

THE BEHAVIOR OF PLAIN-BROWN WOODCREEPERS, *DENDROCINCLA FULIGINOSA*

EDWIN O. WILLIS

IN forests of tropical America, woodcreepers of the genus *Dendrocincla* follow swarms of army ants persistently (Willis, 1960:158-159; Skutch, 1969:136; Oniki and Willis, 1972). Intensive studies of ant-following birds on Barro Colorado Island, Panamá Canal Zone, and brief studies in other areas show that Plain-brown Woodcreepers regularly follow army ants. The changes in foraging niche when these woodcreepers confront different sets of competing antbirds at some of the localities have been detailed elsewhere (Willis, 1966). Here social and individual behavior will be considered.

Feduccia (1970:1) lists many brief references, mostly in annotated lists, on the behavior of woodcreepers. The only extensive studies have been Skutch's (1969) of Tawny-winged and other woodcreepers. Slud (1960, 1964) and several others, including Johnson (1954) and Snow and Snow (1964) and Oniki (1970) among references not listed by Feduccia, have commented briefly on the natural history of Plain-brown Woodcreepers. The species and its genus and family are not well known ethologically.

Appendix 1 lists common and scientific names of birds mentioned herein, following Meyer de Schauensee (1970), except for Central American birds listed only in Eisenmann (1955) and for northern birds listed in the A.O.U. Check-list.

THE PLAIN-BROWN WOODCREEPERS

Plain-brown Woodcreepers wait on or hitch up the trunks of trees like slender woodpeckers or overgrown Brown Creepers. They live in the middle and lower levels of humid lowland forests from Honduras to central Brasil. Occasionally they wander to the edge of the forest, into cacao and coffee orchards, or into second growth more than 5 m tall. Instead of hammering or probing at bark or epiphytes, they peck prey off the surface of vegetation or sally out like flycatchers to snap prey off nearby vegetation, the ground, or out of the air. Commonly they follow army ants and capture arthropods they flush. Occasionally they flycatch away from ants, alone or with wandering interspecific flocks of insectivorous birds.

This is a brown bird with a dark malar streak below a pale gray face (Fig. 1); as in many woodcreepers, the flight and tail feathers are rufous. The yellow linings of wings and mouth and the pale throat seldom show as the bird waits stolidly. A dark streak from bill to eye and a yellowish streak behind the eye are similarly inconspicuous.



FIG. 1. Plain-brown Woodcreeper on Barro Colorado Island, Panama Canal Zone from slide; seen from below.

On Barro Colorado Island, weights of eight Plain-brown Woodcreepers ranged from 38.5 to 43.4 g (mean 41.6); these birds were captured over ant swarms, where food is abundant. James Karr (pers. comm.), netting mostly birds away from army ants nearby in the Canal Zone, found a range in seven birds (ten weights) from 35.0–44.4 g (mean 40.4). Culmens of 39 Panamanian birds in the American Museum of Natural History range from 27.1–32.5 mm (mean 30.2) without sexual differences.

Wing lengths (chord) for Panamanian specimens at the American Museum and at the Museum of Comparative Zoology are 96–106 mm (mean 101.4) for 21 females and 102–113 mm (mean 108.6) for 31 males. Some “males” with short wings and “females” with long wings may have been sexed incorrectly, since labels of these particular specimens indicate gonads were not enlarged. However, short-winged males may have been young. (Birds with very worn, damaged or molting wings were excluded from samples). Birds from other countries have different wing lengths, but males always average longer in

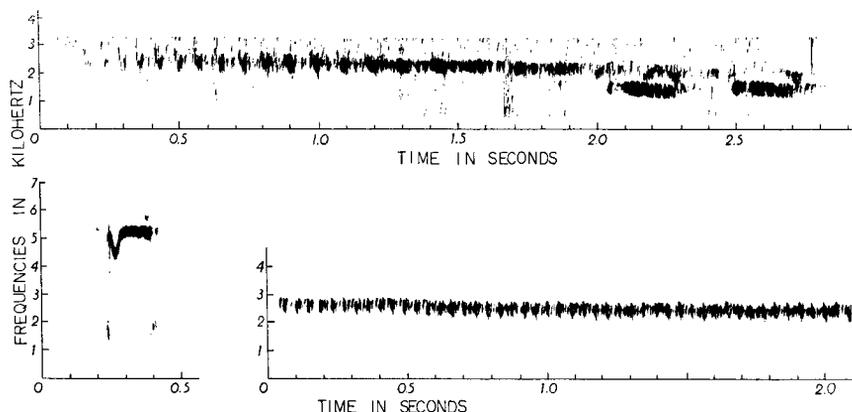


FIG. 2. Audiospectrograms of vocalizations of Plain-brown Woodcreepers. Above, "song"; two caws of a Slaty Antshrike overlap the end of the song. Below left, a "stiek" alarm note. Below right, "long rattling."

wing length than do females from any given region. The dimorphism in wing length helped me sex some birds captured on Barro Colorado Island. Eight adult females there had wings 101–105 mm long (mean 102.5), and four adult males had wings 108–110 mm long (mean 109). Two other birds, with wings of 104 and 106 mm, were judged by their later activity to be nearly-grown fledglings. Adult females also have vascularized, featherless brood patches while nesting.

THE STUDY AREAS

The climate, forest, and study area on Barro Colorado Island and several other localities where I watched Plain-brown Woodcreepers are described in Willis (1967). This reference also describes the behavior of army ants (especially the important species, *Eciton burchelli* and *Labidus praedator*) and methods of study. Many woodcreepers were banded with color bands; female RBYM, for instance, had a blue band above a red one on her left leg and a yellow band above red/white one on her right leg.

I studied woodcreepers over or away from army ants on Barro Colorado from 28 September, 1960 to 25 November, 1961, and for a few months each year to 1971. Information on Plain-brown Woodcreepers comes mainly from observations at swarms of army ants while I was watching many species. However, nearly as many hours have been spent censusing birds while looking for ants, so that the woodcreepers have occasionally been studied away from ants.

VOICE

Plain-brown Woodcreepers have only five calls that seem worthy of separate names, and none is varied, complex, or musical.

Stieking.—This is a piercing, sudden, high-pitched (Fig. 2) *scheek* or *stiek* given by an alarmed bird. The beak flaps open suddenly, showing the

yellow lining more prominently than at any other time. The call is given at a rate of less than 40 per minute unless the bird is extremely disturbed.

Rattling.—This is a faint series of short grunting noises like the distant put-putting of an outboard motor or clacking of a train. The whole body quivers for the notes, but the bill is closed or barely open. The series may be brief (“rattlet”) or continue for several minutes at a time (“long rattle”). *Chut-ut-ut-ut-u-u-u-u, a-a-a-a-a-a, ri’i’i’i’i* *chew-ew ri’i’i’i* and similar notations are in my field notes for this call. It often varies in pitch and speed, but usually is at about 23 notes per second (Fig. 2).

Singing.—The rough “song” of this species (Fig. 2) is a descending series of 25 or so notes, each one like a grunt during rattling but less rough in quality and given more loudly. Notes are longer toward the end of the song. *Whee-hee-he-hah-huh-huh-huh-huh-huh-huh-hu-hu-hu-hu-hu-hu-hoo-hoo-hoo-hoo, wee-i-woo!* is one rendering. The sudden up-and-down ending, the greater speed, and the loudness of the song distinguish it from the rather similar but longer descending song of Black-striped Woodcreepers. Unlike rattling, singing is rather stereotyped. Males, females, and young birds all sing; songs occur in every month of the year, and seem communications of isolated birds hunting others rather than aggressive calls or sexual ones.

Hissing and Growling.—When a bird follows another closely a hissing or growling *chauhh* or similar sound is given. At increased speed the hissing or growling grades into rattling.

Screaming.—In the hand or when pecked by a supplanting bird, a woodcreeper screams roughly and piercingly. The burst of noise, *screeah* or the like, is more like hissing than like the clear and distinct stieking.

POSTURES AND MOVEMENTS

While clinging to a vertical trunk, the Plain-brown Woodcreeper often takes what may be designated the “standard posture” (Fig. 1 shows a slightly crouched bird, close to the standard posture). The slender and rather long body angles away from the trunk about 15 degrees and is clearly separated from it in side view. The bird is suspended by the front claws as it rests on the stiffened and somewhat incurved bare tips of the tail feathers. When seen from behind, as the bird clings to the trunk, the three front toes on each foot spray from just below the horizontal to 70 or so degrees above it, while the rear toe follows the line of the tarsus at about 60 degrees below the horizontal. The long, curved front claws dig into the thin and smooth bark usual on tropical trees, and the rear claws clamp in to some extent. Ordinarily the toes and sole of the foot are off the perch. The bill points about 15 degrees toward the trunk, or some 30 degrees from the line of the body. The wings meet above the base of the tail, and the bend of the wing is exposed.

