

NESTING BIOLOGY OF THE LONG-TAILED MANAKIN

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The Long-tailed Manakin (*Chiroxiphia linearis*) is a strongly dimorphic species in which the brightly colored males perform conspicuous communal displays (Slud 1957, Foster pers. observ.). The dull olive-green females, however, who are solely responsible for nest building and rearing of the young, are considerably more secretive. Thus, very little is known about the nesting biology of this species although it is common over much of its range from southern Mexico to northwestern Costa Rica (Friedmann et al. 1957).

For 19 months in 1971 through 1974 I studied this manakin in Guanacaste Province, Costa Rica. Although the study focused primarily on ecology and social organization, some data on breeding biology were gathered. I discovered 39 nests, 12 of which contained eggs or young. Herein I provide an analysis of these nests and observations on eggs, young, and nesting behavior of females.

METHODS

The study was conducted on the property of Estación Experimental Enrique Jiménez Nuñez (Finca Jiménez), a research station owned and operated by the Costa Rican Ministry of Agriculture and Livestock. It is located approximately 13.6 km SW Cañas in Guanacaste Pr. Two nests located at the Palo Verde Field Station of the Organization for Tropical Studies were examined also. Except where noted specifically, Palo Verde nests did not differ from Finca Jiménez nests, and data for both are combined.

All nests were checked at least once a day to determine their progress. Nests under construction and those containing eggs or young were observed for extended periods as often as possible concomitant with other studies. Observations were made with 7 × 35 binoculars at distances of 6 to 10 m with and without the use of a blind. By climbing a tree, standing on a stump, etc. I was able to see into all nests from a distance of 3 m or more. Therefore, in an attempt to minimize disturbance and its effects on nest success, nests were approached closely only when absolutely necessary, for example, to mark and measure eggs or young.

Nests were measured and collected after I was certain that they no longer were in use. Some nests were destroyed by predators before data were taken. Data taken in the field include location in the study area, height above ground (measured to the top of the nest rim), distance from the trunk of the nest tree, and greatest inner and outer depths and diameters. In addition notes about nest form and habitat were taken, the nest tree was measured, and plant material was pressed for later identification. Voucher specimens of the trees are deposited in the herbarium of the University of South Florida, Tampa. Although most nest measurements were made in the field, they represent only an estimate of actual dimensions at the time of nest completion. Nest dimensions may be modified by weather, predators, and normal use by the birds. Measurements of associated branches were made in the laboratory along with analyses of nest construction and composition.

One nestling, briefly and unsuccessfully maintained in captivity, also was observed. Another unsuccessful attempt was made to hatch 2 eggs deserted by a female. The young contained in these eggs were sufficiently developed to provide some morphological and anatomical information although their ages are unknown. Pterylographic designations follow Clench (1970). Young were preserved in 10% formalin. Measurements taken of young include wing chord (bend of the unflattened wing to the tip of the longest primary), tarsus length (juncture of the tibia and metatarsus to the anterior, distal edge of the lowest undivided scute), length of the middle toe without the claw (anterior distal edge of the lowest undivided scute to the tip of the toe pad on the ventral surface of the toe), and bill length (anterior margin of the nostril to the bill tip), depth (culmen to lower edges of rami), and width (one tomium to the other). Bill depth and width were measured at the level of the nostril.

Females were aged using degree of skull pneumatization and external measurements. Ovaries were examined macroscopically in dead or laparotomized individuals. Ovum measurements are diameters in millimeters.

Vocalizations were recorded at a speed of 7.5 ips with a Uher 4000 Report-L tape recorder and M516 microphone on 1 mil polyester tape. Sound spectrograms were made using a Kay Electric Co. Audio Spectrum Analyzer, model 7029A, at a wide band, 80–8000 Hz setting. Weights were taken with a Pesola balance graduated in 0.5 g divisions. Measurements were made with a 30 m tape, a 15 cm plastic rule, and Helios dial calipers.

Data on 9 nests and 18 eggs from Oaxaca, Mexico were provided by L. F. Kiff from material in the collections of the Western Foundation of Vertebrate Zoology (WFVZ). Localities represented by nests are Rancho Sol y Luna (5), Rancho Sol y Luna, 10 km NW Tapanatepec (1), El Novillero, 3.2 km N Tapanatepec (1), and 16 km NW Rancho Vicente, Cerro Baúl. All eggs were collected at the second locality noted above. N. G. Smith provided a nest of the Lance-tailed Manakin (*Chiroxiphia lanceolata*) which he collected at Rodman Ammo Dump, West Bank of Canal Zone, Panama.

RESULTS

Habitat and nest placement.—The Long-tailed Manakin occupies primarily tropical dry forest habitat (Holdridge et al. 1971) although it may extend into areas of tropical moist forest or “cloud forest” (Griscom 1932, Dickey and van Rossem 1938, Slud 1964, Monroe 1968). My observations were concentrated in a riparian woodland located in the arid tropical zone of northwestern Costa Rica. The water table in the woodland is higher than in nearby areas resulting in a taller, more luxuriant, and largely evergreen forest. However, manakins are abundant on the adjacent drier hillsides as well. Some parts of the study area are greatly disturbed, having been subjected to grazing by cattle and patchy clearing. The greatest portion, however, shows only minimum disturbance, this from occasional selective cutting for lumber. The canopy is closed for the most part, resulting in a shady forest floor. The understory is quite open and characterized by many small trees and saplings, lianas, and a lack of shrubby undergrowth. Several detailed descriptions of the area are available (Holdridge et al. 1971, Janzen



FIG. 1. Long-tailed Manakin nest from Finca Jiménez, Guanacaste Province, Costa Rica. Note roofing provided by adjacent leaves and camouflaging leaves hanging vertically from the rim and underside of the nest.

