole she had much loose debris to eject. Once she removed 14 billfuls in quick succession.

At 7:13 the male returned to do his share of the work and the female flew away. He did not labor as energetically as his mate, but hammered less and threw out fewer billfuls of chips. When he appeared in the doorway with his bill and mouth overflowing with wood flakes, he often held them awhile before releasing them; then he would delay, looking out instead of promptly descending for more, in the efficient manner of the female. After he had labored in this leisurely fashion for 35 minutes, he flew off without waiting for his partner to return.

For 37 minutes the hole remained deserted, and then the male returned to resume the task. He worked, still unhurriedly, for 11 minutes, when his mate arrived to relieve him. She joined him inside the hole, and there was a low trilling such as I had heard earlier in the morning. Then for a while the male trilled with his head in the doorway. Next he slipped out and loitered in front, obstructing the entrance.

The female, eager to resume operations, hurried him off with a few gentle pecks, then began to throw out chips. She toiled for 26 minutes, then departed without waiting for the male to return.

Five minutes later, he flew up and promptly resumed the work of excavation. He labored harder than early in the morning and remained at his task for 13 minutes. Then he left without waiting for his mate. This hole was finished in 4 or 5 days.

On January 7, 1948, I watched another hole, so recently begun that sometimes the piculets worked from outside and sometimes while they were within. The male of this pair was taking the leading part. In two hours, his work periods lasted for 26 and 47 minutes, but the female labored for only 15 minutes. These piculets also trilled when they met at the nest.

The piculets' completed chamber is ovoid in form, widest near the bottom. A typical hole extended to a depth of 4 inches below the lower edge of the doorway. Its greatest diameter was $2\frac{3}{8}$ inches from side to side. Another cavity was only $3\frac{1}{2}$ inches deep and $2\frac{1}{4}$ inches in diameter. The doorway varies from $\frac{7}{8}$ to $1\frac{1}{16}$ inch in diameter. The chamber is not lined for the reception of the eggs, which rest on loose chips in the bottom, as with other woodpeckers.

The piculets must often try again and again before they find wood of just the proper degree of hardness for their nest cavity. One fence post that contained a hole in which a pair were incubating held also five other cavities which apparently had been made by the same pair in vain attempts to complete a chamber. The most advanced of these abandoned diggings penetrated the wood for 2 inches. In other posts of the same row were several of these uncompleted cavities, some of which had been barely begun. The minute birds must have made many futile attempts, and labored much in vain, before they found a spot in the posts which met their needs.

THE EGGS

The piculet nests early, and in El General, 3000 feet above sea level, I found a set of eggs well advanced in incubation as early as January 24, 1937. In one nest, the three eggs were laid on consecutive days, the last before 8:30 a.m. Of 12 accessible nests, 8 held three eggs or nestlings, 3 had two eggs or nestlings, and one contained a single nestling. The eggs are pure white and glossy. Those in one set, which had been abandoned, measured 16.3 by 12.7, 17.5 by 12.3, and 15.9 by 11.9 mm.

In 12 nests in the valley of El General, 2000 to 3000 feet above sea level, eggs were laid as follows: January, 3; February, 4; March, 1; April, 3; May, 1. Thus the piculet nests chiefly in the dry season, which in this region extends from December or January to March or early April.

INCUBATION

The male and female sleep together in the nest cavity before the eggs are laid. On January 15, 1939, I found a piculets' hole 10 feet above the ground. It was in a decaying stub in a grove of coffee and bananas but was close to the forest edge. No egg was present. The male was usually the first to retire into the cavity in the evening. On several occasions, I saw his head framed in the doorway about sunset. One evening I found him looking out of the hole at 5:10, and he lingered constantly in this attitude until his mate joined him for the night at 5:48. He was very tame and did not leave his chamber when I stood close beside the low stub. The first egg

was laid on January 27, after the pair had been sleeping in the hole for 12 days or more. I had a similar experience with another nest later in the season.

After incubation has begun, the pair, as I have seen at a number of nests, continue their habit of sleeping together in the nest chamber. By day they sit alternately, in the manner of all other woodpeckers I have studied. On January 28, 1937, I began at 1:10 p.m. to watch nest 2, where incubation was in progress. I continued watching until 6:00 p.m., and on the following day I watched without intermission from 5:30 a.m. until 12:06 p.m. Although on this day I started to watch at dawn when other birds were becoming active, for the next 20 minutes everything remained still about the chamber in the fence post where the piculets nested and slept. Then, at 5:50, I heard low trills issuing from the tiny round doorway, and almost at once the male looked out. A minute later he flew away. Then the female peered through the orifice, but she promptly went down again to keep the eggs warm. After an absence of a little over half an hour, the male returned at 6:23 and entered the nest, without giving his mate time to leave. She delayed for 3 minutes looking through the doorway before she went to forage. She took a longer outing than the male and was absent for three-quarters of an hour. Returning at 7:09, she alighted beside the doorway, gave a low, short trill, entered, then looked out several times before she disappeared inside. Now the male looked out and soon flew away.

Thus, in their mode of replacing each other on the eggs, the piculets departed from the custom of the majority of the woodpeckers that I have studied, for these rarely enter the hole before the mate has left. But they acted as Golden-naped Woodpeckers sometimes do. In this species, the male and female also sleep together in the nest, and they likewise may stay inside together for brief intervals when one replaces the other on the eggs. Usually the two piculets were in the hole together for only a minute or two as they exchanged places, but once, in the evening, the female delayed inside for 8 minutes after her mate had entered to relieve her. At other times, the member of the pair which had been incubating slipped out and flew away while the newcomer clung to the outside of the post near the entrance, thus effecting the change of occupancy in more conventional woodpecker fashion. This happened at only two of the ten changeovers which I witnessed.

Usually the piculet arriving to enter the nest delivered a low, musical trill while it clung in front of the doorway, then it slipped inside. These diminutive woodpeckers were not as cautious in entering their hole as are many of their larger relatives or many hole-nesting birds of other families. Even when one returned to the nest and found it unoccupied by the mate, it did not cling below the entrance and delay whole minutes while it alternately looked about and peered inside, to make sure that no enemy was lurking within or watching it from outside, but it slipped rather promptly into the little cavity. Frequently, however, one would interrupt its sitting to climb up to the doorway and survey the landscape, often continuing this for several minutes together. When the female returned for the night at 5:10 p.m., the male, which had been inside the hole since 3:55, did not fly forth to feed. But, as the sun set, he frequently came to gaze through the doorway, while his mate remained hidden, evidently warming the eggs. Finally he, too, retired into the bottom of the chamber as the light faded.

The piculets' day may be taken to extend from 5:51 a.m., when the male first left the nest in the morning, to 5:10 p.m., when the female entered for the night. Considering only those portions of my record which fell between these hours, each

member of the pair took five sessions on the eggs, alternately. The male's completed sessions ranged in length from 40 to 112 minutes and averaged 66 minutes. The female's turns in the nest ranged from 30 to 69 minutes and averaged 50 minutes. The male's total time in the nest was 331 minutes, the female's 251 minutes. After the first three quarters of an hour of my watch, when the piculets seemed to be disturbed by my presence, their nest was continuously attended. Since each member of the pair remained in the hole until its mate returned to replace it, its own time in the nest was determined by the mate's eagerness to return, rather than by its own willingness to sit. Largely because the female enjoyed the longer recesses, the male spent considerably more time on the eggs than she.

A few days after I watched this nest, it was discovered by somebody who cut out the side, exposing the cavity, but leaving the eggs unharmed. I replaced the slabs which had been split from the wall of the chamber and tied them in position, but they did not fit closely. The pair of piculets continued to attend their nest for a day or two, but then their eggs vanished. Nevertheless, the birds slept in their ruined nest for two or three nights more, after which their post was pushed or fell over.

Eighteen years later, at a point about ten miles from the foregoing nest, I studied another nest in which the piculets were incubating a second brood. My watches extended from 12:05 to 5:45 p.m. on May 5, 1955, and from 5:25 a.m. to 12:05 p.m. on May 6, thus covering all hours of the daytime. This hole was occupied at night by a young bird of the first brood in addition to the two parents; since the former, as far as I could learn, took no part in incubation but remained away all day, its presence hardly influenced the movements of the incubating adults. On May 6, the female was the first to leave in the morning; she flew out at 5:44 a.m. The young piculet left at 5:48, and at 6:28 the male departed without waiting for his mate to relieve him. After an absence of 35 minutes he returned, but 2 minutes later the female at last came back and replaced him.

In the evening, the male entered the nest at 4:24, the female at 5:14, and the young bird at 5:32; all remained for the night. The parents' active day may be considered to extend from 5:44 a.m., when the female first left the hole in the morning, to 5:14 p.m., when she retired for the night. In this interval of 11.5 hours or 690 minutes, the female took five sessions on the eggs, ranging in length from 7 to 89 minutes and averaging 55.2 minutes. The male's five completed sessions ranged from 2 to 76 minutes and averaged 44.4 minutes. In addition to this, he remained with the eggs for 44 minutes after his mate's departure in the early morning and had been with them for 50 minutes when she returned for the night. Moreover, he happened to be in the nest when I began and ended my study at midday, and parts of two sessions which were not timed in full add 17 minutes to his time in the nest. Thus, in the diurnal period of 11.5 hours, the male was in the nest for a total of 333 minutes, the female for 276 minutes, and it was unattended for three periods which totalled 81 minutes. The eggs were incubated for only 88.3 per cent of the day, instead of 100 per cent of my observation periods, as at the first nest.