TABLE 1
PERCH CHARACTERISTICS OF PLAIN-BROWN WOODCREEPERS

HEIGHT ^a		ANGLE ^b		DIAMETER ^c	
Height (m)	Records	Angle (deg)	Records	Diameter (cm)	Records
0.1	4	20 or less	31	0-1	11
0.2	19	40	37	-2	107
0.3	99	60	74	-3	206
0.4	242	80	284	-4	213
0.5	308	100	2525	-5	202
0.6	201	120	153	-15	1177
0.7	177	140	12	-25	471
0.8	218	160	4	-50	259
0.9	164			-100	138
1.0	148			100+	22
1	1580				
2	1676				
3	1167				
4	1084				
5	650				
6	497				
7	360				
8	340				
9	200				
10	158				
15	234				
20	14				
25	3				
30	3				
Totals	7966		3120		2806

^a Barro Colorado Island, 1960-1964 data over army ants. Records are 0-0.1 or 0-1 m up to 26-30 m.

^b Barro Colorado Island, 1960-1961 data over army ants. Records over 90° represent clinging to the underside of a perch. Records are for 0-20°, 20-40° etc.

^c Barro Colorado, 1960-1961 data over army ants. Records are 0-1.0, 1.1-2.0 cm etc.

A tailless bird, in heavy molt, rests against the undertail coverts and upper parts of the legs when clinging to a vertical perch.

On the rare occasions (Table 1) when this woodcreeper perches on a horizontal or nearly horizontal perch, it frequently stands across it like a perching bird rather than along it like a woodpecker. Commonly the woodcreeper sits close, splay-legged and somewhat humped around the perch (Fig. 3,D), but at times one stands almost as upright as a thrush. One bird that tried to perch crosswise on a wet limb kept sliding backward (Fig. 3,E). A woodcreeper

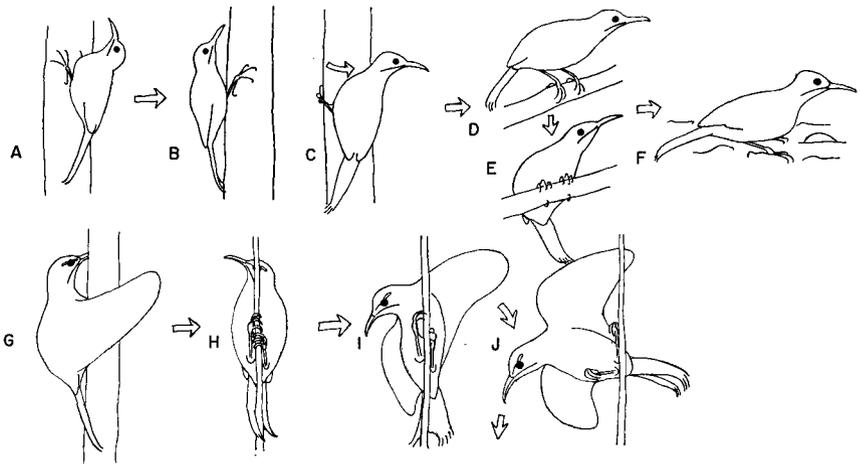


FIG. 3. Perching and travel of Plain-brown Woodcreepers. A bird alarmed by the stieking of another holds its head out (A), flies to another trunk and crouches (B), swings around the trunk (C) and on to another foraging area, where it perches briefly on a horizontal limb (D) but keeps sliding back on the wet bark (E); it flies to the ground briefly but has its crest raised (F). Another bird flashes its wing to flush a prey (G), waits on a slender sapling above ants (H), dives toward prey on the ground (I, J) by using its wings. From scattered field sketches at Simla, Trinidad.

perching crosswise reminds one of a leafscrapper (*Sclerurus* sp.) or other furnariid. The plain brown leafscrapers often cling vertically to a tree trunk or buttress when first flushed, and then resemble Plain-brown Woodcreepers remarkably. Feduccia (1969) suggests from morphological studies that the genus *Dendrocincla* may have evolved from Furnariidae, but from the foliage-gleaners (Philydorinae) rather than from leafscrapers (Sclerurinae).

Plain-brown Woodcreepers stay on perches near the vertical far more often than they stand on horizontal perches or cling underneath perches (Table 1). Their woodpeckerlike adaptations also seem better suited for perching on trunks larger than 2 cm in diameter (Table 1), particularly for poles 5 to 15 cm in diameter. In this respect they differ from such competing birds as Bicolored Antbirds, which cling horizontally to vertical perches but cling to perches more than 4 cm in diameter only with great difficulty (Willis, 1967). The vertically-clinging types of birds and the horizontally-clinging types, both usual at swarms of ants, complement each other. Occasionally a Plain-brown Woodcreeper clings to slender saplings, especially on Trinidad where competing antbirds are absent. If the sapling is 1–2 cm in diameter, the bird simply interlaces its toes. On perches less than 1 cm in diameter the bird has to put one foot above the other (Fig. 3,H) or oppose

the first and second toes of each foot while the outer toes hang freely. The outer feathers often slip forward and do not support the bird on such narrow perches.

Plain-brown Woodcreepers perch near the ground when few antbirds compete with them and high in the trees when antbirds are present (Willis, 1966). Table 1 summarizes the vertical distribution of the Woodcreeper over swarms of army ants on Barro Colorado Island.

HOPPING AND FLIGHT

Plain-brown Woodcreepers move up or down trunks by hopping or "hitching." In hitching upward, the bird catches itself with the tail at the end of each backward extension of the legs, then flexes the legs and catches hold of the bark again. In contrast to Barred Woodcreepers, hitching up and around perches is far more common than hitching downward. However, Plain-brown Woodcreepers do back downward occasionally. I have never seen hitching with head down like a nuthatch. On a horizontal perch or on the ground the bird may hop sideways, body angled at about 60 degrees from the line of progress; but the short legs force the bird to fly or flutter-hop for progressive movement. Adaptations for perching like a woodpecker definitely restrict freedom of movement on a perch compared with species like Bicolored Antbirds (see Willis, 1967).

In taking flight, the main push comes from the wings rather than from the short and forward-angled legs. These woodcreepers seldom hop from one perch to another without flapping the wings, and rapid movement up a trunk is often performed by fluttering vertically rather than by hitching. The long claws, which keep the feet off the trunk, probably do not permit rapid hopping or the effective use of the legs in taking wing in many situations.

Flight is strong. The long and broad wings flap rapidly, with occasional pauses, as a bird weaves rapidly through leaves and branches. The flight is slightly undulating. Long flights in one direction are rare, but the birds are expert at frequent changes of direction and at darting in and out of moderately dense vegetation. At times a fluttering or slow flight is adopted when one bird chases another. Flight is silent unless the bird hits leaves. These woodcreepers hover readily for brief periods: they can hover in any direction but backwards. In general, they combine speed with maneuverability very well.

In alighting, the Plain-brown Woodcreeper seldom glides up and in with wings outspread as do larger woodcreepers (especially the Barred Woodcreeper); it usually flaps as it comes to the perch, then quickly closes the wings when it alights. The yellow wing linings are seldom conspicuous in flight.

TABLE 2
ACTIVITIES OF PLAIN-BROWN WOODCREEPERS AWAY FROM SWARMS OF ANTS

Activity	Occasions	No. Birds	No. minutes
1. Wandering			
a. With other ant-followers ^a	12 (4.4%)	13	53
b. In to playback ^b	8 (2.9)	8	50
c. Singing	59 (21.5)	65	163
d. Rattling or quiet	38 (13.9)	48	159
2. Foraging			
a. With bird flock ^c	38 (13.9)	47	498
b. Not with flock	20 (7.3)	26	231
3. Bathing	8 (2.9)	11	54
4. Resting	1 (0.4)	1	7
5. Search for nest site	3 (1.1)	4	29
6. Stieking at predator or me	67 (24.4)	84	314
7. Activity uncertain	20 (7.3)	22	41
Total	274 (100.0)	329	1599

^a Bicolored Antbird, Ocellated Antbird, Spotted Antbird, or Barred Woodcreeper. Recorded with Gray-headed Tanagers elsewhere (Rio Agua Salud, Panamá Canal Zone).

^b Of songs of Bicolored Antbirds.

^c Followed flocks of birds for at least one minute.

WANDERING AND INTERSPECIFIC FLOCKS

Johnson (1954:45) proposed that Plain-brown Woodcreepers typically follow the wandering interspecific flocks through the forest but are easily attracted to flocks of birds that follow army ants. I would reverse the order of importance. These woodcreepers follow army ants whenever they are available, even when no other bird is present, but occasionally join the wandering flocks when no ants are available. At other times the woodcreeper drifts through the forest alone, waiting and foraging as it goes, until it encounters a swarm of ants.

Away from swarms the Plain-brown Woodcreeper typically travels singly. Two adult birds together are generally unmated and unrelated birds, together for a short time. Most groups of two and three birds are a female with dependent young. Away from swarms on Barro Colorado, I have 210 records of one bird, 46 records of two, and 6 records of three together. The activities of these birds are listed in Table 2. For this table, a bird was considered to be "wandering" if it rapidly changed perches in a given direction and spent little time looking about at stops; a "foraging" bird stays and looks about from a perch, and changes perches first in one direction and then in another. Wandering birds forage to some extent.