1973, Sawyer and Lindsey 1971). The nests from Palo Verde were taken in a very similar though somewhat drier habitat.

The nests were placed throughout this woodland although they generally were absent from the more open areas associated with tree falls or cutting by man (e.g. along fence lines). They usually were built in small trees (36 in trees < 3m, 2 in trees > 5m) although one was found in a moderate sized shrub. Within the tree the nests are suspended from a fork at or near the end of a small branch. The fork selected invariably is located so that adjacent shoots and leaves provide a roof over the nest (Fig. 1). Quantitative aspects of nest placement are summarized in Table 1.

Manakins apparently are quite selective with regard to species of tree used. Of 39 nests, 17 (43.6%) were placed in trees of 2 species, 25 (62.4%) in trees of 4 species (*Eugenia* sp., 9; *Terminalia lucida*, 8; *Ardisia revoluta*, 4; *Psychotria* sp., 4). The remainder were in individuals of another 8 species. Although no complete list of tree species present is available, a preliminary survey of trees in the Cañas area (Hartshorn 1971) cites more than 140 species. The relative abundance of these forms is not known. However, it is generally apparent that *Ardisia revoluta* and *A. belizensis* are the most

TABLE 1
 QUANTITATIVE ASPECTS OF NEST PLACEMENT BY THE LONG-TAILED MANAKIN
 IN GUANACASTE PROVINCE, COSTA RICA, 1971-1974

Character	No.	Range	Mean
Height nest tree (m)	38	1.3-8.0	2.47
DBH nest tree (cm)	38	0.8-12.0	2.65
Distance, nest from trunk (cm)	34	20.0-142.0	55.65
Height, nest above ground (m)	38	0.7-1.7	1.26
Diam. fork rami (mm)	73	2.1-7.5	3.55

abundant components of the understory. Only 10.3% of the nests were found in individuals of the former species. None was found in the latter.

Nesting period.—Nesting occurs in both the dry (Dec.-April) and wet (May-Nov.) seasons. Nests with eggs or young were located in the months of April, May, June and July. However, several lines of evidence suggest that nesting begins in March or perhaps in February. Males initiate reproductive displays in late February (C. R. Carroll, pers. comm.). Such displays rarely, if ever, are given in the absence of a receptive female (pers. observ.). In addition, several females captured in March had developing brood patches and/or enlarging ova. One female taken 21 March contained a yellow-orange ovum 8 mm in diameter. Several completed nests located in the first half of April and followed for several weeks never were observed to contain eggs. Possibly these nests were built and abandoned, but it is more likely that at one time they contained eggs or young which fledged or were preyed upon prior to their discovery (nests do not persist from year to year, see below). They easily could have been initiated in March.

Although no active nests were located, I also believe that Long-tailed Manakins are reproductively active into September. Males display actively until about 1 September, and one female collected on 17 August carried a shelled egg in her oviduct. A second female mist-netted on 13 August had an active brood patch. Nests with eggs and one with recently hatched young were located during the last half of July, indicating fledging in August or perhaps September. One nest was initiated on 30 or 31 July 1974, but construction was not completed on 13 August when I left the area. Another nest was discovered on 10 September 1973, when it contained a broken egg shell. It was located in a small tree within a few cm of a quadrat boundary line which I set out on 21 August. Finally, I have located a few nests in late August and September which appeared quite new. During the rainy season, abandoned nests rarely persist intact for more than a few weeks, if that. The combined effects of weather and perhaps

theft of nest materials by other species rapidly bring these delicate structures to a state of marked disarray.

Although nesting is confined to a 7-month period, data suggest that once the ovary becomes active, it remains in an active state continuously. Adult females from all months except October, January and February were examined. All had ovaries with well defined ova. For example, 9 individuals examined between 22 November and 14 December had ova of at least 1 mm. Young females breed the year following hatching. Their ovaries probably first become active at this time. Three immature females examined between 23 and 28 November contained smooth ovaries showing no evidence of ova externally.

Nest form and composition.—The nest of the Long-tailed Manakin is a small, shallow cup suspended from the fork between 2 small branches (Fig. 1). Usually the nest is attached to each branch only at 2 points though occasionally fibers are wound around the entire length of the twig. Attachment sites range from 3 to 30 mm in width, averaging around 16.5 mm. The anterior connections often are heavier than posterior ones and may reach a thickness of several millimeters. The connection is formed by a dense mat of fibers tightly wrapped around the branch and extending into the cup of the nest. A single fiber may form several loops of the connection. As much as 50% of the attaching fibers may be delicate white or silvery-gray strands apparently from some type of spider web, egg case, or insect cocoon. These fibers are sticky, elastic, and quite strong. Equally common in the connecting mass are black rhizomorphs of the fungus *Marasmius* sp. which measure only a few tenths of a millimeter in diameter. Occasionally larger fibers, usually extensions of components of the nest cup, are included. Pieces of crushed leaf blade, moss and other materials often are bound up in this mass.