The reason why this pair of piculets did not attend their nest continuously seemed to be that the female's rhythm was somewhat slower than the male's. Not only did she sit continuously for periods somewhat exceeding his longest, but she remained away for still longer intervals, once for 81 minutes, once for 91 minutes, and once for 103 minutes. Her partner apparently could not endure such long fasts. Accordingly, on three occasions he deserted the eggs before her return. But then he

probably came back sooner than he would have if he had known that his mate was covering the eggs. On two of these occasions, he incubated until she arrived, 2 and 10 minutes later. The third time that he returned to the eggs which he had left unattended, he found that the female had entered the nest in his absence, but she relinquished it to him, although she had been sitting for only 7 minutes. Apparently, the male did not make contact with his mate when he went off to forage before she arrived to replace him.

At this nest I witnessed nine changeovers. Twice the newcomer waited beside the doorway until its mate emerged, and seven times it entered first, then its partner left from about 15 seconds to 1½ minutes later. Sometimes the male trilled while he awaited his mate's departure. In making the calculations given above, I disregarded the brief overlaps when both of the piculets were in the nest together and counted each partner's session as beginning when the bird entered the hole, ending when its mate entered to replace it on the eggs.

At nest 4, the three eggs were laid on January 27, 28, and 29. One hatched on February 10. By the following day, another egg had hatched, but one of the nestlings lay dead in the bottom of the nest. By the early morning of February 12, both nestlings were dead in the nest beside an unhatched egg. The cavity had been invaded by small ants, which crawled over the bodies of the newly hatched piculets and apparently had caused their death. Nocturnal incubation, at least, had evidently begun with the laying of the first egg. Assuming that but for the interference of the ants the third egg would have hatched on the day after the second, that is on February 12, the incubation period was 14 days. At another nest, I found two eggs that were apparently newly laid on May 1. One had hatched by dawn of May 14, and the other hatched in the following night or in the early morning of May 15, 12 hours or more after the first. The incubation period was at least 14 days.

THE NESTLINGS

Newly hatched piculets have naked pink skin and tightly closed eyes. The parents often leave the empty shells in the nest for several days. Looking into a nest with mirror and light four days after the last egg hatched, I saw a nestling whose eyes were not yet opened trying to swallow a piece of shell, but it did not succeed while I watched. The shells gradually vanished, and perhaps this observation furnishes the clue to their disappearance. There were still fragments of shell in this nest five days after the last egg hatched. The parents remove all waste except the shells and at all times keep the cavity irreproachably clean.

Although both eggs hatched in a second-brood nest, one of the nestlings vanished after a few days. From 5:30 to 10:31 a.m. on May 21, 1955, I watched the parents attend the survivor, now six or seven days old but still sightless and naked. In the 5 hours, the male brought food 5 or 6 times and the female 8 times, so that the nestling was fed at the rate of about 2.8 times per hour. The food consisted almost wholly of small white objects which appeared to be the larvae and pupae of ants, although some seemed rather long for this and may have been the larvae of beetles or other insects which when immature inhabit the interior of dead twigs and vines. Once the female brought a small, dark object of unknown kind. The male once removed waste from the hole. In the 5 hours, he brooded the nestling six times, for periods ranging from 11 to 25 minutes and averaging 16 minutes. The female's seven periods of brooding ranged from 4 to 28 minutes and averaged 17.9 minutes.

The male was in the nest a total of 96 minutes; the female was in the nest a total of 125 minutes. In all the nestling was brooded 221 minutes or 73.7 per cent of the time. The young piculet of the first brood, now 87 days old, still slept in the nest, but it did not feed or otherwise attend the nestling, as far as I could learn.

On April 18, 1939, I watched a nest from dawn until 8:00 a.m. This nest held two nestlings, nine and ten days old. As the light grew stronger, the adult female was the first to look through the doorway. After lingering for 15 minutes with her head framed in the orifice, she drew back inside. Four minutes later she looked out again, this time for 11 minutes. Finally, at 6:05, a whole hour after the first birds had begun to sing in the gray dawn, she sallied from the nest to begin her day's work. Her mate then took possession of the doorway. Although the female began to forage late, she was efficient, and after only 3 minutes she returned with a billful of white ant pupae, only slightly less than she was accustomed to bring later in the day. As she came to the doorway, the male tried to leave, but her breast blocked his exit. Finally he managed to slip past her and fly away. Then she entered, doubtless fed the young down inside where I could not see them, and stayed to brood. After 15 minutes inside she emerged with a billful of waste material and carried it away. After another 15 minutes, the male and female came together with bulging billfuls of white larvae or pupae. The female entered after slight hesitation, but the male, when he saw me sitting without concealment at no great distance from the nest, went off and did not return for 4 minutes. He was always more timid than she; if he happened to be in charge of the eggs or nestlings when I came to inspect the cavity, he would fly away and remain out of sight. The female, on the contrary, would flit around within a yard or two of me as I looked into her chamber.

The female, as was to be expected from her greater devotion to the nest, brought food much more frequently than did her mate. She brought food five times and he brought food twice in the first 2 hours of their active day. The female scarcely hesitated to enter the hole in my presence; the male often hung back for several minutes, yet not long enough to account for his less frequent visits with food. The two piculets always entered the nest hole in this manner. The parents always came with bill and mouth laden to overflowing with elongate white bodies that projected on both sides, forming a miniature grape-like cluster. Although I could not positively identify these objects, from having watched piculets extract bodies of the same appearance from ant-infested slender branches, fill their bills with them, and fly off as though to a nest, I have little doubt that they were larvae and pupae of ants, which seem to be the principal food of nestlings of all ages, and almost their only nourishment during their first ten days of life. The nestlings, still in pinfeathers, were brooded three times by the female, for 15, 18, and 11 minutes, and once by the male, for 16 minutes—a total of 1 hour during my two-hour watch.

The nestlings, it will be recalled, were blind and naked when hatched. When they were five days old, the black buds of the pinfeathers were sufficiently prominent beneath the skin to be noticed in the mirror that I used to examine them. When the nestlings were eight days old, the pinfeathers were pushing through the skin and the eyes were opening. Now, when I stuck a finger into the nest, the young would reach up almost to the doorway and make a continuous buzzing sound, as doubtless they did when a parent came with food. When the piculets were 16 days old, their feathers began to unsheathe, and at 18 days they were fairly well feathered. The oldest was 22 days old before I saw a nestling's head in the doorway.

On the morning of May 2, when these young piculets were 23 and 24 days of age, I again watched their nest. When I arrived in the half-light at 5:34 a.m., the adult female was looking through the doorway. She continued in this position for 6 minutes, then some small animal shook the vines that hung close about the nest and sent both parents prematurely into the open. As soon as they left the doorway clear, a young bird looked out, but it withdrew into the interior at once. Nearly an hour passed before the adult male arrived with a billful of ant pupae at 6:35. A nestling was in the doorway and called with sharp little notes when it saw the adult approach. The male clung below the doorway and passed the food to the nestling. Then he hastily flew off, for the young piculet pecked hungrily at him for more. At 6:44 the adult female, whose hunting had apparently been unproductive, arrived with an empty bill. She seemed about to enter, but the young bird pecked so vigorously at her that she desisted and promptly fled. She brought no food until 7:14, by which time her mate had already fed the nestlings twice.

Although a fortnight earlier the female had fed the nestlings five times and the male had done so only twice, now in the first 2 hours of activity the male fed the nestlings five times and the female fed them four times. The male had overcome his distrust of me and was scarcely more shy than his mate in approaching the nest in my presence. This day for the first time I saw the piculets bring something other than white pupae and larvae to this nest. The dark bodies that I saw in their bills were apparently mature ants, but one dark object that was passed to a nestling seemed too long and slender to be an ant and was probably a larva of some kind. Yet ant pupae still formed the great bulk of the nestlings' diet.

Now all the food was delivered to the nestlings while the parents clung in front of the doorway. The young piculets, instead of gaping widely and waiting passively for the parents to place the food into their open mouths, as passerine nestlings usually do, snatched it from the bills of their attendants with rapid, grasping bill movements which from a slight distance resembled pecking and biting. The nestlings continued these movements—sharp forward thrust of the head, closing of the opened bill—after they had taken all of the food that the parent had brought, and it appeared that they were vigorously pecking their parents. Frequently, after having delivered all the food, the parent moved a little higher, bringing its breast opposite the doorway; then, through the binoculars at close range, I could see that a nestling plucked rapidly and vigorously at the breast feathers, as though trying to eat them, but it did not actually peck.

This treatment was not at all agreeable to the parents, who usually fled the moment they had delivered the last morsel—and sometimes before. Once when the female had brought a billful of ant pupae and passed most of them to a nestling, the latter's plucking at her breast feathers drove her away before she had delivered the last item. She rested briefly on a neighboring vine, brought forward to the tip of her bill a white object which had evidently been far back in her mouth, then returned to the doorway and quickly passed it to the hungry nestling. I have watched similar behavior at mealtime on the part of other woodpeckers which are fed with particles carried in the bill rather than by regurgitation. Occasionally I have seen a young Golden-naped Woodpecker actually pull a feather from its parent's breast.

By noon of May 3, both young piculets had left this nest, one certainly not more than 24 days old, the other either 24 or 25 days of age. From another nest, a single fledgling departed when it was 25 or 26 days old. In Surinam, Haverschmidt (1951:

200) found the nestling period of a Sundevall Piculet to be about 28 days. Accordingly, the nestling period of piculets is substantially shorter than that of larger tropical woodpeckers. Although the Olivaceous Piculet commonly lays three eggs, I have not known it to rear more than two young. Sometimes the third egg fails to hatch, and sometimes one or two nestlings vanish a few days after they hatch. In plumage, all the fledglings that I have seen resembled the adult female, except that the spots thickly sprinkled over the top of their heads were grayish instead of white, and the ground color of the crown was a lighter shade of brown, so that the spots did not contrast so conspicuously as in the adult. After the departure of the young, I found the nests perfectly clean.