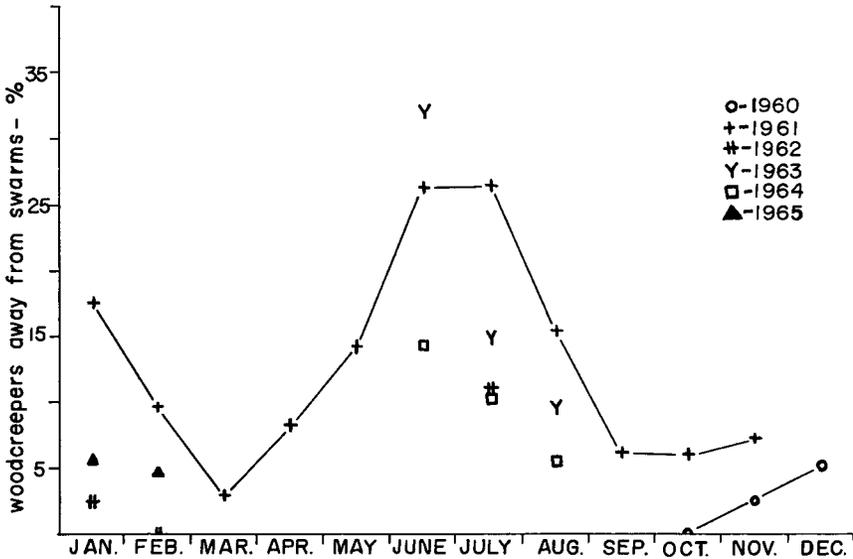


FIG. 4. Percentages of Plain-brown Woodcreepers away from swarms of army ants on Barro Colorado Island, 1960-1965.

Plain-brown Woodcreepers forage readily away from swarms of ants, in contrast to such ant-following species as Bicolored Antbirds (Willis, 1967). The percentage of woodcreepers away from swarms of ants on Barro Colorado rises during the rainy or nesting season (Fig. 4), when arthropods are more numerous away from swarms of ants. Highest use of swarms is in the late rainy season and in the dry season, when the young of the previous breeding season swell the ranks of ant-following birds (Fig. 5). There is some variation from year to year. In January and February of 1961 an unusually high percentage of woodcreepers wandered away from swarms. Perhaps this was a case of what Tinbergen (1946) calls "specific search images." During the preceding three months there had been an unusual number of swarms of *Labidus praedator*, which emerged frequently in the wet year of 1960. Disappearance of swarms of *praedator* in early 1961 apparently left many woodcreepers searching for them, even though swarms of *Eciton burchelli* were not overcrowded during these months (Fig. 5). In 1964 and 1965 there were unusually many swarms of *Eciton burchelli*, so that the percentage of woodcreepers away from swarms (Fig. 4) and number per swarm (Fig. 5) were both low.

On 58 of 255 occasions when Plain-brown Woodcreepers were recorded away from swarms and ant-following birds on Barro Colorado, they were

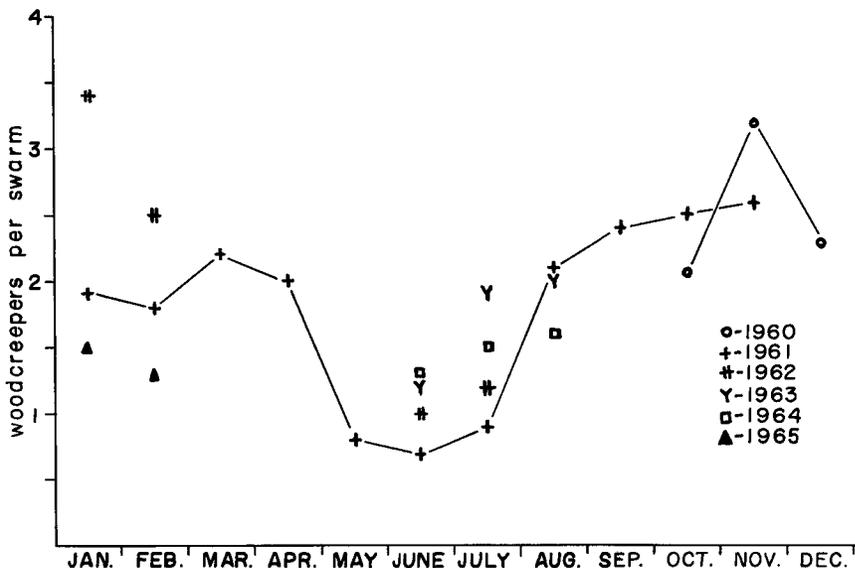


FIG. 5. Numbers of Plain-brown Woodcreepers at swarms of *Ecton burchelli* on Barro Colorado Island, 1960-1965.

with the wandering interspecific flocks of the forest interior (Willis, 1972). These flocks, which are entirely different from the ant-following interspecific flocks even though a few species occur in both, are characteristic of many forested areas in the tropics. Plain-brown Woodcreepers rarely lead such flocks or attract other species; they are desultory joiners and followers, or what Moynihan (1962) calls "active attendant species." Moynihan's term "active" implies joining rather than activity; the woodcreepers do not forage by moving actively, and often are rather inactive in following flocks about.

I doubt that other small birds often flush the large insects favored by woodcreepers. It is more likely that mixed flocks are efficient at detecting hawks and other predators, so that individual birds can then devote more time to finding food and specialize in foraging niches or use otherwise unsafe niches rather than watch in all directions for predators (see Willis, 1972). Plain-brown Woodcreepers stiek loudly from their elevated perches when hawks or distant ground predators such as tayras (*Eira barbara*) appear. The small birds near the forest floor are the first to call when predatory mammals pass in dense vegetation. Thus the high-foraging woodcreepers must often get advance warning of danger in a zone where they are not foraging actively.

I sometimes detected a Plain-brown Woodcreeper away from swarms by

its loud stieking when I or a predator passed (Table 2). At other times woodcreepers sang as they wandered through the forest. Most singing birds wandered as if looking for a swarm of ants; such songs are sometimes answered by birds at swarms, and the singer homes on the replier. Females separated from their young also sing, and the young sing, stiek or hiss to their mother. The song is thus often used in the way Bicolored Antbirds use "loud-songs," (Willis, 1967), as a locating or "lost" call rather than as a territorial, agonistic, or sexual call. Songs occasionally follow agonistic encounters. Rattles and other calls were occasionally used by wandering birds, but silence was more usual if birds were not singing or stieking.

Playing recorded loud-songs of Bicolored Antbirds in the forest (see Willis, 1967:25 for methods) brought Plain-brown Woodcreepers up to the loud-speaker on 10 out of 79 trials. On several occasions the woodcreeper flew past the speaker and then flew back to it when the next loud-song was played. On a separate occasion the chirring of Bicolored Antbirds near their recently-fledged young brought up a Plain-brown Woodcreeper. A woodcreeper is thus able to home on the calls of the noisy Bicolored Antbirds, which as professional ant-followers usually are close to swarms of ants. It also homes on the calls of other species that follow army ants, especially the noisy and common Spotted Antbirds. On 3 October 1961 one woodcreeper arrived as two male Spotted Antbirds disputed away from a swarm. On several other occasions woodcreepers flew to the songs of Spotted Antbirds or associated with them in wandering flocks at points distant from known swarms; in some of these cases the two may have stayed together after leaving a folded or inactive swarm nearby, however. Plain-brown Woodcreepers occasionally follow other professional ant-followers when they move between branches of a swarm or to other swarms distant in the forest (Table 2).

Besides homing on the calls of other species that follow army ants or following those species about, Plain-brown Woodcreepers show several other behavior patterns usual among "professional" ant-followers. Interest in ants is not confined to swarms that are actively flushing insects, as is usual for the many "non-professional" ant-followers on Barro Colorado and elsewhere. Plain-brown Woodcreepers commonly visit "statory" (sedentary) army ant bivouacs, peer around the tree trunk, and follow any line of ants to the distant swarm. The woodcreepers occasionally wander near inactive bivouacs for hours until the ants finally start swarming. Plain-brown Woodcreepers, like other professional ant-followers, move along lines or trails of ants between nomadic bivouacs and swarms rather than stumbling on swarms by accident. Individual woodcreepers follow the same colony of the army ant *Eciton burchelli* for days or weeks at a time, return to it periodically during a statory period, and may resume following the colony when it becomes active

again during the nomadic period. They shift readily from one colony to another, even when they have to travel a kilometer or more to do so.

Plain-brown Woodcreepers show by their behavior that they are strong ant-followers, and they are certainly "professional" ant-followers (ones that get more than 50 per cent of their food over ants) even though they forage readily away from ants. On Trinidad, where competing ant-following antbirds are absent, the woodcreepers rarely forage away from swarms. In other regions they probably depend on swarms of ants for most (60-90 per cent) of their food.

FORAGING BEHAVIOR

When following army ants a Plain-brown Woodcreeper waits on the trunks of trees or saplings, turning its head at intervals, until a large prey moves; then the bird darts over and snaps the prey out of the air or off the vegetation. Occasionally a bird hitches up or down, perhaps spiraling rapidly, and pecks prey while on a perch. These birds rarely poke in epiphytes or under bark as do many species of the Dendrocolaptidae. At times there is an involved aerial or semiaerial pursuit, with fluttering or hovering or rapid changes of direction.

When foraging off the ground, Plain-brown Woodcreepers forage most actively around rotten trunks and stubs, tangles of lianas in the crowns of saplings, near epiphytes, in the crowns of palms, at places where a dead limb or tree has jammed above the ground, and near other tangled places. Usually the birds wait on vertical lianas or saplings near the tangle or palm crown and sally to the periphery of the tangle for prey. At times, however, a bird hitches or flutters to deep within a tangle. The vicinity of a tangled treefall on the ground is another favorite site. When the ants pass through open forest, the woodcreepers scatter to vertical trunks and forage little unless competing antbirds are absent. Then they forage rapidly, and capture many prey items on the ground.