The nest proper is a circular cup although the attachment areas and supporting twigs give the nest as a whole a trapezoid appearance. The nest is not lined with any soft material but can be separated into 3 (rarely 4) relatively discrete layers. The outermost layer consists of a very sparse network of fungal hyphae which extends between the connection points. These hyphae form a sling supporting the middle layer which is composed of leaves or of mixed leaves and moss (Leskeaceae). Very rarely, both a layer of leaves and then a layer of moss are present. In about 35% of the nests the fungal hyphae also provide a site for the attachment of leaves which hang vertically from the outer surface of the nest for a distance of up to 8.5 cm. These may be few or many, but usually they are concentrated around the outer perimeter of the cup. The hanging leaves generally are quite large and often different from those in the middle layer and

TABLE 2
 QUANTITATIVE ASPECTS OF LONG-TAILED MANAKIN NESTS IN
 GUANACASTE PROVINCE, COSTA RICA, 1971-1974

Character	No.	Range	Mean
Inner Diam. (cm)	23	4.3-6.0	5.87
Outer Diam. (cm)	25	5.8-8.8	7.22
Inner Depth (cm)	24	1.5-3.0	2.24
Outer Height (cm)			
A ¹	22	3.5-4.5	3.84
B ²	11	6.0-11.0	9.08

¹ Excluding vertically hanging leaves.

² Including vertically hanging leaves.

apparently serve to camouflage the nest against predators. The middle layer always contains leaves, or more often pieces of leaves, of many species and may be from one to several leaves thick. Four nests also included grass blades in the leaf layer; 10 nests included strips of bark. Nineteen included pieces of moss (*Leskeaceae*) and 20, leaflets of the fern *Lygodium venustum*.

Beneath the leaf layer is the innermost and thickest layer which forms about half the bulk of the nest. It consists primarily of fungal hyphae (*Marasmius*) and leaf midribs from various species, although small diameter twigs, grass blades, bark fibers and fern petioles (*Adiantum*) also are found occasionally. The fibers forming the rim of the nest and the centimeter just below the perimeter are wound circularly while those in the cup usually are interwoven at right angles across the nest.

Palo Verde nests showed only minor differences from those at Finca Jiménez. They contained a greater percentage of fungal hyphae (*Marasmius*), and the leaf layer of one nest consisted primarily of blades of grass (*Panicum fasciculatum*). Both lacked leaflets of *Lygodium venustum*.

Measurements of various nest parameters are summarized in Table 2.

Nest construction and use.—I did not observe nest building from its inception but did locate 3 nests in which construction had been in progress for less than half a day. The female building one of these nests was observed for 9.2 hours. The other 2 nests were checked periodically to determine their progress toward completion.

Construction begins at the attachment sites. A limited amount of material is added at these sites throughout the building process, but attachment is quite strong from the beginning. The circular fibers forming the upper centimeter of the rim and the outer sling of fungal hyphae extending between the various attachment sites are added next. By this time the



FIG. 2. Long-tailed Manakin nest under construction at Finca Jiménez, Guanacaste Province, Costa Rica. Note the leaf midrib lying across the upper perimeter of the nest; it is partially interwoven with other fibers but not shaped into the cup of the nest.

general shape of the nest is apparent. Approximately half a day is required for construction to reach this point. Next the leaves hanging from the rim or bottom of the nest are added, if they are to be included. At approximately the same time the leaf-moss layer is laid down from the inside. The innermost layer of hyphae and midribs is the last to be added. This is done in several ways. The most common is by placement of several strands of material across the nest so that they protrude on either side (Fig. 2). The female then lands on the center of the nest cup bending the strands with the weight of her body. She wiggles her body laterally as if settling in on the nest at the same time rotating her body slightly. Initially then, the nest is a half sphere which is periodically pushed down in the center. Often when settled in the nest the female leans over to the outside reaching with her bill to poke and rearrange material. She also perches on the rim of the nest or on the supporting twig between connection points leaning to the inside to rearrange material or to reinforce connections. Some fibers are poked into the outside of the nest, brought up over the supporting twig and attached on the inside.

The leaflets of *Lygodium venustum* are green when brought to the nest as are the tufts of moss. The *Marasmius* rhizomorphs used probably are

live also. Other leaves and nest materials always are brown and dry, even those apparently coincidentally of the same species as the nest tree. I never observed a female collecting nest material from the tree in which the nest was built. Although these dry materials must be brittle, there is little evidence of broken twigs or midribs. Leaf blades, however, often are represented by nothing more than an extensive vein network. During the rainy season, of course, materials are considerably more pliable.

It takes a female approximately 3 days to build a nest. She works at it throughout the day, though work bouts periodically are interrupted by absences from the nest of 30 to 60 min. When actively building, the female visits the nest fairly regularly at intervals of approximately 5 min. On entering the nest area she usually perches 3 to 5 m from the nest carefully scanning the area. This may last for a few seconds or several minutes involving several perch changes. Occasionally she will leave the area without visiting the nest site. Usually the female carries only a single piece of nest material at one time. The visit to the nest site may last only a few seconds, the length of time required to leave the material carried, or it may last up to 35 sec.

Observations at one nest indicate that the female may interrupt nest building for several days. This nest was begun on 24 May. No work was done on 25 May nor any day thereafter until 1 June. It was completed on 2 June. Another nest observed was begun 31 July. No additional building occurred between 1 and 13 August when I left the area. In each instance the initiation or reinitiation of building directly followed one or several days of rain. Once the rainy season begins, usually in late May, interruptions of building seem to coincide with dry periods. Therefore, it is tempting to suggest that rainfall in some way stimulates or controls nest building behavior. However, nesting apparently occurs in both March and April when rains are absent, or at best rare, sporadic and unpredictable. Records of several nests built during this dry period indicate construction following periods of up to two weeks without rain. One would suspect that nest building would be easier after a rain as construction materials would be more pliable.