POSTFLEDGING FAMILY LIFE

In the late afternoon of May 3, 1939, I watched a hole which two fledglings had left for the first time earlier in the same day. At 4:10 p.m., the adult male came alone to the vicinity of the nest. He repeated over and over a clear, sharp monosyllable and more rarely he trilled, the while flitting among the vines before the doorway, nervously twitching his wings, and at times pecking on a vine or twig. He lingered alone near the nest until 4:35, when the fledglings appeared, but soon all drifted off through the thicket again.

After 10 minutes, the whole family returned. The adult female went to the doorway of the nest to look in, and while she was there a fledgling followed and clung to her back. Both birds dropped away, but when the parent again went to the doorway, the fledgling followed once more and entered the hole without difficulty, at 4:58. The adult female then went in, also. Soon the second fledgling flew toward the nest, but it struck the trunk well above the hole. It then dropped down too far and toilsomely worked its way upward to the entrance, while the adult female looked down at the young bird, and the male flew to the orifice. When the fledgling reached the opening both adults made way for it, and it entered the nest without further delay, at 5:02. Soon after the second young piculet had entered, the female flew out and away. Then the male went in and threw a few particles of wood out through the doorway. At 5:07 he also flew away.

At 5:16 the female returned and entered for the night, but she looked frequently through the doorway until her mate arrived at 5:40. As he came to the entrance, one of the fledglings, sticking forth its head, plucked hungrily at the feathers of his breast, but the young were not fed after they entered the nest.

Next morning, I watched the piculets begin their day. At 5:30 the female's head appeared in the doorway, and a minute later she left. Then the male promptly took possession of the aperture and remained there for 6 minutes. After his departure at 5:37, a fledgling looked out. Two minutes later, the parents trilled among the vine tangles nearby; the fledgling answered with sharp monosyllables and flew forth to join them. At 5:41 the second young bird followed. Then all four flew away to seek food. I looked into the nest and found it perfectly clean, although the parents had removed nothing since the preceding evening. Later in the morning, I saw the fledglings pecking on slender branches, but they found nothing to eat while I watched.

During the remaining four weeks of May, the two young piculets continued to pass the nights with their parents in the hole where they had been hatched. One

afternoon when a light rain was falling, I found all four in the chamber at 5:25, although it was still broad daylight, an hour before dusk. In June, when their slender dead trunk toppled over and leaned against a neighboring one, the piculets abandoned it as a dormitory.

The first return to the nest of two fledglings of another family was even more promptly accomplished. On March 17, 1955, two young piculets left a nest 15 feet up in a dead burio trunk close by our house, and that evening I watched them re-enter it. A few minutes before 5:00, the family of four flew into the top of an orange tree about 10 yards in front of their nest. From this, one of the parents flew to the stub and entered the hole, then it rejoined the others in the orange tree. This round trip was repeated half a dozen times, and all except possibly one of these trips were made by the adult male. Then, while he was at the nest, his mate joined him there and clung in front. The two fledglings now followed their parents to the burio trunk. They alighted on neighboring parts of the bark instead of at the doorway, as their parents had done, but without difficulty they climbed to the orifice and went in. Ten minutes after arriving in the vicinity of the nest, the whole family was settled within for the night. In this interval, there was much conversation in high, weak voices and some trilling, followed by silence when the last of the four had entered.

Next morning, the adult male left the hole at 5:43 a.m., the female at 5:51, and the fledglings at 5:53 and 5:54. In the following days, they usually sallied forth before sunrise. By the middle of April, this cavity was abandoned. As far as I have seen, young piculets who have once left the nest are not fed after their return to it, in the evening or early morning, as fledgling Golden-naped Woodpeckers sometimes are. After their first flight, the young birds retire in the evening and leave the dormitory in the morning at about the same time as their parents. Haverschmidt (1951:200) found that a young Sundevall Piculet slept in the nest hole with its parents for at least 62 days after fledging.

In 1945, a pair of piculets nested in a decaying fence post in front of my house. Their single surviving fledgling took wing on March 22. From then until at least the following July 5, or over a period of three and a half months, the young piculet continued to lodge in the hole in this post along with his parents. On quitting the nest, he resembled all the other fledglings that I have seen, but by mid-May, two months after he could fly, he had an orange-streaked crown like the adult male.

On April 23, 1936, I discovered, among rank second-growth vegetation near the forest's edge, a piculets' hole about 10 feet up in a weak, tottering stub. Watching at the following dawn, I saw four piculets leave this cavity, in which they had slept. One was a male and at least two had light-spotted heads as do the females and young; the fourth popped out so suddenly that I did not see it well. I continued to watch, and at 6:26 a.m. a female returned, remained in the cavity for 18 minutes, then darted forth bearing in her bill something large and white. Although I did not have a satisfactory view of this object, I could not imagine what it might have been if not an egg. On several visits later in the same day, I failed to find the hole occupied, and no piculet arrived to sleep in it that evening. Such behavior was difficult to explain. Possibly the egg was thrown out because it was unseasonable or infertile. I have seen a Black-checked Woodpecker remove a yolkless egg from its nest, and an Acorn Woodpecker carry out one that I could not examine. Moreau (1942:39) reported that a White-rumped Swift ejected from its nest an infertile egg

that had been incubated for a week. But I cannot surmise why the family of piculets abandoned their dormitory after this episode.

Piculets may carve their sleeping holes at any season. About 100 feet from the stub where four individuals had slept in April and vanished, I found, on the following October 25, another hole in a low stump in a newly made clearing close by the forest. The doorway was only 5 feet above the ground. The bright color of the wood surrounding this orifice, and the fresh chips that littered the herbage below it, showed that the hole had been quite recently carved. Next morning, after the light had grown bright, I watched a male, then a female, evidently a mated pair, emerge from this cavity and fly to the neighboring woodland. On the morning of November 14, a male and then two females came out of this hole, where they had slept. At day-break on December 25, only a single female emerged from the hole. Looking about for a new dormitory, I discovered a freshly carved hole in the stump of a burío tree 50 feet from the old one. This was also only 5 feet above the ground. On the morning of December 30, I watched two piculets leave this new hole. The old hole was now abandoned. By January 25, 1937, this new cavity was also deserted, and I tried in vain to discover where the pair took shelter from the cold air.

Piculets sometimes sleep singly, for in April, 1937, I discovered a freshly carved hole which during the next fortnight, at least, was the dormitory of a lone male.

From the foregoing observations, and others which need not be given in detail, we may conclude that young piculets continue to sleep with their parents for at least three or four months after they are fledged. The greatest number of individuals that I have found in a dormitory is four, which is in accord with my experience that usually no more than two young are reared in a nest. After the dispersal of the young, the adults sleep in pairs, but even as late as November they will hospitably receive in their dormitory a third individual—possibly their own offspring, or maybe an adult left single by the loss of its mate. Piculet families apparently do not remain intact as long as do those of the Golden-naped Woodpecker, which often stay together until the beginning of the following nesting season. Because their holes are in low stumps in very soft wood that quickly decays, they do not last as long as the high cavities which Golden-napes carve in trees of more resistant wood. Thus, piculets must change their domicile more frequently, so that it is more difficult to follow their history throughout the year.

THE SECOND BROOD

Thus far, except for incidental references, we have followed the history of piculet families as though only a single brood were reared in a year. This appears to be the usual course in El General, where I have found only one nest definitely known to contain a second brood. Early in February, the piculets that attended this nest laid their first set of three eggs, from which a single young was fledged. After its departure on March 21, the young bird continued, as usual, to lodge in the nest cavity with its parents. By May 1, this hole contained two fresh eggs, and no more were laid. As already related, the young piculet of the first brood slept with its parents in the nest while they hatched out these eggs, but it took no interest in them, as far as I could learn. On May 22, the hole was invaded by fire ants, which devoured the nestling. Ants appear to be one of the chief enemies of nesting piculets, and I have known two nests to be destroyed by them.

Some years earlier, I had found a similar situation in a nest of the Lafresnaye

Piculet of the eastern foothills of the Andes. On August 17, 1939, the nest held two eggs, which the piculets had already begun to incubate. To my surprise, I found three full-grown piculets sleeping in the cavity with the eggs. One was a male with orange-red streaks on his head. The other two had the white-spotted brown forehead and crown of females. Apparently, the third occupant of the Lafresnaye Piculets' nest was the parents' offspring from an earlier nesting (Skutch, 1948*b*). So, too, the second male which Haverschmidt (1951) found sleeping in a nest of the Sundevall Piculet in which incubation was in progress may have been the offspring of the breeding pair. One of the two males at this nest disappeared before the eggs hatched. On the rare occasions when the Golden-naped Woodpeckers rear a second brood, the young of the first brood lodge in the nest with their parents and the eggs and then with the nestlings. These young Golden-napes may bring a little food to the nestlings.

SUMMARY

On the Pacific slope of southern Costa Rica, the Olivaceous Piculet inhabits shady pastures and plantations, second-growth vegetation, and the forest edges, from sea level up to at least 4500 feet. It finds its food chiefly in thin dead branches and twigs, to which it clings in the most diverse positions, without using its rounded tail for support. Ants and their immature stages form an important part of its diet, which includes also insects and larvae of other sorts.

Its call or song is a fine rapid twitter or trill, which at best is clear, soft, and melodious. It also utters a clear, sharp monosyllable. Apparently it does not beat a tattoo with its bill.

The neatly rounded cavities used both for nesting and for sleeping at all seasons are carved in dead trunks of very soft wood (*Helicarpus* being a favorite tree) or in decaying fence posts. The holes are at heights ranging from about 3 to 30 feet above the ground, although those above 15 feet are rare. Male and female share the task of carving out the chamber. Each works in the absence of the other and may continue for from one half to three quarters of an hour at a stretch. One hole was completed in four or five working days.