Table 3 lists foraging motions for Plain-brown Woodcreepers over ants on Barro Colorado Island. Birds take prey on the wing ("sallying") more frequently than they "lunge" or peck for prey from a perch. Prey taken on trunks is commonly pecked, however. Although these woodcreepers sally to the ground rather frequently, they take a large proportion of their prey from leaves and other vegetation above the ground. A greater proportion of prey is taken above the ground when such competing ground-foraging antbirds as Ocellated Antbirds are present (Willis, 1966).

The woodpeckerlike foraging position of the Plain-brown Woodcreeper seems a distinct disadvantage compared to the crosswise positions of competing ground-foraging antbirds. The woodcreeper uses small trunks only

TABLE 3
FORAGING MOTIONS OF PLAIN-BROWN WOODCREEPERS^a

Place of capture	Foraging Motion			
	Sallying	Lunging	Leaf-tossing	Prying
Ground, root, log	328	5	3	—
Trunk	219	263	—	1
Stem or liana	230	83	—	—
Limb or twig	27	8	—	—
Leaf or petiole	410	23	—	—
Dead leaf or debris	26	7	—	—
Air	182	7	—	—
Unspecified	204	7	—	—
Total	1626	403	3	1

^a From 1 October 1960 to 30 September 1961, over army ants on Barro Colorado.

with difficulty (Fig. 3,H). Large perches, besides being uncommon, block part of a bird's view. The woodcreeper must fly upward for a short distance or turn in midair (Fig. 3,I,J) to get away from the trunk if it is to capture prey below it, since it starts from a head-up position, but it is not delayed more than a fraction of a second by the conflict of adaptations for clinging with those for pursuing prey below it. Still, when a fast-leaping antbird and a woodcreeper go for the same prey the antbird usually captures it. The short legs and long toes of the woodcreeper also make hopping after prey on the ground rather difficult. If the woodcreeper misses prey on the first sally it must fly up again, fly short distances along the ground, or stay flopping, wheeling, and pecking in the midst of attacking army ants. A long-legged antbird hops nimbly about, exposing its feathers and body to the ants only rarely.

Away from swarms, I have never seen a woodcreeper sally to the ground. The woodcreepers forage 3–15 m above the ground at such times, in the mid-levels of the forest. Probably this is the zone in which the perching behavior and foraging motions of woodcreepers are most effective. Moreover, there probably are few prey items large enough on the ground unless ants flush them. Foraging strategy away from ants involves short waits on tree trunks, hitches upward to new waiting sites, flights to other trunks, and the like. To get food, a woodcreeper away from ants usually sallies to distant foliage or trunks, and hovers to catch the prey or chases it in flight. Less often it pecks off prey as it alights or as the prey alights, or pecks prey off a surface while hitching upward. They are unlike most woodcreepers (genera *Xiphorhynchus*, *Glyphorhynchus*, etc.), which forage by peering and pecking at or into trunks

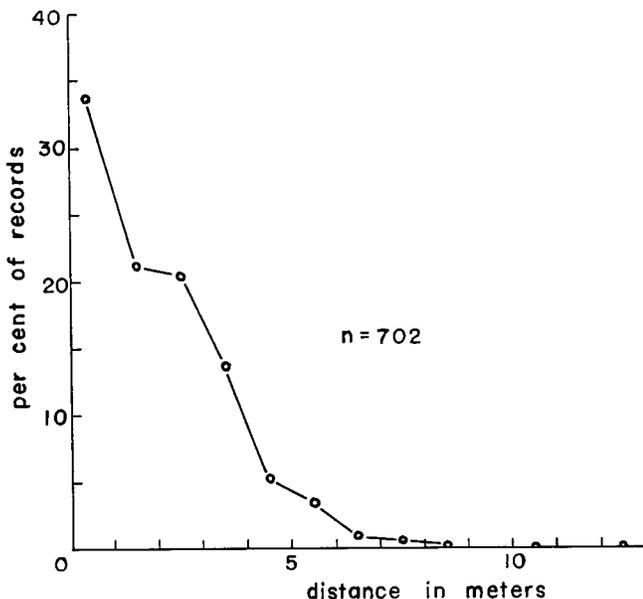


FIG. 6. Distances that Plain-brown Woodcreepers flew to try for prey ("sallying").

and epiphytes close-by, but are like other ant-following woodcreepers (genera *Dendrocincla*, *Dendrocolaptes* and *Hylexetastes*), in being "flycatchers" to distant surfaces.

Prey at and away from ants is captured both above and below a foraging bird. The distances of sallying are shown in Fig. 6. The Plain-brown Woodcreeper has a larger foraging radius than do such species as Bicolored Antbirds (Willis, 1967). However, 75 per cent of the prey of Plain-brown Woodcreepers is captured within 3 m from the perch and 98 per cent within 6 m.

Plain-brown Woodcreepers frequently use "wing-flashing" when prey stops and is concealed. The bird moves to the trunk where prey disappeared and briefly flashes one wing widely along the surface of the trunk. On slender trunks the bird may simultaneously sidle and peer around the trunk from the opposite direction (Fig. 3,H), so that it will run into prey fleeing the wing. At times a woodcreeper flashes its wings alternately, sidling and feinting back and forth around the trunk as if shadow boxing. The bird may also angle the head one way and then the other in the direction opposite the wing flashed instead of sidling bodily. On larger trunks the bird may crane the head or sidle in the direction of the flashed wing rather than in the opposite direction. Thus wing-flashing is not just a way to sidle more rapidly, although it could easily have originated from such rapid sidling motions.

TABLE 4
FOOD OF PLAIN-BROWN WOODCREEPERS^a

Food	Size of prey in mm						
	?	0-10	10-20	20-30	30-40	40-50	50-125
Unspecified		110	60	34	4	1	
Sowbug	1						
Whip scorpions			2	3			
Scorpions			1	4	4		
Spiders	6		11	24	4	1	
Egg case	1						
Centipede				3	3	5	4
Millipede	1						
Roaches	7	3	18	23	6		
Orthopterans	12		15	32	17	4	6
Walkingstick							1
Mantids	1					1	1
Odonatans							1
Cicadas	6		1	3	1		
Heteropterans			1	2			
Beetles			2				
Beetle grubs	1			1			
Neuropteran				1			
Moths	10	2	7	4			
Caterpillars				2	1		
Ants	4	1	1	1			
Ichneumon			1				
Hymenopterans		1	3				
Lizards				1		2	3

^a Barro Colorado Island, 1960-1971.

In 89 out of 105 recorded observations of wing-flashing, the presence or absence of foraging motions was noted. In 32 cases (36 per cent) the bird peered intently after wingflashing one to several times but made no try for prey. In one case the bird flashed at an insect covered by army ants; although unsuccessful here, wing-flashing may occasionally flush prey already captured by army ants. In a second of the 32 cases a Black-breasted Puffbird sitting above captured prey flushed by the wing-flashing woodcreeper. In 57 cases (64 per cent), the woodcreeper immediately sallied or lunged for fleeing prey. The woodcreeper is thus somewhat less successful at wing-flashing than is the Mockingbird which tries for prey after 74 per cent of its wingflashes (Hailman, 1960).

I recorded successful wing-flashing to flush prey by a White-chinned Woodcreeper at Cashibococha, Perú. Tawny-winged Woodcreepers flash the wings

even more frequently than do Plain-brown Woodcreepers. Perhaps the conspicuous tawny wing patches of the Tawnywing and the yellow undersides of the wings of all three species are adaptations for flushing prey. There is some use of double wing-flashing in aggressive displays in all these species, however.

Orthopterans (mostly long-horned grasshoppers, katydids, crickets), roaches, and spiders are the primary large food of Plain-brown Woodcreepers at swarms of ants (Table 4). Moths, centipedes, scorpions, cicadas, and lizards (mostly *Anolis limifrons*) are also taken readily. Only prey that was held in the bill long enough for size to be estimated as a fraction of exposed bill length (about 25 mm) or for reasonably certain identification is listed in this table. The size range indicated is skewed toward the maximum sizes of prey, since small prey was often swallowed before I could see it. This distribution of maximum-sized prey centers on the bill length of the species, although slender prey (centipedes, orthopterans, damselflies, lizards) were sometimes three to five times the length of the beak.

Small prey is swallowed at once. Large prey is frequently chewed vigorously and hammered or flailed against the trunk. The woodcreeper may hitch up the trunk now and then, hammering the prey at each stop, or fly to a new perch to continue work. The feet are never used for holding prey. One woodcreeper drooped its wings toward the trunk as it hammered prey, in the fashion of a hawk "shielding" its prey. Moth and locust wings are usually dropped. Legs and other small pieces of prey that fall are ignored, but the bird may dive after a major piece. If dropped prey falls to near the ground it is readily snapped up by Bicolored Antbirds. At other times other Plain-brown Woodcreepers may catch dropped prey.

Some small prey items are dropped or thrown away immediately or dropped after some chewing in the tip of the bill. These are probably prey with chemical defenses, for the woodcreeper often wipes the bill and shakes the head after such an encounter.