Eggs, egg laying, and incubation.—The Long-tailed Manakin eggs from Costa Rica are covered by a thin, delicate shell of beige-tan ground color. It is lightly to heavily marked with medium to dark chocolate brown spots. They may be present over the entire shell or just toward the larger end where they usually are concentrated, especially in a 4–5 mm band at the point of greatest egg diameter. Nine clutches from Oaxaca, Mexico, are of the same color and markings (L. Kiff, pers. comm.). Egg dimensions, weights, and clutch size data are summarized in Table 3. These parameters

TABLE 3
EGG DIMENSIONS AND CLUTCH SIZES OF MANAKINS OF THE GENUS *CHIROXIPHIA*

Character	No.	Range	Mean
<i>C. linearis</i> —Costa Rica (this study)			
Length (mm)	10	20.3–24.0	22.40
Greatest width (mm)	9	15.5–18.0	16.52
Weight (g) ¹	9	2.5–3.25	2.94
Clutch size	10	1–2	1.6
<i>C. linearis</i> —Oaxaca, Mexico (L. Kiff, pers. comm.)			
Length (mm)	18	21.1–22.8	22.13
Greatest width (mm)	17	15.6–16.8	16.09
Weight (g)	0	–	–
Clutch size	9	2	2.0
<i>C. lanceolata</i> —Panama, Colombia (Allen 1905, Hallinan 1924)			
Length (mm)	7	21.0–22.0	21.67
Greatest width (mm)	7	14.7–16.0	15.31
Weight (g)	0	–	–
Clutch size	5	1–2	1.8
<i>C. pareola</i> —Brazil, captivity (Burmeister 1856, Pinto 1953, Olney 1973)			
Length (mm)	7	21.5–25.0	–
Greatest width (mm)	7	14.5–17.0	–
Weight (g)	1	2.2	2.2
Clutch size	7	2	2.0
<i>C. caudata</i> —Brazil, Paraguay (Burmeister 1856, Nehr Korn cited in Ihering 1900, Euler 1900, Ihering 1902, Chubb 1910)			
Length (mm)	? ²	21.6–26.0	–
Greatest width (mm)	? ²	16.0–17.0	–
Weight (g)	0	–	–
Clutch size	? ³	2	2.0

¹ Includes fresh eggs (N = 2, R = 2.75–3.25) and eggs located some time after laying (N = 7, R = 2.50–3.25, \bar{x} = 2.93).

² No. = at least 7.

³ No. = at least 3.

do not differ significantly between the countries. The 9 clutches from Mexico all consisted of 2 eggs. Of 10 from Costa Rica, 6 included 2 eggs and 4 one egg, which suggests a difference. Sample sizes are too small for meaningful statistical testing. Three of the 1-egg clutches were located after completion of egg laying and may reflect partial loss of the clutch.

In 2 instances eggs were laid in nests whose construction had been followed. At both, 2 full days intervened between the day of nest completion and the day the first egg was laid. A second egg was laid in one nest the following day. Four eggs for which information is available were laid

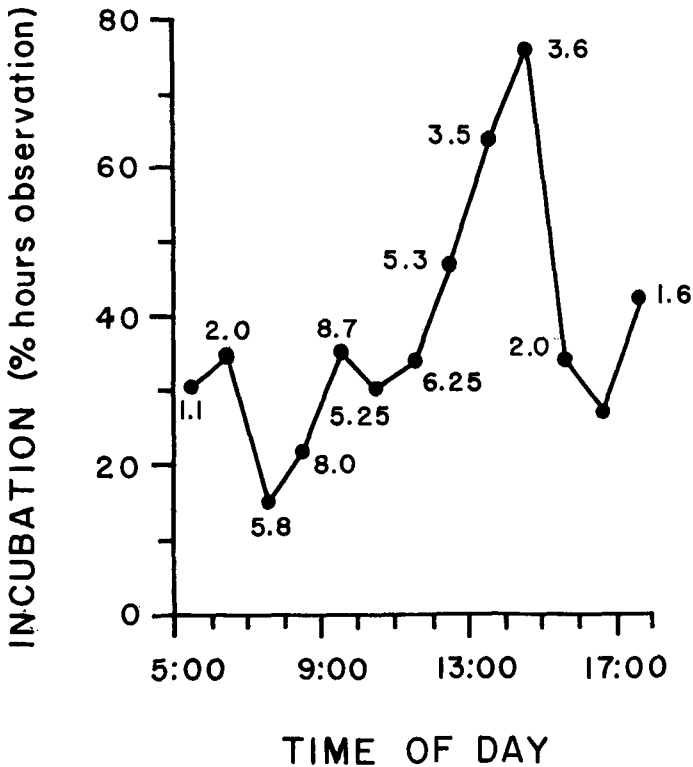


FIG. 3. The amount of incubation by females during each daylight hour expressed as a percentage of hours of observation (numbers adjacent to dots) during each of those daylight hours.

in the morning, 2 prior to 07:30 and 2 between 09:00 and 10:00. In no instance were nests observed to be used more than once.

Incubation was observed at 6 nests for approximately 55 hours. Because hours of observation were not equal for each daylight hour, data were transformed by hour into the percentage of observation time spent by the female on or off the nest (Fig. 3). Females do not incubate during much of the morning. This absence may be attributed in part to time spent feeding, but I suspect that this is a relatively minor factor. Manakins are frugivores feeding in trees that are quite abundant in the study area. Observations on feeding suggest that they know the location of the trees and travel directly to them. Feeding bouts are usually quite short, a few minutes at most. In addition, much of the time when a female is not incubating, particularly during the morning hours, she is present at the nest

site. A female often was seen perching quietly in a tree adjacent to her nest tree, preening, or quite alertly examining the area. Sometimes it appeared as if she sensed some disturbance in the area and for that reason was avoiding the nest. For example she would settle on the nest for a minute or 2 and then with no apparent provocation would leave the nest and perch in an adjacent tree. After carefully eyeing the area for 15 to 20 min, she would return to the nest again only for a minute or 2. However, this behavior was observed only during the morning, not in the afternoon. The dip in incubation time in the late afternoon also may represent absence for feeding although again, the birds appear to be absent for more time than necessary, and the female may remain near the nest during this period. The increase in incubation time between 17:00 and 18:00 hours is indicative of females coming to the nest to spend the night. The number of hours of incubation each day also seems to increase as the incubation period progresses.