The piculet nests chiefly in the dry season, from January to April, but laying continues until at least May. Three or, less often, two pure white eggs are laid on consecutive days.

Both sexes sleep together in the breeding nest, sometimes for two weeks or more, before the eggs are laid, and they continue to do so throughout the period of laying, incubation, and rearing the nestlings. By day they sit alternately, usually from one half to nearly 2 hours at a stretch. One pair kept the eggs constantly covered, but another pair attended them for only 88 per cent of the day. In their mode of replacing each other on the eggs, piculets differ from most woodpeckers in that one usually enters the hole before the other comes out, and they may remain inside together for a few minutes at the time of the changeover. The eggs tend to hatch on successive days, and the period of incubation is about 14 days.

Newly hatched nestlings have pink skin with no trace of feathers and their eyes are tightly closed. When they are eight days old, their pinfeathers are becoming prominent and the eyes are partly open. The feathers begin to unsheathe at about 16 days, and two days later the nestlings are fairly well clad with plumage. When three

weeks old, they begin to look through the doorway; they emerge from the nest when 24 or 25 days of age.

The nestlings are brooded and fed by both parents, which bring food in the bill and mouth rather than regurgitate it. Immature stages of ants appear to form the bulk of the nestlings' diet, especially when they are younger. Later, mature ants and the larvae of other insects are added. The parents keep the nest scrupulously clean.

The nestlings take food with a forward thrust of the head and grasping movement of the bill. This is continued after they have received all that the parents have brought for them, and greatly annoys the latter.

After their first flight, the fledglings are led back to sleep in the nest cavity with their parents, and they may continue to do so for at least three or four months. The family retires early, especially on rainy evenings, and emerges late in the morning, after most birds of other kinds have become active. Frequent changes in dormitories, often caused by the falling or crumbling of the decayed stub, make it difficult to follow the history of a family for a long period.

In the second half of the year, piculets are most often found sleeping in pairs. Occasionally three birds occupy the same dormitory, and rarely one lodges alone.

When eggs for a second brood were laid in a hole where one first-brood fledgling was reared, the young piculet continued to sleep in the nest with the parents throughout the period of incubation and the early part of the nestling period, until ants destroyed the nestling about a week after it hatched. Three grown Lafresnaye Piculets, two of which wore female plumage, were likewise found sleeping with eggs.

GENERAL SUMMARY OF INFORMATION ON THE PICIDAE

The approximately 225 species of woodpeckers, piculets, and wrynecks inhabit all of the earth's larger land areas that support trees, with the exception of the Australian region, Polynesia, and Madagascar. They are found from the equator to the northern limit of woodland, among the sparse vegetation of semi-deserts no less than in the most humid forests, and from sea level to—and beyond—timberline on the high mountains. Some have even colonized treeless plains. They are most numerous in species, however, in warm woodlands.

In size, woodpeckers exhibit an amazingly great range, from piculets, about 3 inches long, to the Imperial Woodpecker, about 22 inches in length. In coloration, woodpeckers are extremely varied and many are brilliant. Bold, contrasting patterns of black and white are frequent in the family, but a number of species are clad largely in shades of brown and olive, whereas others have large expanses of red, yellow, and green. The North and Central American woodpeckers alone display all the bright colors except blue, violet, and brilliant green. Species in which the sexes are nearly or quite indistinguishable, such as the Red-headed and Lewis woodpeckers, are exceptional in the family, as are species in which the male and female are colored quite differently over most of the body, as in the Williamson Sapsucker. In the majority of woodpeckers, the sexes have different colors only in small, sharply defined areas, usually on the head and neck. Often all or part of the red or yellow on the male's head is replaced by black or some other dull color in the female's, or the male may have red or black malar stripes which the female lacks. That these small patches of color on which the birdwatcher depends to distinguish the sexes of woodpeckers convey the same information to the birds themselves was demonstrated by Noble (1936) in the Yellow-shafted Flicker. He found that when a black "mustache," the mark of the male in this species, was artificially attached to a female, she was treated by her mate as a male and rival.

Despite their great range in size and their extremely varied coloration, the woodpeckers are, structurally, a fairly uniform and well-defined family. With the exception of the three-toed woodpeckers of the genera *Picoides*, *Dinopium*, and *Sasia*, they have two toes directed forward and two backward; sometimes the four sharp-nailed toes radiate at about equal intervals from the end of the tarsus, forming an apparatus which serves admirably to clamp the bird to an upright trunk. The tail feathers, with stiff shafts and acuminate tips that engage irregularities in the bark or wood, function as a prop to support the bird as it clings upright to vertical surfaces, or ascends them in a jerky progression the details of which are difficult to observe. Woodpeckers' tails, however, are less specialized than those of woodcreepers, for the shafts of their rectrices do not project beyond the vanes as spine-like, decurved points, as in the latter family. Piculets and wrynecks, which do not use their tails for support, have soft rectrices with rounded ends, like those of perching birds. Instead of dropping their central tail feathers first, as in many other avian families, molting woodpeckers retain them until all the other rectrices have been replaced. The old central rectrices continue to give support to the climbing woodpecker during the period of feather renewal, and evidently also provide some protection to the growing lateral rectrices until they harden.

The woodpecker's strong bill, straight or slightly curved, laterally compressed and, in the larger species, tapering to a wedge-like apex rather than to a point, serves as a drill for digging into wood, in which these birds find much of their food and excavate chambers for nesting and sleeping. The nostrils of most woodpeckers are covered by tufts of short, forwardly directed feathers, the function of which is to prevent particles of wood from flying into them while the birds are chiselling, as seems evident from the fact that these tufts are present in both typical woodpeckers and piculets, which carve holes, but absent from wrynecks, which do not peck into wood.

The slender, flexible, white tongue of a woodpecker, which in some species may be protruded to a length of 4 inches, is an instrument admirably adapted for extracting wood-boring larvae from their burrows or ants from their tunnels. The tip of the extensible tongue, pointed and barbed like a spear, is used to transfix soft grubs and similar prey and draw them from burrows which have been opened by blows of the bill. Smaller creatures, such as ants, adhere to the sticky saliva that liberally coats the tongue and are drawn into the mouth when the tongue is retracted. In species which subsist largely on ants, such as the Green Woodpecker of Europe, the tongue may have a flattened tip that helps to collect larvae and pupae from deep galleries, whereas in sapsuckers the tongue is unusually short and brushy, with hairlike bristles replacing the barbs of the more typical woodpeckers. The accommodation of a woodpecker's long tongue in its relatively short head has been effected by passing the two basal branches of its framework, the hyoid apparatus, along the forks of the lower jaw, thence back around the occiput and forward over the crown, to enter (in the species with longest tongues) the hollow of the upper mandible, or else to curl like a spiral spring around the eyeball. Finally, the skull is thickened and the articulation of the mandibles with it has been modified to protect the delicate organs of the head from the effects of the hammer blows that the woodpecker delivers with its bill.

The flight of woodpeckers is typically undulatory, a consequence of the intermittent flapping of their wings, but a few of the larger kinds, such as the Pileated and Lewis woodpeckers, can fly as steadily as a crow.

With such pronounced anatomical peculiarities, one might expect woodpeckers to be as narrowly circumscribed in their mode of foraging as swifts, skimmers, anteaters, and sloths. One of the surprises that awaits the student of woodpeckers is the discovery of their great versatility in procuring food. Many woodpeckers spend much time drilling into dead or even living trunks or branches to extract boring insects, the presence of which they may detect by slight sounds which these creatures make as they move or gnaw in their deep burrows, although visual or olfactory clues may perhaps also betray their position. Large woodpeckers, such as the Pileated and the Pale-billed, hack off chips or splinters that may be several inches long, and open great holes in insect-infested trees. Ivory-billed, Black-backed, and other woodpeckers pry the bark from dead and dying trees, often decorticating extensive areas of the trunks in their search for the beetles which bore beneath it. Ants enter largely into the diet of many species, from diminutive piculets to great Pileated Woodpeckers. Flickers, Green Woodpeckers, and wrynecks collect them from anthills or the ground; Pileated Woodpeckers open deep, rectangular holes in trunks to remove large carpenter ants; Lineated Woodpeckers prey upon the small

ants which inhabit the hollow internodes of living *Cecropia* trees in the tropics; and piculets extract ants and their pupae from slender twigs of trees and shrubs.

Many woodpeckers make long flights to catch flying insects. Sometimes they extend their forays in intricate aerial maneuvers which rival those of the larger American flycatchers, or they may circle back and forth over open ground in company with swallows, remaining aloft continuously for more than half an hour, as has been reported of the Lewis Woodpecker (Bent, 1939:230). A few woodpeckers, including the Red-headed of North America and the Great Spotted of Europe, devour the eggs and nestlings of other birds; but such predatory habits are exceptional in the family and may be confined to a minority of the individuals of these species.

Fruits in great variety, wild and cultivated, are included in the diet of many woodpeckers, as are the seeds of conifers and a wide range of angiosperms. Woodpeckers also eat quantities of acorns and hard-shelled nuts, which they wedge into a convenient crevice in a stub or branch while they split them open with strokes of the bill. In a mild December long ago, I watched Red-headed Woodpeckers, both mature individuals and young birds with gray heads, fitting acorns beneath loose bark, into the irregular ends of broken-off branches, and into cracks in fence posts. Whole acorns were tucked into the larger crannies, but many halves and smaller pieces were forced into fissures too narrow to contain whole ones. A few living insects and earthworms had also been wedged into splits in the wood, so firmly that they could not wriggle out. Seven fence posts in a row held these stores, as well as many of the surrounding trees above my reach, and the woodpeckers often removed an article from one cache and transferred it to another. Sometimes these Red-headed Woodpeckers hammered pieces of bark and fragments of decayed wood into crevices where evidently they had earlier deposited acorns. I did not then realize the full significance of this activity, which has since been elucidated by Kilham (1958*a*), who has described how Red-headed Woodpeckers fill cavities in trees with acorns, insects, and other food, then seal in their stores by plugging the opening with splintered wood, pieces of bark, and the like. This may be compared to the manner in which jays cover their caches of food with leaves, lichens, and other materials; and I once saw White-breasted Nuthatches hide a bit of food in a crevice in bark and then stuff in fragments of bark to cover it. Eckstorm (1901:60-67) believed that Red-headed Woodpeckers had acquired recently the habit of storing food.