ANTING

Some small prey items elicit "anting" behavior. Instead of dropping the prey and wiping the bill, the bird chews the prey in the tip of the bill, brushes the prey through the rectrices or the under tail coverts (Fig 7,F), and resumes chewing. Often the bird shakes the prey before brushing it through the rectrices or regimes repeatedly. I recorded anting 67 times. On 35 occasions the prey was eaten. On one occasion the bird dropped the prey and bill-wiped repeatedly; on another, the prey was thrown away. On the 30 other occasions I did not record what happened to the prey, but think it was generally eaten. After a woodcreeper eats such prey, it often champs the beak or wipes it.

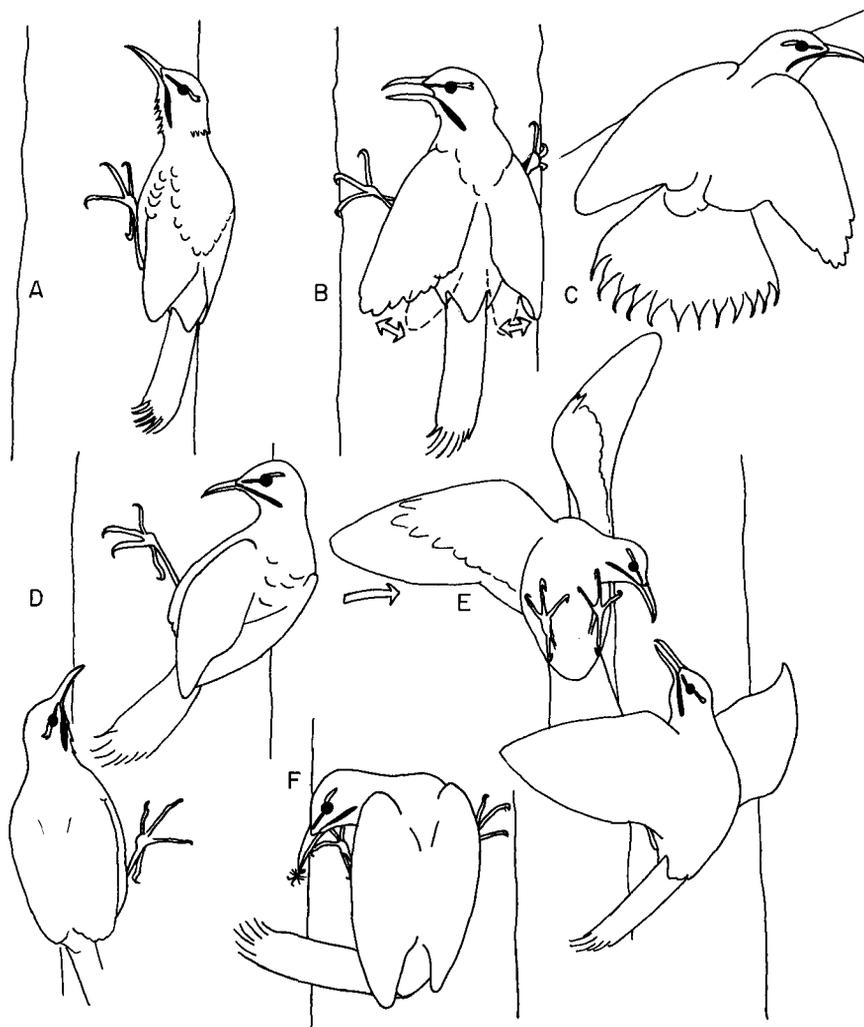


FIG. 7. Postures of Plain-brown Woodcreepers. A, during long rattling. B, wing-fluttering by a subordinate bird as a dominant one approaches. C, sunning on a log. D, a dominant bird takes an aggressive posture as a subordinate one hitches up below it, then (E) fights with it in the air. F, "anting" requires a C-shaped posture if the undertail coverts or tail is to be used.

Anting in this species is probably a standard method for treating distasteful prey; it does not seem to reach the level of non-foraging anting as is recorded for some birds (see Whitaker, 1957; Simmons, 1966; and Potter, 1970, for summaries).

Southern (1963) and Potter (1970) suggest that anting soothes skin irritated by molt processes. Potter does not cite Dubunin's (fide Kelso and Nice, 1963) evidence that anting kills feather mites, nor my (Willis, 1967:33) evidence that subordinate Bicolored Antbirds have to take distasteful prey and ant with it. Perhaps there are two preening and one foraging uses for anting, rather than the single use suggested by Potter. Her main argument for anting as a molting poultice is that anting has been recorded more frequently in months when birds are molting.

I have recorded Plain-brown Woodcreepers anting every month of the year, but in 1960-61 I had more observations from September to November, 1961. (In summer visits later, I have obtained many records for July and August). September and October seem to be the main months of wing and tail molt in Panamanian Plain-brown Woodcreepers, judging from my observations and from the few specimens in museums. Some birds start molting in July and August. Although molting may be the reason for a peak of anting in the late months of an annual cycle, there are several alternatives that Potter does not consider: since molting follows nesting in most passerines, there are more birds present in molting months; the large number of young birds in months of molt means that more can make mistakes and pick up insects with chemical defenses; competition is high as young birds crowd in to local food sources, forcing some to take prey with chemical defenses; there may be more insects with chemical defenses about in late months of the annual cycle, since early insects of such a cycle are not so subject to predation and can be fast-reproducing ones without chemical defenses; observations of anting may be less frequent in spring and early summer because most observers are distracted by songs, bright colors, and territorial and reproductive activities of birds; winter observations are rare because few insects are out in northern areas and because few observers are out.

For Plain-brown Woodcreepers, the brief time of most anting episodes tends to indicate that care of the skin or use against feather mites is not as important as use as a part of a foraging strategy. Occasional sequences in which a bird anted with several prey usually seemed reactions to absence of more suitable prey rather than attempts to extend skin exposure to ants. Most anting episodes came when other Plain-brown Woodcreepers or Ocellated Antbirds were interfering with the bird's foraging, although some birds anted when few or no competitors were about. While young and subordinate birds sometimes anted, some adult and dominant birds also did so. There is not the clear correlation of subordinate status and anting that I found for Bicolored Antbirds. However, Plain-brown Woodcreepers are a subordinate species that uses a variety of prey items, and such birds might be expected to ant with prey with chemical defenses more often than do dominant species.

Simmons (1966) and I (Willis, 1967) have suggested that the original use of anting may have been wiping off distasteful secretions of prey, and that anting as a preening method may be learned individually. That such tropical species as Plain-brown Woodcreepers and Bicolored Antbirds show anting as a foraging pattern rather frequently may reflect the well-known diversity of tropical insects. Species of distasteful prey are likely to vary tremendously in appearance and to look like mimicking palatable prey rather often. It may be better strategy for a hungry or young bird to try for prey and then find if it is palatable rather than wait until species known to be palatable appear. Species of intermediate palatability may provide suitable prey for hungry birds if they are detoxified by chewing and by rubbing their secretions on the wings or tail.

MAINTENANCE BEHAVIOR

After chewing distasteful prey or large, juicy prey the bird often wipes the bill in the usual fashion: alternate sides, base to tip. Fluffing the head, a frequent movement in bill wiping in many species, was not detected. However, the feathers of the head are so short that it is difficult to detect head fluffing.

To egest fecal material, the Plain-brown Woodcreeper lifts the tail off the trunk by flexing the femora briefly, ejects the dropping forcefully, and quickly drops the tail to the trunk. Probably front and hind claws oppose each other at such times. Occasionally a woodcreeper coughs up parts of insect exoskeleta. It gapes one to several times as if choking, then shakes the head briefly as it is turned to one side; the exoskeleta drop out of the open beak.

Periods of inactivity or preening frequently interrupt periods of foraging. In addition, when competing antbirds are present, the woodcreepers are partly excluded from the continuous source of food near the ground and must depend on occasional probes of ants into tangles above the ground. During periods when ants are inactive above the ground the woodcreepers may cling and look about for long periods or wander widely about the swarms. They disappear for minutes at a time, but reappear as soon as the ants start up a tree. Johnson (1954:60) was also struck by similar behavior patterns when he watched these woodcreepers at swarms.

When preening interrupts periods of waiting or resting, the woodcreeper generally perches vertically in woodpeckerlike fashion. To preen the body, the feather tract is fluffed and the bird pokes the bill down in to the feathers, then out. In addition to movements of the feathers and neck, the bird extends the legs when it preens the underparts and flexes the legs when it preens its back. In the latter case the bird may rest on the ventral feathers for a time. There is also no difficulty when the wings are preened; extension of one wing at a time does not interfere with perching. However, preening the tail

and scratching the head require awkward contortions. To preen the tail the bird raises it and directs it laterally, then falls back on the tail coverts or the sides of the tail so the body forms a C-shaped arc. Plain-brown Woodcreepers always scratch the head over the wing. When one foot is released from the trunk the bird seems to rest on the abdominal area on that side while the other foot grasps strongly and the tail forms the other leg of the tripod. Scratching the head is often awkward and hasty even when the bird rests in this position.