Although my data are limited, they suggest that females do not incubate right after laying. Three nests with a total of 4 eggs were observed at length or spot checked several times on the days the eggs were laid and for several days thereafter. It was noted for the 2-egg clutch that the female did not incubate until the second day following the laying of the second egg. At another nest the female did not incubate the day she laid the first egg. The nest was destroyed by a predator the next day. At the third nest no incubation was observed the first day after laying. The nest was not checked again until 3 days later at which time the female was incubating one egg.

No nest was observed from egg laying through hatching, so the length of the incubation period is not known. The longest any nest was observed was 10 days. In this instance, eggs were present, and the female was incubating when the nest was located. One egg hatched on the tenth day of observation.

When I first located a manakin egg and weighed and measured it, I also numbered the shell with India ink. I was thus able to determine that the position of the eggs changed during the day, throughout the incubation period. Individual eggs were rotated side to side and end to end and even were moved to new positions relative to another egg in the nest. I do not know if this was an accidental result of movements by the female during incubation or if she actively changed their position from time to time.

Nestlings.—Only 3 young were observed in the nest. The first, one of a clutch of 2, apparently hatched prior to 07:00 when I arrived at the nest to begin observations. The female was incubating, and the contents of the nest were not observed until 10:10. No shell or remnants were present in

or under the nest at that time, and the female did not dispose of them between 07:00 and 10:10. She also did not feed the young bird during this period, and it did not have the bulging stomach often characteristic of nestlings. The nestling weighed 3.0 g, hatching from an egg weighing 3.15 g nine days before. When disturbed, the nestling repeatedly gaped widely but made no sound. Its mouth lining was golden-yellow, its eyes were closed, and the black-tipped bill was 3 mm long with a small distal caruncle. Grayish-tan natal down was present in the superciliary and occipital elements of the capital tract, all elements of the dorsal tract, the scapulohumeral and femoral tracts, and the area of the secondaries in the alar tract.

The other 2 young were present in a single nest. They weighed 9.5 and 8.5 g, 50 to 60% of the average adult weight. Their measurements (mm) were, respectively, bill length, depth and width: 3.0, 2.5, 4.0 and 3.0, 2.7, 3.5; chord of the wing: 15, 13; tarsus plus middle toe: 22, 19. Neither had rectrices. Their gapes and mouth linings were golden-yellow, their skin reddish to light brown, and their natal down grayish-brown. These feathers were present in the superciliary and occipital elements of the capital tract, all elements of the dorsal tract, and the femoral tract. All pterygiae were clearly defined by developing pins just beneath or barely protruding through the skin. Sheath tips were unruptured.

The young were observed from 13:45 until 17:00 on the day of discovery. They were not visited by the female during this period nor was any female seen in the vicinity. However, the young must have been fed shortly before my arrival as they were regurgitating seeds in the nest. All seeds but one (unidentified) were from fruits of *Trichilia cuneata* on which the adults feed commonly. The regurgitated seeds landed in the nest, and all seemed relatively fresh. No seeds were apparent on the ground beneath the nest. This suggests that the female removes the seeds after the young regurgitate them. No food or fecal remains were present in or under the nest which was quite clean. All 39 nests examined were noticeably clean and free of any fecal material.

The young were able to flex their appendages but did not seem capable of moving around the nest. When the nest was jiggled, they raised their heads and gaped repeatedly; when they were not begging, however, their heads drooped, and they crouched low in the nest. When handled, the nestlings made a series of soft *cheeps*.

Because I was to be away from the area for the 4 days subsequent to the discovery of the nest, I took one nestling in an attempt to rear it. This effort was unsuccessful. The nestling rapidly lost weight, and so I preserved it 20 hours after collection. However, a few observations were made in

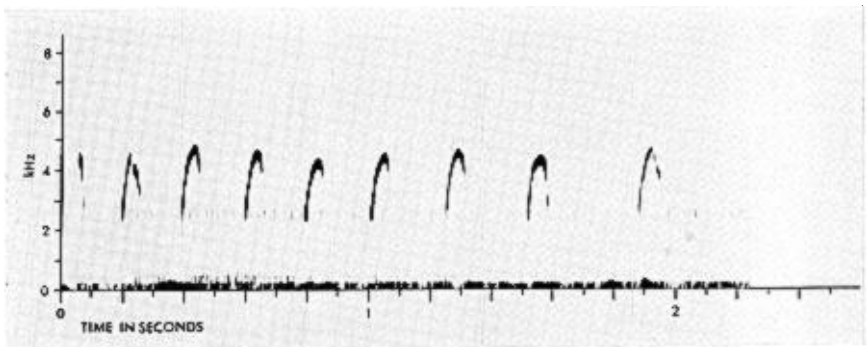


FIG. 4. Sound spectrograph of *cheep* notes of a nestling Long-tailed Manakin from Guanacaste Province, Costa Rica.

the laboratory. Vibration of the nest (apparently simulating the arrival of the female) stimulated the bird to gape. If the nestling accepted a food item, it would not gape again for several minutes. Food was taken into the bill and "mouthed" for a second or 2 before swallowing. If the food item was too large or too dry, it was dropped. The preferred size of items seemed to be about 5 mm in length and 3 mm in diameter, although larger pieces were taken. This means that fruits such as those of *T. cuneata* would have to be broken up by the parent into component carpels before feeding. The seeds regurgitated in the nest ranged to 9 mm in length and 4.5 mm diameter. The nestling in captivity was fed field collected fruits of *T. cuneata* and *Muntingia calabura* as well as a few insects. Seeds of the *Trichilia* were regurgitated, usually several in succession. The tiny *Muntingia* seeds and insect exoskeletal parts were voided in the feces.