Lewis Woodpeckers (Bent, 1939:230-231) and some tropical populations of the Acorn Woodpecker store whole or fragmented acorns in such crannies and crevices as they find in trees, much in the manner of the Red-headed Woodpecker, although evidently they do not seal in their stores. Northern races of the Acorn Woodpecker, to which such reserves of food are of great importance in the winter and spring, lay up their stores more seriously and systematically, drilling innumerable holes into the thick bark of trees, each just large enough to accommodate an acorn snugly, or sometimes a pecan or some other nut or even a pebble, when it is driven in with a blow of the bill, as has been described in great detail by Ritter (1938) and other writers. Red-bellied Woodpeckers hide acorns, insects, and fragments of perishable fruit pulp in trees and fence posts, and a Hairy Woodpecker dropped two bushels of decapitated potato bugs into a hollow pine stub (Bent, 1939:18, 242-243; Kilham, 1963). In Europe, the Great Spotted Woodpecker has been reported to store food (Coward, 1928:259). Aside from the Acorn Woodpecker, I have no information on food storage by any woodpecker within the tropics.

Among more special modes of foraging are those of the sapsuckers of the genus *Sphyrapicus*, which drill in the bark of a variety of coniferous and broad-leaved trees many shallow, round, or elliptical pits, usually arranged in neat transverse rows, and deep enough to reach the cambium. The sapsucker eats these tender meristematic tissues, drinks the sap which flows into the holes, and catches the insects attracted to the sweet fluid. These feeding stations are visited by hummingbirds and other small birds, from which the sapsucker makes some attempt to defend them. The habit of pecking through bark to obtain cambium and sap is found, in less developed form, in the Downy and Great Spotted woodpeckers (Bent, 1939:62-63, 71; Witherby *et al.*, 1938).

On the treeless plains of southern South America, as likewise on the bleak puna of the high Andes above 12,000 feet, flickers (*Colaptes*) forage wholly on the ground for the worms, insects, and spiders on which they subsist, thus intensifying a propensity already quite evident in northern flickers that inhabit wooded regions. That the southern flickers are better adapted for a terrestrial life than are their northern relatives is evident from the fact that at least some of the former (for example, *C. campestris*) walk over the ground rather than hop like the latter (Mitchell, 1957: 121). The Ground Woodpecker of southern Africa is likewise terrestrial.

Because of the varied sources of their nourishment, including abundant stores in some instances, and the protection provided by their dormitories, woodpeckers of many kinds are able to endure the freezing weather, ice, and snow of high latitudes. The annual migration of a number of species, including the Red-headed and Lewis woodpeckers and the Yellow-shafted Flicker, is largely a withdrawal from the more northern to the more southern portion of the breeding range. The extent of this movement, in which all individuals may not participate, may depend on the severity of the winter or on the abundance of the nut crop on which the birds depend for food at this season. Flickers migrate by night as well as by day. Among the more highly migratory woodpeckers are the Wryneck, which breeds in Europe and northern Asia and winters in tropical Africa and India, and the eastern race of the Yellow-bellied Sapsucker. The latter, which nests in northern United States and over much of the wooded parts of Canada, is the only member of the family which migrates into Central America, where it winters as far south as western Panamá, usually at middle and high altitudes. A substantially higher proportion of females than of males come to the tropics at this season (Howell, 1953). In this race (*Sphyrapicus varius varius*) sexual differences in coloration are more pronounced than in many other woodpeckers; in the less highly migratory western races of the same species the sexual differences are less pronounced, and in the nonmigratory *S. varius ruber* of the northern Pacific coast the male and female wear the same brilliant attire. A number of other groups of birds, including tanagers, wood warblers, and American orioles, exhibit a similar correlation between plumage and migration; in migratory species, the male is often far more brilliant than the female, whereas in nonmigratory species the two sexes more frequently wear the same bright colors.

Woodpeckers apparently never unite in large, closely integrated flocks like those of some parrots and pigeons. Many of them exhibit the minimum of sociability compatible with reproduction. In the least social woodpeckers, the male and female maintain, in the nonbreeding season, separate territories, either in the locality where they nest, as in the Downy, Hairy, and Black woodpeckers (Bent, 1939:66; Kilham, 1960; Sielmann, 1958), or in their winter home, as in the partly migratory Red-

headed Woodpecker (Kilham, 1958*c*). In many resident species, however, the male and female live throughout the year on a territory which they hold in common, as in the Pileated Woodpecker (Kilham, 1959*c*) and the Red-crowned Woodpecker. Intermediate between these two groups appear to be the Red-bellied Woodpecker and Central American races of the Hairy Woodpecker. In Maryland, Kilham (1958*b*: 318) found the former solitary from late summer until early in the following year, and in Guatemala, I usually saw Hairy Woodpeckers alone from the close of the breeding season until late November or December, when they were paired. The territories of all the species mentioned in this paragraph and numerous others contain holes in which individuals lodge singly. In the nonbreeding season, males carve these dormitories more often than do females, which are often content to sleep in the dilapidated chambers abandoned by the former, as Burroughs (1886) discovered long ago of the Downy Woodpecker and as has since been found true of a number of other species. Territorial and other conflicts among woodpeckers are usually settled by posturing and display, and members of this family only exceptionally strike or grapple with each other. Rarely an individual is savagely pugnacious. Yellow-bellied Sapsuckers are unusually quarrelsome and often engage in physical combat (Kilham, 1962*a*:32).

In the more social species, exemplified by the Golden-naped, Crimson-bellied Black, and Acorn woodpeckers and the piculets (Skutch, 1943) and the Blood-colored Woodpecker (Haverschmidt, 1953*a*), each family remains united after the close of the breeding season and its members lodge in the same chamber, or occasionally they divide up in two or three holes that are close together, one or several birds in each cavity.

Among the more gregarious woodpeckers are the flickers, which often form loose flocks composed of what appear to be family groups. Thus Dorst (1956) observed, on the high plateau of Perú, a flock of about 30 Andean Flickers spread over a pasture in knots of five or six. A dozen pairs of these flickers may nest in as many burrows close together in a river bank. Although the Yellow-shafted Flicker of North America is less colonial, two pairs occasionally nest in the same tree (Bent, 1939:260). In the Lewis Woodpecker, as many as three occupied nests have been found in the same tree, and 10 or 12 pairs of Red-cockaded Woodpeckers may breed in 50 acres of pine woods (Bent, *op. cit.*:228, 74). Most woodpeckers, however, are far more strongly territorial than these few species.

Although woodpeckers are among the more loquacious of birds, none that I know of can be said to sing melodiously. But, especially when mellowed by distance, the loud, far-carrying voices of some of the larger kinds, as the flickers and the Lineated Woodpecker, may appeal to the human listener because of their peculiarly attractive tone quality. Often the call, especially of the smaller species, is a roll, a *churr*, or a rattle, formed by the rapid repetition of a single basic note. In the little Olivaceous Piculet, this roll has been reduced to a twitter or trill, which is at times clear, soft, and melodious. The larger Hispaniolan Piculet delivers six whistled notes, which earn for it the local name "flautero" (Wetmore and Swales, 1931:297).

The rather limited range of voice of most woodpeckers is supplemented by mechanical sounds. Although certain other birds produce instrumental sounds by means of specially modified feathers of the wings or tail, or by striking the wings or mandibles together, woodpeckers appear to be unique in the whole class of birds in habitually using a sound-producing object which is not a part of their body. By

striking its bill very rapidly against an appropriate sounding board, usually a hard, dry part of a tree but sometimes a metal roof or some similar object, the woodpecker drums a roll or rapid tattoo. Since a number of kinds of woodpeckers often inhabit the same locality, it is evident that if these mechanical sounds are to achieve their fullest use in proclaiming possession of territory and attracting mates, they must be species specific, just as the vocal sounds of birds are specific and enable one to identify their source without seeing it. The loud, double tap of the Pale-billed Woodpecker can hardly be confused with any other sound of the Central American forests. The Ivory-billed Woodpecker delivers single or double raps, apparently never a long sequence (Bent, 1939:11). The rolling tattoos of the several kinds of woodpeckers, however, sound much alike to unpracticed human ears, save as they vary in intensity with the size of the drummer or its distance from the hearer. Nevertheless, the analysis of recordings reveals that the tattoos of different species vary significantly in structure. Thus a single roll of the Great Spotted Woodpecker consists of 12 to 14 taps and lasts from 0.76 to 0.98 second, whereas that of the larger Black Woodpecker consists of 35 to 44 taps which occupy from 2.10 to 2.69 seconds and are, moreover, lower in tone in consequence of the greater weight of its bill (Sielmann, 1958:25). In most, if not all, woodpeckers, both sexes utter essentially the same notes and beat the same tattoos, although one may call or drum more frequently than the other.