Perhaps the requirements of grasping during egestion and preening partly account for the large size of the rear toe, which Bock and Miller (1959) consider a hindrance or functionless in climbing birds that use the tail for support. In the Plain-brown Woodcreeper the rear toe is shorter and thicker than the front toe; the rear claw is less curved but is longer and thicker than a front claw. The rear toes and claws of this bird probably have a different function from the front ones rather than being vestigial, and in perching may act as wedges to prevent backward rotation. Perhaps a small bird that clings to smooth-barked tropical trees and to the under sides of smooth trunks or limbs occasionally clamps front and rear toes into the bark. Plain-brown Woodcreepers also use their rear toes to perch horizontally.

Woodcreepers stretch in the ways usual among birds: yawning, half-flexing both wings, or stretching fully on one side or the other (see Willis, 1967). When the bird does a left or right stretch the leg on that side is stretched and the bird swings against the trunk. I have not recorded toe-standing, which should be difficult for a clinging bird. After stretching movements the bird usually flies off.

Occasionally a woodcreeper suns itself on a log (Fig. 7,C) or on a limb of a tree. One wing and side of the tail are spread more fully than the others, and the face on the same side is turned toward the sun. Ordinarily Plain-brown Woodcreepers avoid full sunlight, although they readily cross clearings, openings in the forest, and esteros on Barro Colorado Island. They are by no means as strongly restricted to forest as are Bicolored Antbirds and similar species. On Trinidad, Plain-brown Woodcreepers follow swarms of ants through open cacao groves and to isolated trees in yards and pastures. Rivers and clearings should not be strong barriers to this species. There is little evidence of subspeciation across large rivers in the tropics, except across the "inland seas" of the Amazon, Tapajoz, and Madeira. There is much reason to suspect any subspeciation arose in isolated forest refugia during dry climatic periods, not because of the rivers (Haffer, 1969).

On many occasions woodcreepers bathed in holes in trees. I repeatedly found one or two woodcreepers bathing in one hole in a fig crotch in the evenings. On one occasion another bird drank after peering in the knothole, then backed in carefully and repeatedly, emerging and shaking briefly be-

tween dips. Investigation of cavities above ground is frequent, perhaps for roosting or nesting sites as well as for drinking or bathing.

Although this woodcreeper is a victim of the bites and stings of army ants less often than are birds that perch near the ground, one occasionally bends down quickly and throws an attacking ant into the air. Once a woodcreeper ate a soldier of *Eciton burchelli*. Occasionally a woodcreeper jitters, shaking one leg or shifting back and forth from one foot to the other rapidly, when ants attack. Normally the bird hitches a few centimeters away and waits in a position out of the stream of ants.

REACTIONS TO HUMANS AND PREDATORS

When predators appear, Plain-brown Woodcreepers occasionally freeze in place by clinging very close to the trunk and staying very still. Often the reaction includes loud stieking. In addition to the yellow flash from the gape as the lower mandible flaps down for each call, occasional flitting of the wings may betray the position of the bird. The yellow under wings flash inconspicuously when a bird flits. Often one wing seems to extend more than the other, but flitting never extends as widely or as close to the trunk as does wing-flashing, which is normally a movement of one wing. Commonly a stieking or silent bird whisks around the trunk so that it is hidden from the predator or the observer. At times it hitches up the trunk, flitting the wings at each jump, or darts suddenly and repeatedly from one tree to another, circling trunk after trunk. There is relatively little fluffing or sleeking, although a freezing bird is slightly more fluffed than usual and a hyperactive stieking bird is more sleeked and stands out farther from the trunk than it does in the standard posture. However, birds freezing on slender saplings seem sleeked, as if hiding behind the saplings. Often the bird jerks its head one way and then the other with or between stieking notes.

Stieking is commonly set off by a hawk, although it is also a common reaction when I first appear at a swarm unless the individual bird has seen me frequently. Stieking was recorded as reactions to hawks on 29 occasions involving seven species of hawks. Other records included stieking at a Spectacled Owl (1), Mottled Owls (2), Turkey Vultures (3), Collared Araçaris (1), Chestnut Woodpecker (1) in Brasil, a large bird flying over (1), the alarm note of a Buff-throated Woodcreeper (1) in Brasil. Once a woodcreeper stieked at a tayra, once at a jaguarundi (*Felis yagouaroundi*), once at running agoutis (*Dasyprocta punctata*), once at squawking of a squirrel (*Sciurus granatensis*), twice at the grunting and stick-dropping of white-faced monkeys (*Cebus capucinus*), once in Peru at red titis (*Callicebus cupreus*), and several times at my swinging my cap at mosquitos.

Many other birds react to stieking by freezing, fleeing, or giving alarm calls: Ocellated Antbirds (31 records), Bicolored Antbirds (43), Spotted

Antbird (12), Gray-headed Tanagers (3), Buff-throated Woodcreeper (1), Chestnut-backed Antbird (1), Streaked Flycatcher (1), and Barred Woodcreeper (1). In Peru a Lunulated Antbird keened; in Brazil, a Harlequin Antbird chipped. In Guyana, Rufous-throated Antbirds (2), White-plumed Antbirds (2), White-browed Antbird (1), and a Black-banded Woodcreeper (1) fled. At times, other Plain-brown Woodcreepers repeat stieking or flee when one bird starts calling. Usually only one or two birds stiek at a time while the others hide or stiek infrequently.

The reactions of Plain-brown Woodcreepers often precede those of other ant-following birds when a predator appears in the canopy, partly because these woodcreepers forage high in the vegetation rather than concentrating on ground prey as is the case for many ant-following birds. Once a woodcreeper, seeing a tayra approach on the other side of a hill, stieked and alarmed ground antbirds before the latter could see the tayra. However, Plain-brown Woodcreepers are also prone to hysterical outbreaks of stieking with no obvious cause after a hawk disappears or I take a position behind the swarm. Other birds at swarms may start a "dread," becoming hyperactive and giving alarm calls, when a woodcreeper continues stieking or resumes it long after danger has passed. Since the woodcreeper sometimes moves down and forages in the zone deserted by the antbirds even though it continues to stiek, one wonders if its seeming hysteria may help it by relaxing competition from domineering antbirds. I have suggested this for another subordinate bird, the Spotted Antbird (Willis, 1971). Another possibility is that the hair-trigger hysterics of Plain-brown Woodcreepers discourage types of predation which are probably quite common in tropical forests. In central Brasil the Lined Forest-Falcon, which occasionally follows ants for hours, often returns time after time to the same area. It sits and waits quietly for long periods. Although I have seen it capture only large insects, it undoubtedly gives the antbirds and woodcreepers reason for hysteria. Stieking may annoy such predators so that they move away, or keep the birds on their guard against still-hunters and hawks that return repeatedly. Plain-brown Woodcreepers, which work the middle levels of the forest in a zone where there is light and space for a hawk to maneuver, have to be more careful than do antbirds foraging in dim and tangled areas near the ground. On Trinidad, where the woodcreepers work near the ground on an island that has few species of forest hawks, they were far less prone to hysterical stieking than in other areas.

Plain-brown Woodcreepers react to the alarm calls of other birds. At chipping notes of Bicolored Antbirds or stieking of another woodcreeper, a woodcreeper often presses close to its perch, sleeks, and freezes. At chipping of Spotted Antbirds, one looked about quickly.

Woodcreepers that have had some experience with me quickly become tame, especially if I scare away Ocellated Antbirds or other domineering competitors so that the woodcreepers can forage near the ground. At times the woodcreeper changes from flitting and then sleeked hiding behind trunks to open foraging via the "displacement activity" of preening. However, I never saw any evidence of the "curiosity" or investigating behavior so characteristic of tame Bicolored Antbirds. Woodcreepers use peering and investigating behavior very little in foraging, in contrast to Bicolored Antbirds; the seeming lack of curiosity may be related to their noninvestigative type of foraging. Still, tame woodcreepers often hide behind trunks of trees when one tries to observe them closely.

Woodcreepers that were semi-tame or ones that I forced to fly from a swarm sometimes reacted with long rattles. Once long rattles were a reaction to marmosets (*Saguinus geoffroyi*). The bill is closed and the bird hardly moves, except for a pulsing low on the neck. The neck seems long, probably because of extending the angles between vertebrae (Fig. 7,A). The feathers of throat and forehead, possibly those of the entire head, are raised as the bird clings close to the trunk. The feathers of the vent are also fluffed. The bend of the wing is sometimes exposed. One bird ended its rigid display by ejecting feces, doing a half-flex of both wings, and spiraling up the trunk.

Woodcreepers held in the hand for banding commonly scream loudly and persistently. Some individuals squeak rather faintly or growl softly. Clawing stops if the bird is allowed to grasp a finger. Pecking is often vigorous, but these woodcreepers do not hold and twist so vigorously or for such a long time as do antbirds.

AGONISTIC BEHAVIOR

The frequent interspecific supplantings when Plain-brown Woodcreepers and other species compete over swarms of ants have been discussed elsewhere (Willis, 1966).