Fecal material contained in a sac-like membrane was voided directly into the nest. Apparently the female removes these sacs in the wild. Birds would not gape when about to void a fecal sac. This act was preceded by a series of peristaltic contractions running posteriorly along the length of the body, and by lifting and rhythmic contraction of the anal protuberance.

The nestling cheeped almost continuously except immediately after being fed, so this vocalization may function in begging. Spectrographic analyses of several calls are shown in Fig. 4. The *cheep* begins at an average frequency of 2.258 kHz (N = 15). It has a rapid upward inflection to an average of 4.519 kHz followed by a turn downward. The depth of the downward inflection is variable, reaching frequencies ranging from only 3.875 kHz to 2.375 kHz. Each *cheep* element lasts an average of 0.062 sec. The *cheep* is given in series of varying length (R = 19-64 calls; \bar{x} = 31.8;

N = 12) without any observable pattern. Within each series from beginning to end, however, the calls are spaced at intervals of increasing length. Initially, *cheeps* are given at a rate of 6 calls/sec; toward the middle of the series they occur at a rate of 5/sec and at the end, at 4/sec.

The *cheep* call is characterized by a well-defined beginning and end, and covers a wide frequency range. Thus, it should be easy to locate. However, it is not likely to attract predators from any great area as it is a very low intensity vocalization inaudible to my ear at a distance of about 1.5 m. Despite its low intensity, some variation between calls is noticeable (this is not evident in the spectrograms). "Louder" calls appear to alternate with "softer" ones at a ratio of one to one.

Two other young nestlings taken from unhatched eggs that had been abandoned were examined. They had been incubated for at least 6 and 7 days though probably more. Both weighed approximately 1 g without the yolk sac and though both were well developed, one was obviously more advanced. Each had a well developed egg caruncle, and the pterygiae were moderately to well defined. Down feathers with intact sheaths were present in the areas noted above for the other nestlings.

Nesting success and predation.—Although only a small number of eggs and nestlings was followed, nesting success seems to be quite low in the Long-tailed Manakin. Only one of 15 eggs observed (6.67%) hatched. This nestling plus one from another nest (I collected a third) did not fledge.

Though nest predation never was observed, it was presumed on the basis of egg or nestling disappearance, and in some instances on the basis of nest damage. In 3 instances pieces of broken shell were found in or beneath the nest. Predation apparently is accomplished in at least 2 different ways. In one instance the nest seems perfectly intact with only its contents missing. In the second, the central portion of the nest is pushed (pulled?) downward and occasionally completely separated from the four connection points and adjacent portions of the nest rim. It appears as if an animal of considerable weight has rested on or pulled down the central part of the nest.

Snakes would appear to be the most likely predators in the first instance. The nests generally are placed low enough so that ground dwelling as well as arboreal forms may be responsible. Of the many snakes known from the area, at least *Boa constrictor*, *Drymarchon corais*, *Leptophis mexicanus*, *Mastigodryas melanolomus*, *Oxybelis aeneus* and *Trimorphodon biscutatus* may be expected to prey on eggs or nestlings (Keiser 1975, D. R. Paulson, R. W. McDiarmid, N. J. Scott, W. van Devender pers. comm.). Various species of birds also may rob the nest causing minimal damage. Likely

candidates common in the area include Turquoise-browed Motmots (*Eumotoca superciliosa*), White-necked Puffbirds (*Notharchus macrorhynchos*), toucans (*Pteroglossus torquatus*, *Ramphastos sulfuratus*), Magpie Jays (*Calocitta formosa*) and others.

Nests that were pulled apart could have been damaged by large lizards or mammals. Both *Ctenosaura similis* and *Basiliscus basiliscus*, which are common arboreal lizards in the area, might be expected to take bird eggs or nestlings (R. W. McDiarmid, W. van Devender pers. comm.). Local mammals reported (Goodwin 1946, Leopold 1959) to feed on birds and eggs include several opossums (*Didelphis marsupialis*, *D. virginianus*, *Philander opossum*, *Caluromys derbianus*), White-throated Capuchins (*Cebus capucinus*), Kinkajous (*Potos flavus*) and probably Coatis (*Nasua nasua*). At one nest between my observations late one afternoon and early the following morning, some large predator weighed down the limb with the nest far enough to hook the limb on a bush below. Although the nest was undamaged, the eggs had fallen to the ground. I restored the eggs and nest to their former positions, but the female never returned to incubate.

DISCUSSION

Nest site selection.—Trees used for nesting apparently are selected on the basis of growth form, size, and fruiting time. The suspension of the nest requires the presence of forked branches of approximately equal diameter lying in the same horizontal plane. Although this criterion would seem to be one easily met by a large number of species, some trees are particularly suitable and are commonly selected. *Terminalia lucida*, in which the branches occur in whorls in a single horizontal plane, is one of these. In addition, branching must be such that adjacent rami will form a roof over the nest site without hindering access by the female (Fig. 1). The roof probably is of great value in mediating the effects of the physical environment. Although none of the nests was directly exposed, all received filtered sun for several hours each day. The adjacent leaves helped to shade eggs, young, and the attending female. Protection provided from rain during the wet season would be of equal importance. In most instances, the shading vegetation appeared to reduce substantially the amount of water falling into the nest during a storm or from adjacent vegetation afterward.