A number of species whose rapid rolls defy analysis by the unaided human ear also tap more slowly, at the countable rate of two or three times per minute. This tapping is of considerable importance in maintaining the bond between the members of a pair and in signifying their agreement on a nest site. In some species, including the Red-bellied and Red-headed woodpeckers, the male and female tap simultaneously, while one is in the nest cavity and the other clinging to its outer wall, or while both cling together in front of the doorway. Yellow-shafted Flickers give similar taps which have the same significance, but the members of a pair tap at different times rather than simultaneously (Kilham, 1958*b*, 1959*a*, 1959*b*). Black Woodpeckers exchange these countable taps when they replace each other at hole-carving, incubation, or brooding the young (Sielmann, 1958:38).

In courtship, the woodpeckers' loud calls and drumming announce the presence of an unmated individual, usually a male, and draw a potential partner from a distance. When the two approach each other, they display by swaying the forward part of the body sideward, up, and down, so that the bill "weaves" or traces an irregular scroll in the air. These movements give each an opportunity to notice the marks distinctive of sex that are nearly always situated on the head. The wings are often raised to display their striking color pattern, and in the case of flickers the tail is elevated and spread to reveal its bright lower surface. Yellow-bellied Sapsuckers make undulating courtship flights to and from the nest hole (Kilham, 1962*a*). Nuptial feeding seems not to have been reported in this family, but the male and female Ivory-billed Woodpeckers clasp bills, mated Downy Woodpeckers rub bills, and Yellow-shafted Flickers touch and seize each other's bills (Bent, 1939:3, 57; Kilham, 1959*b*). Bill touching is sometimes regarded as incipient or symbolic feeding.

A male Yellow-bellied Sapsucker had two mates, and all three attended a nest with an unusually large set of eggs (Howell, 1952:255). Otherwise, polygamy has not, to my knowledge, been reported in this family. In four species of woodpeckers of eastern Canada studied intensively by Lawrence (1967), all pairs remained mated

for life. This fidelity seemed to result from the woodpeckers' strong attachment to the territory in which they had once nested rather than from attachment to the mate of the preceding year.

The nest site may be chosen by either sex. The male often selects it in the Red-bellied and Red-headed woodpeckers (Kilham, 1958*b*, 1959*a*), the Great Spotted Woodpecker (Bussmann, 1946), and the Red-crowned Woodpecker; in the last the male's dormitory may become the nest. In the Yellow-shafted Flicker, the nest site may be chosen by either the male (Sherman, 1910; 1952:239) or the female (Kilham, 1959*b*). In the Downy and Hairy woodpeckers, the female appears to choose the nest site, at least in some races (Bent, 1939:56; Kilham, 1960). In the Black and the Green woodpeckers of Europe, the nest is usually carved in the female's winter territory, but the male selects the actual site (Sielmann, 1958:27).

The nest of most woodpeckers is a hole which they carve in a tree. Typically, a neatly rounded entrance penetrates the wood for a short distance, and then the excavation turns downward to form a deep, roughly cylindrical chamber, which may be widest at the top, middle, or near the rounded bottom. Usually the cavity is in a dead trunk or branch of a tree, a fence post, a telegraph pole, or in some other similar situation. In Central America, I have never found a woodpecker nest carved in living wood, but in other regions such a site is not infrequently chosen. The Red-cockaded Woodpecker prefers living pines, and it pecks the bark around the doorway to make the resin exude freely, although this is detrimental to its plumage, which becomes matted. If, for any reason, the resin ceases to flow, the woodpecker abandons its nest tree for another (Bent, 1939:74). The Gilded Flicker and Gila Woodpecker often carve their holes in living giant cacti, the Hispaniolan Woodpecker in living royal palms, and western races of the Yellow-bellied Sapsucker in living aspen trees (Bent, 1939:143, 151, 252, 302; Wetmore and Swales, 1931:292). Many other instances of the use of living wood for nests have been recorded. Frequently the living tree chosen by the woodpeckers has a soft, decaying heart, the presence of which they apparently detect by tapping on the trunk and listening to the sound, and which they then reach by carving through several inches of sound, and often hard, green wood. Flickers (*Colaptes*), whose bills are less adequate for wood carving than those of many other woodpeckers, often nest in a cavity caused by decay, which they may enlarge, or provide with a suitable doorway. Although North American flickers usually breed in trees, they sometimes lay their eggs in burrows in banks, and in the treeless regions of southern South America and the high Andes, flickers regularly dig tunnels for their nest. These burrows, which may be 4 feet long, run inward and upward to an enlarged chamber where the eggs are laid (Dorst, 1956). When Pampas Flickers, lacking suitable banks or old mud walls, excavate a nest in the soft wood of an ombú tree, they direct it upward, like a burrow, rather than downward, in the usual manner of tree-nesting woodpeckers (Hudson, 1920, 2:11-12). The Ground Woodpecker of Africa also nests in a tunnel which it digs in a bank.

A few woodpeckers share with some kingfishers, jacamars, trogons, puffbirds, parrots, and others, the custom of excavating their nest chamber in a termitary; among them are the Gray and the Buff-spotted woodpeckers, both of which inhabit Africa. The latter also digs a nest chamber in the carton nests of tree-dwelling ants. The Rufous Woodpecker of India habitually breeds in a cavity which it carves in the large, roughly globular nests built in trees, of a material resembling papier mâché, by ants of the genus *Crematogaster*. The woodpecker chooses for this

purpose occupied nests, but, strangely enough, the insects do not harm the birds, their eggs or young, although they fiercely attack any other animal that molests their home (Hume, 1889-1890; Hindwood, 1959:26-29).

The nest is carved by both sexes in all woodpeckers for which information is available. The male often takes the lead in this as in other domestic tasks, but nearly always his partner helps. Even in species which on occasion breed in the male's dormitory, the female will join him in carving a new hole if the first nest is lost. In the Hairy Woodpecker, Kilham (1960) witnessed the excavation of a hole, apparently intended for nesting, entirely by a female, as far as he saw, but in Central American races of this species, both sexes share the undertaking. In carving a nest chamber, woodpeckers loosen the wood by using their bill as a pick, sometimes and possibly regularly delivering the blows with the tips of the mandibles slightly separated (Sielmann, 1958:116), then removing the loosened particles from the cavity with their mouths or bills. Nearly always the debris is simply thrown from the doorway, often many billfuls in succession, with a sideward twitch of the head to scatter it. Yellow-shafted Flickers, however, are reported to carry away some of the excavated material (Bent, 1939:268; Kilham, 1959*b*). While one partner works, the other usually forages at a distance, instead of waiting close by for its turn, in the manner of trogons, motmots, kingfishers, and many other hole-nesters. Spells of carving usually range from a quarter of an hour to an hour, but they may be shorter or longer. From one to four weeks is the period usually required for the completion of a chamber, but a much longer time may be spent on one begun well in advance of the breeding season.

The burrow-nesting flickers of South America have so far departed from the habits typical of their family that, instead of casting out the loosened material with their bills, they eject it from the shaft by kicking backward with their feet, in the manner of kingfishers, motmots, and jacamars (Dorst, 1956:122). Although the tiny piculets carve holes which are miniatures of those of the typical woodpeckers, the larger wrynecks nest in cavities which they find ready made, in a tree, a bank, or a masonry wall.

Nearly always, woodpeckers lay their eggs in a newly carved hole, or at least in a recently carved dormitory, but a few species, including the Red-cockaded and Lewis woodpeckers, nest in the same chamber in successive years. Deepened before each nesting, a cavity of the Lewis Woodpecker may become 30 inches in depth (Bent, 1939:74, 228). From this, the nest chambers of woodpeckers range in size down to those carved in very soft wood by piculets, which may be only 3 or 4 inches deep, with a doorway somewhat under an inch in diameter. This may be compared with the orifice of an Ivory-billed Woodpeckers' nest, which is about 5 inches in height by 4 in width and gives access to a cavity from 14 to 20 inches deep. No matter what the size of its chamber, the woodpecker never lines it with soft material but lays its eggs on a bed of wood particles on the bottom. This bed appears to be of some importance in the economy of the nest, for if it is removed the woodpeckers replace it by chipping fragments from the wall of their chamber (Sielmann, 1958:116). However, when woodpeckers carve their nest in a giant cactus, it lacks this layer of wood particles on the floor.

The eggs of woodpeckers seem invariably to be white, often with a high gloss that makes them resemble thin, translucent porcelain, although sometimes they are a dull white. In the Golden-naped Woodpecker, the Yellow-shafted Flicker, and a

number of European species, the eggs are laid early in the morning on consecutive days (Sherman, 1952:241; Sielmann, 1958:49). In eight species of Central American woodpeckers, I found sets ranging from two to four eggs; those of two eggs belonged to the smallest and largest species, the Olivaceous Piculet and the Pale-billed Woodpecker. In Trinidad, Belcher and Smooker (1936:796-798) found sets of two and three in nests of five species. In extra-tropical North America, as in Europe, woodpeckers usually lay larger sets, ranging from three to eight eggs and sometimes more. Woodpeckers are prolific egg-producers and include two of the limited number of birds demonstrated to be indeterminate layers. By leaving only a single egg in a nest of a Yellow-shafted Flicker during the period of laying, the female was induced to deposit 71 eggs in 73 days (Bent, 1939:272). A Wryneck laid 62 eggs consecutively (Davis, 1955:82). Many woodpeckers rear a single brood each year, and this appears to be the rule in the family north of about the fortieth parallel of latitude. Two broods may be raised by the Red-headed and Downy woodpeckers in the more southerly portions of their range, and three broods may be undertaken by the Acorn, Red-bellied, and Golden-fronted woodpeckers. Golden-naped Woodpeckers, and apparently also Olivaceous Piculets, only exceptionally rear a second brood.