Large birds that follow army ants supplant (chase from its perch) or displace (cause to move off) the Plain-brown Woodcreeper (Table 5). It is rather nonaggressive, except to a few stolid moderately large birds and to small ant-followers. Buff-throated Woodcreepers are particularly pugnacious to it, and chase it about persistently on the rather infrequent occasions when Buff-throats follow army ants. Black-striped Woodcreepers are also rather pugnacious on the few occasions when they follow ants. Most of the large ant-following birds in Panamá, such as Barred Woodcreepers and Ocellated Antbirds, supplant or displace it rather regularly; but the Plain-brown Woodcreeper is good at keeping out of their way. In other countries, I have seen Plain-brown Woodcreepers supplant Scale-backed Antbirds and White-

TABLE 5
ANTAGONISTIC INTERACTIONS OF PLAIN-BROWN WOODCREEPERS

Species A	Numbers of Wins/Losses by Species A ^a			
	Fights	Supplantings	Displacings	Returns ^b
Plain-brown Woodcreeper	53	1196/	65/	
Barred Woodcreeper		109/	48/	
Ocellated Antbird		80/	28/	4/
Buff-throated Woodcreeper		85/2	18/	2/
Bicolored Antbird	1	60/16	8/11	
Black-striped Woodcreeper		42/	9/	
Gray-headed Tanager	2	9/9	6/1	
Squirrel Cuckoo		2/	7/	
Black-breasted Puffbird		4/	1/	
Bright-rumped Attila		2/1		
Rufous Motmot			1/	1/
Keel-billed Toucan			1/	
Broad-billed Motmot			/1	
Canada Warbler		/1		
Acadian Flycatcher		/1		
Wedge-billed Woodcreeper		/1		
Scaly-throated Leafscraper		/1		
White-whiskered Puffbird		/1		
Slaty Antshrike			/2	
Swainson's Thrush		/5		/2
Spotted Antbird		/9	/4	

^a Barro Colorado Island, over ants, 1960-1971.

^b One bird has to watch until other leaves before moving in.

throated Antbirds. Rufous-vented Ground-Cuckoos, Ruddy Woodcreepers, Red-billed Woodcreepers, Hoffmanns' Woodcreeper, Spix's Woodcreepers, Black-banded Woodcreepers, Rufous-winged Bare-eyes, Black-spotted Bare-eyes, Bare-crowned Antbirds, and Black-headed Antbirds supplant or displace Plain-brown Woodcreepers. Twice I saw White-chinned Woodcreepers displace Plain-brown Woodcreepers, and once a Plain-brown displaced a White-chin.

Generally a woodcreeper surprised by a larger species screams loudly if attacked or pecked but simply flees or stieks and flits as it hitches up a trunk if it is supplanted less strongly. It may ruff the throat, or cling close with feathers fluffed out. The woodcreeper gives rattlets or long rattles if it is gradually crowded out or displaced rather than attacked bodily. Once one shivered the wings as it approached a Barred Woodcreeper, which did not attack it.

Interactions with species close to its own size or dominance are frequently more varied. Once one supplanted a male Gray-headed Tanager (at 30 g,

only three-fourths the weight of the woodcreeper) by spreading the wings and showing the yellow wing linings at it. A minute later the same tanager supplanted the woodcreeper when it did not spread its wings. On another occasion a tanager female, crest raised, gave faint notes as she pecked down repeatedly at a woodcreeper under the limb she stood on. The woodcreeper sidled back and forth, weaving and feinting at her with the beak, before it flew off. When Bicolored Antbirds (30 g) supplant the woodcreeper the latter sometimes stays and growls, pecking back at the smaller bird. However, the woodcreeper is usually forced to sidle back and forth around the perch by the repeated jabbing of the more agile antbird, so that the woodcreeper is often supplanted despite its initial resistance and larger size. Once a woodcreeper supplanted the antbird by flashing one wing at it and growling at it.

The intraspecific agonistic or competitive behavior of Plain-brown Woodcreepers seems as undistinguished as their plumage and voice. Simple avoidance, chasing, and fighting seem to replace aggressive and submissive displays most of the time. When two or more birds are present at a swarm of ants, they often stay apart. At times avoiding each other is not possible; the birds crowd around a palm or liana-covered tree the ants are ascending. At such times peck order is mainly evident in the well developed and rather diverse methods of fleeing and pursuing.

When a dominant bird flies up near a subordinate bird or supplants a third bird, the subordinate commonly sidles quickly behind its perch. If on a slender sapling, the subordinate bird may cling close and sleek the feathers as if to become as narrow as possible. Often one bird hitches up the trunk or around it when another alights below it. It may turn the head one way and then the other, looking down at the dominant bird (Fig. 7,D). When a subordinate bird flies, its flight seems normal unless it is hotly pursued by the dominant bird. It then twists and turns, zigzags in and around trunks, and quickly hitches or spirals around them on alighting. It may stiek at times, give rattlets in flight or on alighting, or end a series of rattlets with a song if completely driven away from the swarm.

Commonly a dominant bird ignores a nearby subordinate as long as it is quiet or sidles behind its perch. At times birds ignore each other even when three or four aggregate within a meter of each other for minutes at a time. Once a watching woodcreeper waited until another finished dissecting a tettigoniid, then hitched up and supplanted it. Most species that follow army ants wait until a subordinate finishes its meal before supplanting it, although Plain-brown Woodcreepers and other species commonly supplant subordinate birds during and immediately after prey capture. The position of dissecting birds in this and other species, hunched close to the perch and with necks

retracted and bodies fluffed, may mimic submissive display and thus inhibit attack.

At other times a dominant bird may pursue the other bird by hitching or spiraling up the trunk after it, extending the neck to jab at it if it hesitates too long, or flying after it for as much as several hundred meters off into the forest or back and forth over the swarm. The pursuer or both birds may adopt a somewhat slow, flapping flight like a dove or a buzzy flight like a Spotted Sandpiper in the more protracted chases. Possibly such forms of flight display the yellow wing linings. At times the fluttery flight is accompanied by "tailgating," when the pursuer seems to slow and speed up when the pursued bird does so rather than try to overtake and attack it. Such flights may have sexual or parental connotations, as is discussed below.

Simple supplanting, often followed by long chases, is common. Fighting, or at least pecking and fluttering duels around and around a perch or down through the air (Fig. 7,E), is less common. Of 1,314 presumably agonistic displacings or supplantings, 53 (4.0 per cent) ended in fighting. This frequency is about ten times that for Bicolored Antbirds, a species with well developed aggressive and submissive displays. The contrast between these two species may support proposals that agonistic displays evolve to prevent dysgenic fighting. Fighting involves pecking with the bill as well as scratching at the opponent with the feet. Growling notes emerge during the more violent fights, which sometimes end on the ground.

A common display of subordinate birds is "rattleting." The beak is closed as a rattlet of 5 to 20 notes is uttered. The rigid, rather sleeked bird often ruffles the throat and lower face, sometimes the whole head. The neck is sometimes extended or ruffled, but more often the head is close to the body. At times the body seems ruffled. The wingtips commonly droop loosely. The legs are flexed, so the bird is close to the trunk. The eyes seem glazed, perhaps because they are diverged rather than focused binocularly. A bird that is consistently chased or forced away from a swarm by another wood-creeper or any other domineering competitor often extends rattleting into long rattles, as described under "reactions to humans and predators." At times the calling is omitted from the display of rattleting.

Another possibly submissive display is gaping and growling, or growling rattlets, during chases. Squealing comes from a bird losing a fight. Possibly growling is restricted to sexual and juvenile-parent chases, described below.

At times the subordinate bird flits the wingtips out sharply and repeatedly as it hitches jerkily up a tree after being supplanted. The dominant bird occasionally flits the tips of the wings. Such actions commonly accompany or lead into a stiek note or two, suggesting the bird may be panicking.

Occasionally the subordinate bird shivers or rapidly flutters the tips of

the wings (Fig. 7,B). In seven out of 21 cases, however, the dominant bird shivered the wings and then chased the other off. In some of these cases the dominant bird seemed hesitant and initially unsure of its dominance, but the meaning of wing-shivering is unclear. Among Bicolored Antbirds it seems a juvenile or submissive activity (Willis, 1967, p. 47).

If there is an aggressive display in Plain-brown Woodcreepers, it is not frequent or conspicuous. Ordinarily the aggressor starts a chase from the standard posture, without calling. At times the legs are extended so that the body is far out from the trunk, as in the more conspicuous aggressive display of Barred Woodcreepers. If so, the head and neck are often arched, the head being flexed toward the neck (Fig. 7,D). Really aggressive birds fluff out the belly, chest, and back feathers; but I have not seen strong ruffling. The head is usually sleeked, so that the dark brown malar and presuperciliary lines seem more prominent than usual but the pale throat and yellowish postsuperciliary line less so. However, at times an attacking bird has the head ruffed; some such birds seemed unsure of their dominance. At times the attacker gapes, especially if defending a spot from an approaching bird. At times the yellow underwings are flashed out as well, especially if the approaching bird persists long enough to start a fight or chase.

One woodcreeper that preceded me to a swarm raised its back and chest feathers as it looked up at a bird one meter above; the latter dropped to half a meter below the new bird and shivered its wings. The newcomer then tailgated the other off. On another occasion an arriving woodcreeper went round and round a pole pecking and gaping at an unbanded bird; the latter tailgated the banded bird off after a pause.

MOVEMENTS AND TERRITORIES

Banding birds on Barro Colorado Island between 1960 and 1971 has given a moderately clear picture of territoriality and movements, even though many birds are not banded. Some banded individual birds (Fig. 8), especially birds known to be less than a year old, wander irregularly. Other banded birds, which I call "settled" birds, occasionally follow a swarm of ants outside the centers of their home areas but return to the areas year after year until they disappear. Settled birds with the long wings and feathered edges of the ventral apterium characteristic of males (Fig. 9) wander out from the centers of their home areas more frequently than do other birds (Fig. 10) with wing lengths characteristic of females; the latter are mostly birds that have vascularized, bare ventral brood patches during breeding seasons and birds that cared for one or more broods of young during the 1960-1971 period.