The roof of leaves also tends to camouflage the nest from above and sometimes from the side. Additional camouflage is provided by the leaves which hang vertically from the rim and underside of the nest. Some nests closely resemble piles of detritus caught in the fork between branches. I

can attest to the fact that this camouflage is very effective at reducing discovery by ornithologists. It undoubtedly reduces predation to some degree also.

Predation may be the selective factor controlling choice of tree species and size. Many of the trees common in the study area produce an abundant fruit crop heavily used by birds and mammals also expected to prey on eggs and nestlings (e.g. *Eumomota superciliosa*, *N. nasua*). Thus the placement of manakin nests in trees of species not in fruit or in individuals below fruiting size minimizes the probability of encounters between fruit eating predators and the nest. Predation also may favor the use of small trees for nesting if the trunks and branches are too small to support the weight or provide free movement of many of the large mammals and lizards. This probably also influences the distance from the trunk at which the nests are built because animals too large to traverse small side branches would be unable to reach into the nest from a position on the trunk.

Although advantageous with regard to predation, the use of distal rami of small branches of saplings and small trees may be disadvantageous during the dry season because of wind. The months of November through April are characterized by strong tradewinds from the northeast. These winds commonly cause small trees or their branches to bend deeply. On one occasion I watched while the wind tipped a branch with a nest from which the female was absent far enough to cause the eggs to roll out.

Other nests of C. linearis.—Wagner (1945) reported on 3 nests from Chiapas, Mexico, which he attributed to the Long-tailed Manakin. However, according to the data he provided, the nests and their eggs differ considerably from those taken in Costa Rica and Oaxaca, Mexico (WVZ).

Wagner indicated that he found his nests at the borders of woods, in direct sunlight, and at heights of 2.5 to 3 m. The nests I located were in the forest proper, received only filtered sunlight and averaged 1.26 m (Table 1) above ground. Eight of the nests from Oaxaca averaged 1.49 m ($R = 0.91-1.83$) above ground, and the 5 with data all were in deep shade. Wagner also states that the nests were not hidden by leaves in contrast to my findings.

On the basis of the descriptions and diagrams which he provided, the Chiapas nests also appear to differ in plan of construction and composition from the Costa Rican nests and the single Oaxacan nest that I have seen. The latter, apparently typical of all of the Oaxacan nests (L. F. Kiff, pers. comm.), is strikingly similar to those from Costa Rica. It is approximately the same size and was suspended from a small fork. Primary components include spiders' web, leaf midribs, fungal rhizomorphs (*Marasmius?*), leaflets of *Lygodium venustum*, and an outer covering of dead leaves. Differ-

ences in the Chiapas nests include (1) crossing of small adjacent branches with the principal ones of suspension to increase nest stability; (2) extensive use of extremely large squares and strips of bark and their deployment in the nest; (3) interior lining of leaves and bark. The suspension of the nest in a small fork, the use of spiders' web and long animal hairs (which I assume were actually fungal rhizomorphs), and the manner of nest construction agree with my findings.

Wagner (1945) also supplied a variety of nest measurements. For one nest illustrated he gave interior and exterior diameters of 4.2 and 8 cm, and an interior depth and exterior height of 4.5 and 7 cm, respectively. He also stated that the upper diameter of the nests varied between 4.2 and 4.7 cm and the height between 4.6 and 7 cm. The diameter measurements are similar to those of the Costa Rican nests, but the other measurements are more difficult to evaluate. He did not mention the presence of leaves hanging vertically from the nest, and in the general diagram of nest construction (Wagner 1945: Fig. 2) they are clearly absent. His diagram of an intact nest, in situ (Wagner 1945: Fig. 1), although not very clear, may show such components. This would account for the differences in height values. The single measurement for inner depth, 4.5 cm, is extremely difficult to explain. The mean depth of the Costa Rican nests was only 2.24 cm ranging to a maximum of 3.2 cm. Long-tailed Manakins are small birds with an average body length (tip of bill to tip of tail, excluding the central pair of rectrices) of only 10 cm (Land 1970), 3 to 3.5 cm of which comprise the tail. It seems unlikely that a bird this size would occupy so deep a nest.

Finally, Wagner described the eggs found in one of his nests as whitish-cream in color with dark spots, which is different from both the Costa Rican and Oaxacan eggs (see above).

On the basis of the data provided in his paper, it seems likely that all or at least one of Wagner's nests were misidentified. Although various aspects of nests may vary between widely separated parts of the range of a species (e.g. Skutch 1969:114, 216), it is unlikely that the nests of Oaxaca and Costa Rica would be extremely similar to each other while markedly different from those in Chiapas. Wagner never mentioned how species identification was determined and did not indicate that any females were sighted in the vicinity of the nest.

The eggs and nests which he described and diagrammed are strongly reminiscent of those of the Barred Antshrike (*Thamnophilus doliatus*) which I have seen commonly in my study area in Costa Rica and which are described by Belcher and Smooker (1936) and Skutch (1969). The distribution of this species overlaps that of the Long-tailed Manakin in Chiapas

(Edwards 1972) where Wagner made his observations. The nests he described should be excluded from a consideration of manakin nests at least until more conclusive data concerning the nature of the Long-tailed Manakin nest in Chiapas are available.