Incubation is performed by both sexes in all woodpeckers for which information is available. In the more solitary species, the male, which in many instances has slept in the nest chamber for a longer or shorter period before laying began, nearly always attends the eggs by night, although exceptionally a female Yellow-shafted Flicker may take her mate's place on the eggs or young on some nights (Sherman, 1952:239). The female Wryneck may also incubate by night (Kendeigh, 1952:228). In the more social forms, including *Tripsurus* and *Picumnus*, both sexes normally sleep in the nest, but if for any reason they pass the night separately, the male stays with the eggs. Woodpeckers vary enormously in the length of their sessions on the eggs, and large species do not always sit more constantly than small ones. A pair of Pale-billed Woodpeckers made only two changeovers in 24 hours: the female sat continuously for 4½ hours of the forenoon and the male remained with the eggs practically all the rest of the time. A female Golden-olive Woodpecker incubated for nearly 5 hours of the morning, but other diurnal sessions of this pair were considerably shorter. A pair of Yellow-shafted Flickers replaced each other on the eggs infrequently, but without waiting for its partner to relieve it, each member of the pair took a number of short recesses while the eggs remained unattended; the flickers seldom sat more than 2 hours continuously in the daytime (Skutch, 1937). Black Woodpeckers generally replace each other on the eggs at intervals of from 70 to 90 minutes (Sielmann, 1958:92). The little piculets sit about as constantly as this. In many hours of watching, I have not known a Golden-naped Woodpecker to incubate for longer than 51 minutes at a stretch by day; at four nests, most sessions by either sex lasted less than 25 minutes. But the most restless sitters of all are the Acorn Woodpeckers. When four males and a female shared incubation at one nest in Costa Rica, they replaced each other at intervals of a few minutes; in nearly 12 hours of observation, the longest session lasted only 17 minutes. Leach (1925:19) watched a group of incubating Acorn Woodpeckers in California come and go with about equal frequency.

The incubation period of woodpeckers is difficult to determine with accuracy, because the eggs can rarely be reached for marking without cutting open the nest. Among the determinations which seem to have been made with some care are the

following: Yellow-shafted Flicker, 11–12 days (Sherman, 1952:243–245); Downy Woodpecker, 12 days (Bent, 1939:57); Great Spotted Woodpecker, about 12 days (Bussmann, 1946); Black Woodpecker, 12 days (Sielmann, 1958:98); Yellow-bellied Sapsucker, 11–14 days (Howell, 1952:248, 255); Wryneck, 12 days (Witherby *et al.*, 1938); Golden-naped Woodpecker, about 12 days; Golden-fronted Woodpecker, 12 or 13 days; Olivaceous Piculet, about 14 days. That the eggs of the tiny piculet should take longer to hatch than those of larger woodpeckers is in accord with the situation in some other families, such as the American flycatchers and the tanagers. The fairly large woodpeckers of the genus *Picus* have incubation periods much longer than all of the foregoing: Green Woodpecker, 18–19 days (Witherby *et al.*, 1938); Gray Woodpecker, about 18 days (Bussmann, 1944). For the Pileated Woodpecker, several writers report the incubation period to be 18 days. Since some woodpeckers lay large sets and often begin to incubate before they finish laying, the eggs may begin to hatch only nine or ten days after the last was deposited. Eggs that fail to hatch appear to be more frequent in this family than in many others.

Newly hatched nestlings have naked skin and never acquire any down. Their lower mandible is conspicuously longer and broader than the upper mandible, and like the latter it bears a white, shield-like eggtooth at its tip, although that on the upper mandible is larger and probably more effective in chipping the shell. At the base of the lower mandible, on each side of the mouth, is a conspicuous, white, knob-like protuberance which, according to Sielmann (1958:65, 100), the parents touch with their bills to stimulate very young nestlings to raise their open mouths for food. The nestlings' eyes are tightly closed, yet they are not insensitive to light, and they lift their gaping mouths when the entrance of their chamber is darkened by the approaching parent or the observer's hand (Sherman, 1952:245). The nestlings' heels or tarsal joints are covered with a pad studded with spike-like projections, which protects them from abrasion that might be caused by the unlined floor of their nest. These ugly, helpless, newly hatched woodpeckers are attended by both parents, which for some days brood them about as constantly as they incubated the eggs.

In their methods of feeding the nestlings, woodpeckers fall into two groups, those which carry the food visibly in their bills and those which regurgitate it by inserting the bill into a nestling's mouth. The first group includes the genera *Dendrocopos*, *Centurus*, *Tripsurus*, *Balanosphyra*, *Sphyrapicus*, *Veniliornis*, *Picumnus*, *Jynx*, and others. Woodpeckers which feed their young by regurgitation include the genera *Colaptes*, *Picus*, *Piculus*, *Picoides*, *Dryocopus*, and others; this method of feeding the nestlings is followed especially by those woodpeckers which subsist largely on ants, except the piculets, for which even an ant's pupa is a fairly large object. Although it is sometimes said that woodpeckers of the first group begin to feed their nestlings by regurgitation and later bring food in the bill, this does not agree with my studies, for I have found that the parents bring the nestlings' food in their bills from the first.

The rate of feeding the nestlings varies greatly according to whether they are given solid particles or regurgitated aliment. When the latter system is followed, food may be brought to the nest no more frequently than once an hour, as I have seen at nests of the Golden-olive and Lineated woodpeckers where there were one or two nestlings. At a nest of the Gray Woodpecker, the maximum rate of feeding was reached on the seventeenth day after hatching, when the nestlings received 26 meals. Thereafter, the frequency of feeding declined until the young were fledged (Bussmann, 1944). A brood of Black Woodpeckers was fed at the average rate of once every 90

minutes (Sielmann, 1958:118). A brood of five feathered Yellow-shafted Flickers was fed more frequently, 25 meals in 4½ hours (Sherman, 1952:250). But even this rate of feeding is slow compared with the frequency of feeding by parent woodpeckers that bring food in the bill, often six or seven times per nestling per hour, and for brief periods, especially in the early morning, much more rapidly than this. A brood of Yellow-bellied Sapsuckers over a week old is fed at intervals of about 2 minutes throughout the day (Howell, 1952:249). An interesting method of feeding the young was recorded for this species by Blackford (1950), who watched sapsuckers soak billfuls of insects in sticky sap in a well in alder bark, then fly off to the nest with them. Similarly, Antevs (1948) watched a male Gila Woodpecker feed his fledglings liquid honey by dipping solid objects, such as lumps of bark and seeds, into a saucer of the sweet fluid and passing them to the young. Thus woodpeckers, with their great flexibility of habit, manage to give their young liquid nourishment even without regurgitation.

Soon after they hatch, nestling woodpeckers become exceedingly noisy, making almost continuously a sound which has been variously described as a buzz, a hiss, or a sizzle, which is intensified when a parent arrives with food. Young flickers continue this noise even by night. After they have acquired plumage and can look through their doorway, nestling woodpeckers are less constantly vocal, but they may now utter from time to time weak versions of the adults' typical calls. Feathered nestlings of the Yellow-shafted Flicker and the Great Spotted Woodpecker may fight furiously for possession of the coveted place at the doorway, which ensures receipt of the next meal, but despite the pecks they exchange, they seem rarely to injure each other (Sherman, 1952:246-247; Sielmann, 1958:74-75).

Sanitation of the nest is not neglected by woodpeckers. At first, the nestlings' excrements, like those of passerines, are enclosed in a tough gelatinous sac, which facilitates their removal. Parent Yellow-shafted Flickers usually remove droppings, at first by swallowing them and later by carrying them in the bill from the nest chamber, after delivering a meal. If a nestling does not defecate after being fed, the parent may solicit the dropping by biting the uropygium of the young bird or its heel joint. As the young grow older and move about more actively in the chamber, the enclosing sac is no longer formed; this is true also of small passerines when, at about the same age, they leave the nest. But young woodpeckers remain in their nursery for a number of days after this occurs, and the parents now try vainly to keep the nest clean (Sherman, 1952:251-252). In some species, the parents neglect to remove the excreta after the young take their food through the doorway and it is no longer necessary to enter the nest in order to feed them. The bottom of the cavity then becomes covered with waste in which maggots batten; the woodpeckers, however, spend much, if not all, of their time clinging to the wall above the filth. But those more social woodpeckers which lead their fledglings back to sleep in the nest never neglect its sanitation; as long as the young remain within the cavity, and even after their emergence, these careful parents enter the nest to gather up the waste matter and carry it to a distance, often making a number of these trips in rapid succession. Even some of the solitary woodpeckers which do not lead their fledglings back to the nest may, after feeding, enter the chamber to remove the droppings of feathered nestlings, as I have seen in the Lineated Woodpecker. In a number of species, the male cleans the nest much more often than does the female, and at some nests he alone attends to sanitation. The droppings of Yellow-bellied Sapsuckers are

not enclosed in a fecal sac, but the parents overcome the difficulty of removing the soft material by sopping it up in wood particles, which they obtain by continuing to enlarge the nest cavity after the young hatch (Kilham, 1962*b*).

Although at first they carefully remove the nestlings' droppings, woodpeckers often neglect for several days to remove the empty eggshells. This is the more surprising in view of the fact that woodpeckers, more than any other birds that I know, carry whole eggs from their nests. Those eggs which fail to hatch usually vanish from the chamber after a few days. A Yellow-bellied Sapsucker removed and ate an egg from a nest which had been cut open (Bent, 1939:145). A captive male Yellow-shafted Flicker carried off and punctured embryonated eggs, after disturbances in the aviary caused his mate to neglect her share of incubation (Kilham, 1959*b*:333). Flickers apparently carried five fresh eggs from the nest of a rival pair (Sherman, 1952:82). Instances have already been given of the removal of eggs from their own nests by Black-cheeked and Acorn woodpeckers and Olivaceous Piculets (pp. 543). One of the eggs removed by the male Black-cheeked Woodpecker was yolkless and the other was eaten by him before it could be examined. This habit of removing and at times devouring eggs from their own nests might lead woodpeckers to prey on the eggs of other birds, but I have found such behavior reported only of the Red-headed and Gila (Bent, 1939:199-200, 254) and Great Spotted woodpeckers.

Injury simulation, which is rare in hole-nesting birds of all kinds, has been recorded in this family only for the Downy and Red-cockaded woodpeckers and the Wryneck (Hebard, MS). When disturbed in its nest, the Wryneck darts out its tongue and hisses—snake-like behavior which, like the similar actions of brooding titmice, may alarm intruders. If taken in hand, the Wryneck often simulates death, but it is questionable whether this reaction ever saves the bird or its offspring (Coward, 1928:265). When sitting on well-incubated eggs or when brooding recently hatched nestlings, Yellow-bellied Sapsuckers sometimes sit so steadfastly that they may be touched, or even lifted from the nest (Bent, 1939:129; Howell, 1952:248). A pair of sapsuckers repeatedly knocked from their nest tree a weasel that attempted to reach their young (Johnson, 1947). A female Golden-naped Woodpecker often lightly struck me when I climbed to her nest, but the bird never struck me when my eyes were directed toward her. A male Pileated Woodpecker attacked with repeated blows of his bill a large Pilot Black Snake which had entered the hole in which he and his mate seemed to be nesting or preparing to nest, evidently killing the reptile (Nolan, 1959). The zeal displayed in defending the nest and young varies greatly with individuals, even in the same species at the same locality; sometimes the male, sometimes the female, is the more devoted guardian.

The nestling period of woodpeckers varies from about three to five weeks. The shorter periods have generally been recorded for northern species: the Great Spotted and Lesser Spotted woodpeckers and the Wryneck, 18 to 21 days (Witherby *et al.*, 1938); Yellow-bellied Sapsucker, 23 to 28 days (Howell, 1952:258); Green and Black woodpeckers, 27 days (Siemann, 1958:88, 119); Yellow-shafted Flicker, 25 to 28 days (Sherman, 1952:257, 263). Tropical woodpeckers remain in the nest longer: Olivaceous Piculet, 24-25 days; Sundevall Piculet, about 28 days (Haverschmidt, 1951); Red-crowned Woodpecker, 31-33 days; Golden-naped Woodpecker, 33-37 days, which is about the same as the nestling period of the far larger Ivory-billed Woodpecker, stated by Tanner (1941) to be about five weeks. In the Great Spotted, Green, and Black woodpeckers studied by Siemann (1958:87-88, 118-119),

during the last days of the young in the nest, the parents diminished their rate of bringing food and tried to call the fledglings from their chamber. Golden-naped Woodpeckers, however, may feed their nestlings most rapidly just before their spontaneous departure from the nest, and they seem indifferent whether their offspring come out or stay inside. For its size, this woodpecker has the longest nestling period so far recorded.

Most woodpeckers are well feathered long before they leave the nest. In a number of species, the first or innermost primary of the juvenal plumage is only a fraction of its length in adults, and in some species the second primary is abbreviated like the first. The postjuvenal molt, in which the innermost primaries are the first to be replaced, begins before the young woodpecker leaves the nest, so that when it emerges the fledgling has primaries of normal length and can fly well. The significance of the short inner primaries of the juvenal plumage, which seem to be found only in woodpeckers, is not clear. Since they are not needed for flight, it may be that the economy of material effected by their reduction in size has promoted the evolution of this peculiar feature (Sibley, 1957).

In the juvenal plumage, woodpeckers of many species essentially resemble their parent of the same sex, although their colors may be duller. When the fledglings differ only in minor details of color pattern from adults of the same sex, those of both sexes may more closely resemble the adult female, as in the Olivaceous Piculet. In a number of species, however, they resemble the adult male. In the Yellow-shafted Flicker, young females as well as young males have black malar stripes, which adult females lack. In the three-toed woodpeckers of the genus *Picoides*, young females have yellow feathers on the crown like adult males, although usually fewer of these feathers, whereas adult females lack yellow on the head. In the Hairy and Red-cockaded woodpeckers, as in other species of *Dendrocopos*, the young of both sexes may have more or less red on the crown, although adult males wear this color only on the occiput or sides of the head and adult females lack it entirely. There is, however, great individual variation in the colors of the crown of juvenal Hairy Woodpeckers (Bent, 1939:16). Species like the Red-headed Woodpecker and the Yellow-bellied Sapsucker, in which juveniles are much duller than the adults, are exceptional in the family, at least in the Western Hemisphere. Even in these woodpeckers, the young acquire plumage much like the adults before the following breeding season. Accordingly, yearlings can hardly be distinguished from older individuals, and woodpeckers, unlike some birds of other families, seem not to breed in transitional plumage.

In the majority of woodpeckers for which information is available, including species of *Colaptes*, *Picus*, *Piculus*, *Dendrocopos*, *Dryocopus*, *Centurus*, and *Campyphilus*, the fledglings do not return to sleep in the nest. If a young Red-crowned Woodpecker tries to enter a hole into which a parent has retired, it is repelled. Each fledgling roosts clinging to a trunk in the open until it can find or carve a hole for itself, as is also true of fledgling Red-bellied Woodpeckers (Stickel, 1964), Hairy Woodpeckers, and apparently of the young of all the genera just mentioned. In these woodpeckers, adults sleep alone in holes at all seasons, and the male may continue to lodge in the nest after the departure of his offspring. But woodpeckers in which the male and female sleep in the nest chamber, including the Golden-naped Woodpecker and the Olivaceous and Sundevall piculets, lead their fledglings back to the nest which they have just left. The parents show the young the position of the doorway by flying repeatedly from them to it, although often the young find their way back

to it with little guidance. The whole family, old and young, may then continue until the following breeding season to lodge in the nest chamber or in other cavities carved to replace it. They may also enter these chambers when it rains in the daytime.

After the young leave the nest, the brood may be divided, each parent taking charge of one or more fledglings, as occurs in the Red-bellied Woodpecker (Kilham, 1961:245) and the Great Spotted Woodpecker. In the latter species, the young are attended by their parents for only a week or two after they leave the nest, or until they are about four or five weeks old (Blume, 1961:62-64). Green Woodpeckers are attended for about a fortnight after they leave the nest (*op. cit.*:64). A Golden-naped Woodpecker, however, may be fed as late as two months after it has left the nest, or until it is about 94 days old.

Helpers at the nest are known only in *Tripsurus* and *Balanosphyra*. On the rare occasions when a pair of Golden-naped Woodpeckers rears a second brood, the young of the first brood sleep in the nest with them. These immatures may bring a little food to the second brood, but because they have not learned the proper way to deliver it, they avoid the grasping thrust of older nestlings. After the second brood is fledged, the young of both broods lodge with the parents, sometimes as many as seven individuals occupying the same hole. The young, including fledglings still being fed, may help the parents to carve a new dormitory. In the Acorn Woodpecker, up to five and possibly more full-grown birds may join in carving a nest chamber, incubating, and feeding the nestlings (Leach, 1925, and my own observations). That such a group consists of a mated pair with their offspring of the preceding year is made probable by an observation quoted by Bent (1939:214-215) of an Acorn Woodpecker, apparently a member of an earlier brood of the same year, bringing a little food to nestlings. In this species, only one individual sleeps in a nest with eggs—a fact which indicates that the social habits of the Acorn Woodpecker have developed farther than those of the Golden-naped Woodpecker, for the presence of a number of grown birds in the chamber with the eggs and young is sometimes detrimental to them and, moreover, it exposes the whole breeding group to the same hazards of nocturnal attack.

The woodpeckers occupy a unique place among the families of birds. By extracting the larvae of wood-boring beetles, they enjoy a source of nourishment available to no other bird and they protect trees. Although occasionally they take a heavy toll of ripening cultivated fruits, their presence is on the whole beneficial to men. To a considerable number of birds which nest in holes but cannot make them, the chambers carved by the woodpeckers are of the greatest importance. These hole-nesters do not always wait until the woodpeckers have abandoned their laboriously carved cavities, but sometimes claim them as soon as they are finished. A bird that occupies a woodpecker's hole cannot be much larger than the woodpecker that excavated it, and one would suppose that, with his powerful bill, the latter would defend his home against the intruder. Yet woodpeckers are, on the whole, unaggressive birds and often relinquish their holes without much resistance; in Europe, Black Woodpeckers abandon their chambers to Jackdaws as meekly (Sielmann, 1958:41) as tropical American woodpeckers of the genus *Tripsurus* give theirs up to tityras. The dispossessed woodpecker patiently carves a new hole for itself, which eventually increases the number of such cavities available to birds and small mammals for breeding and sleeping.

With the protection of the snug chambers that they prepare for themselves and

the abundance of food made available by their exceptionally versatile foraging habits and sometimes also by their forehandedness in laying up reserves, woodpeckers enjoy leisure which contrasts strongly with the ceaseless search for nourishment that fills the days of many birds. With few exceptions, they linger in their dormitories after most of their neighbors have begun to forage at daybreak and they are among the first of the feathered community to retire in the evening. They also take shelter in their holes in inclement weather (Burroughs, 1886; Jourdain, 1936). Because of their remarkable adaptations, coupled with the flexibility of their behavior, their industry, their pacific nature, and the advanced social life of some species, woodpeckers attract and hold the attention of the serious student of living birds as do few other avian families. Sherman (1952:33) wrote: "Were I required to choose from all the birds the single family that has afforded me the greatest amount of pleasure, my choice would fall upon the woodpeckers." And Sielmann (1958:14): "Of all the experiences and knowledge which my work with animals has thus far brought to me, my time with the woodpeckers has become especially dear to me." With these sentiments I agree.

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APPENDIX

Life Histories and Notes on Neotropical Birds Published by the Author Elsewhere than in this Series

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