Comparisons with other Chiroxiphia.—The genus *Chiroxiphia* includes 3 species in addition to *C. linearis*. All species show striking similarities in external morphology (de Schauensee 1970, Land 1970) and male reproductive behavior (Sick 1967). Although very few comparative data about nesting biology are available, it appears that the 4 species are very similar in this respect also.

Nests of the Lance-tailed Manakin (*C. lanceolata*) have been described from Colombia (Allen 1905) and Panama (Hallinan 1924) where they were found in low forest shrubs. The nests consisted of a mat of fine circularly woven fibers with dead leaves forming an exterior covering and hanging loosely from the sides and bottom. Spiders' web was used for binding the nest to its supporting twigs, although Allen suggested that dried, glutinous bird saliva might be used also. The Colombian nests had outside diameters ranging from 6.35 to 7.62 cm, inside diameters ranging about 2.54 cm less, and a depth of less than 2.54 cm (Allen 1905). I also have examined a nest of this species collected by N. G. Smith in Panama. It agrees with the above description but also includes some fungal rhizomorphs (*Marasmius* sp.). The average height of these nests was 1.13 m (R = 1.0–1.2; N = 3) above ground. Burmeister (1856) briefly mentions a nest of the Blue-backed Manakin (*C. pareola*) found in Brazil by R. Schomburgk. It was in the forest and made of moss. Pinto (1953) also described nests of this species from Brazil. They were located in the forest, especially adjacent to waterways, and suspended from forks in small trees at an average height of 1.4 m (N = 4). One nest, treated in detail and pictured, consisted of a small cup of curved petioles and long dark fibers resembling horsehair, neatly arranged in layers. Presumably the horse-hair-like fibers were fungal rhizomorphs, perhaps *Marasmius* sp. Pinto also noted that the outer surface of the nest was covered with dry leaves or pieces thereof, but included no moss. The single nest measured had an outer diameter of 6 cm. Several authors (Burmeister 1856, Euler 1900, Ihering 1902, Sick 1957) have mentioned nests of the Swallow-tailed Manakin (*C. caudata*). These nests generally are suspended from the forks of small branches in forest shrubs and small trees. They are rather weakly built and measure about 7 cm in diameter. Dry plant fibers, black fibers of *Tillandsia usneoides*, rhizomorphs of *Marasmius*, and sometimes moss and wool (?) are used in construction. Dry leaves are affixed to the outsides and may hang beneath the nest.

Egg dimensions of the 4 *Chiroxiphia* species are similar (Table 3), though *C. caudata* is a noticeably larger bird than the others (pers. observ.). Egg color and markings also are quite similar. Eggs of the Lance-tail are described (Hallinan 1924) as brownish-white with reddish-brown markings, or (Allen 1905) as dull creamy-white with markings of a very pale chocolate color mixed with shades of lilac. In both instances, markings are concentrated at the wide end of the egg. Remnants of broken eggs of this species supplied by N. G. Smith are of a beige-tan background with medium brown spots and closely resemble eggs of *C. linearis*. The eggs of the Blue-backed Manakin described by Pinto (1953) ranged from dirty-white to light-brown with chocolate brown, rusty-wine or yellow-brown spots. Thus they differ slightly from those laid in captivity (Olney 1973) which were bluish-buff and heavily spotted with chocolate brown. According to Euler (1900) and Nehr Korn (cited in Ihering 1900), the eggs of *C. caudata* are yellowish-white with light brown spots and dark elongated markings concentrated in a band at the blunt end. The cream-colored eggs described by Chubb (1910) also had spots and blotches concentrated at the large end, but these markings were pale chestnut and lilac. Eggs described in Burmeister (1856), in contrast, were grayish-yellow, covered with a pale reticulum, and marked with bluish-green spots.

With the exception of a notation that the female was incubating at a nest of *C. caudata* (Euler 1900), the only *Chiroxiphia* other than the Long-tail for which data on nesting behavior are available is the Blue-backed Manakin. Pinto (1953) noted incubating females at 4 nests. Additional information was provided by Olney (1973). However, his observations were made on a female nesting at the London Zoo and so do not necessarily reflect activity in the wild. An incubation period of 17 days was suggested, and the fledgling first left the nest after 14 days. The nestling was fed primarily, if not wholly, on fruit. Olney did observe some participation by the male in nest building.

SUMMARY

The nesting biology of the Long-tailed Manakin (*Chiroxiphia linearis*) was studied over several months in 1971-1974 in Guanacaste Province, Costa Rica. Thirty-nine nests were discovered, 12 of which contained eggs or young. These nests were shallow cups suspended from forks in small trees. They were placed so that adjacent branches provided camouflage and protection from weather. Nest materials included primarily spider web or insect cocoon fibers, fungal rhizomorphs (*Marasmius*), moss, leaf blades and petioles, bark fibers, grass blades, and other dry plant fibers.

Nest building normally took about 3 days when not interrupted. Females did not incubate over much of the morning and in the late afternoon, although they often remained in the vicinity of the nest. Clutch size was 1 or 2. Young were sparsely covered with grayish-tan natal down; gapes and mouth linings were golden-yellow.

Older young, at least, were fed on fruit, and they repeatedly made soft, *cheep* notes. Nesting success was very low, presumably because of high predation. Only one of 15 eggs which were followed hatched; neither of 2 nestlings observed fledged.

Growth form, size, and fruiting time are probably the most important features of the tree controlling the selection of trees for nest placement because of their influence on nest suspension, camouflage, and protection from weather and predators.

Long-tailed Manakin nests described from Chiapas, Mexico by Wagner (1945) were probably misidentified. The Costa Rican nests and eggs also are compared to those from Oaxaca, Mexico and to those of the other 3 species of the genus *Chiroxiphia*. All are strikingly similar.

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