It is likely that the home ranges of these settled birds are territories, al-

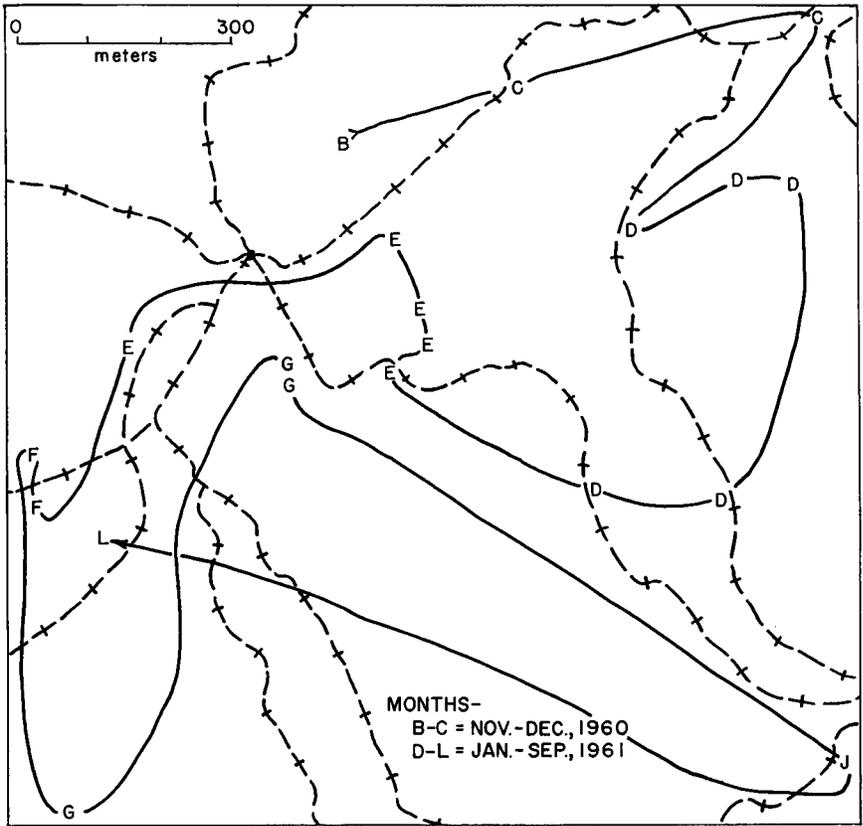


FIG. 8. Wanderings of Plain-brown Woodcreeper "XR" from November, 1960, to September, 1961.

though there is not enough evidence on supplanting and chasing to be certain of dominance. The known females have nearly exclusive ranges; I have yet to observe two banded ones together at the same swarm of ants or to observe two unbanded females with their broods at one swarm. The settled males have home ranges completely overlapping those of settled females. The ranges of settled males overlap each other, so that two or more settled males occasionally follow the same swarm. However, overlapping of ranges is no proof that animals are non-territorial (Willis, 1967); each male may be dominant over other males toward the center of his own range. The centers of ranges of settled males are different suggesting that males do have this form of territoriality.

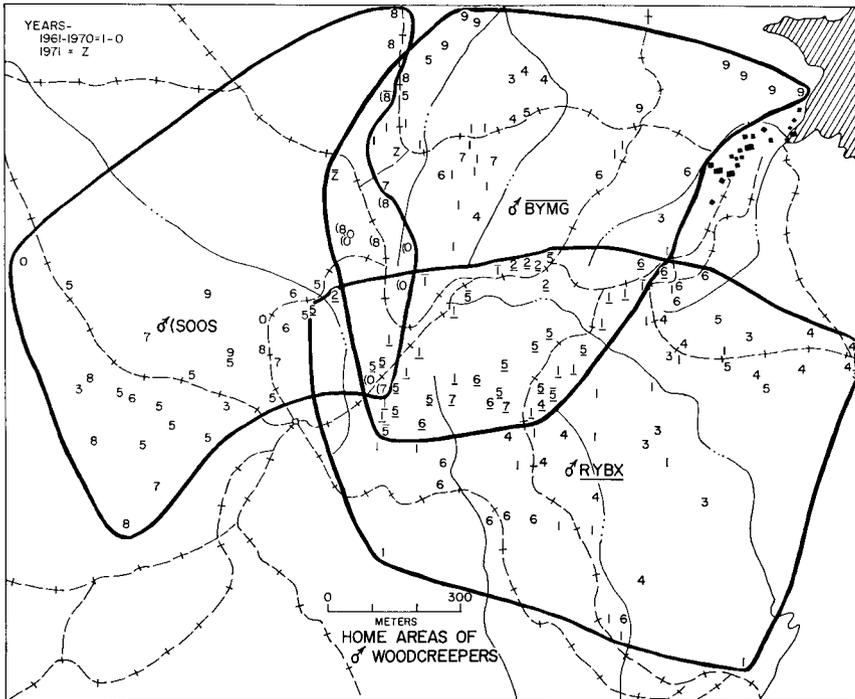


FIG. 9. Observations of three settled male Plain-brown Woodcreepers, 1960-1971. Within overlap zones, records of RYBX are underlined, of BYMG are overlined, and of SOOS start with a parenthesis.

There is some evidence that settled males are subordinate to settled females. The wider wanderings of settled males suggest this, since a subordinate bird must wander more widely than does a dominant one to find an unoccupied swarm. In 37 cases of supplantings involving settled females, the female was the victor in 35 cases. The exceptions may represent meetings of two females at territorial boundaries; in both cases the banded female was chased by an unbanded bird at a place where the neighboring female was unbanded. On 14 August 1961, female RBYM (Fig. 10) supplanted male BYMG (Fig. 9) within the ranges of both. Male RYBX rattled whenever female BRBYM came near him on 18 August 1964; the location was well within the area of the male but peripheral to the area of the female. On August 16 and 21 female PSPM repeatedly supplanted male RYBX; she was near the edge of her range, while he was well within the boundaries of his. On 2 October 1965 female BRBYB displaced male RYBX at the edge of her range but well within his.

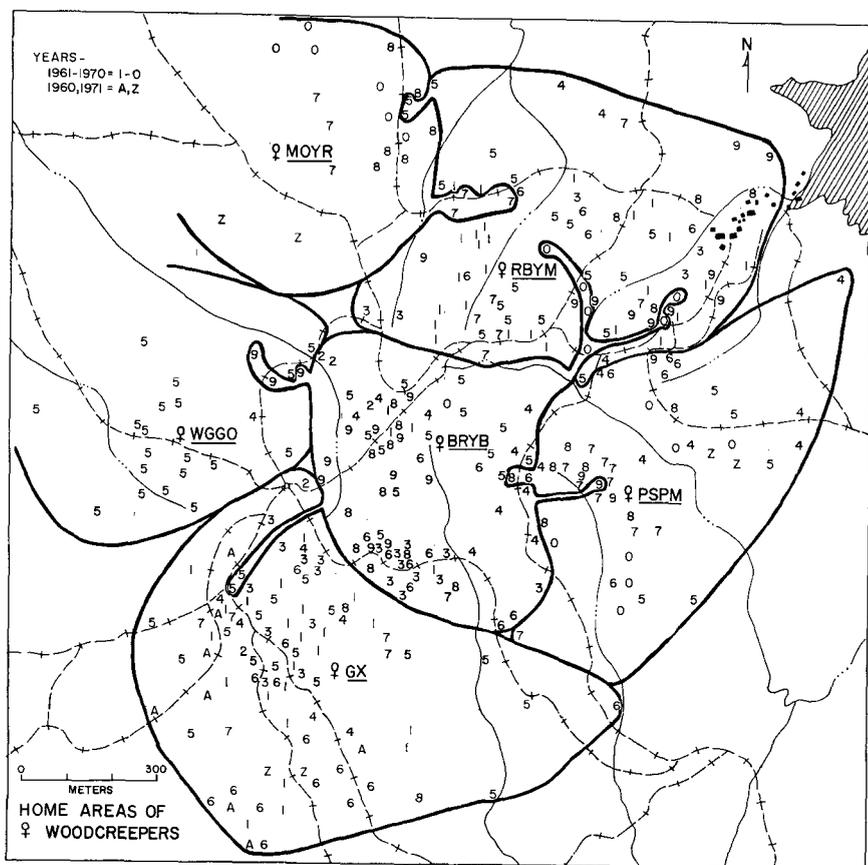


FIG. 10. Observations of five settled female Plain-brown Woodcreepers, 1960-1971. Dark lines separate records of individual females.

There were always unbanded birds wandering through the territories of these settled males and females. Probably most of them were either males with home ranges overlapping those of the banded birds or else wandering birds. I do not know how many years these birds wander before they settle down, for the only banded young rediscovered later (MGYY) was not found until nearly 10 years after banding. The extremely long lives of settled birds, especially settled females (of three females banded in 1961 as adults, two were still alive and on their territories in 1971 and the third disappeared after 1969) suggest that young may wander for years at times waiting for territories.

Preliminary evidence thus indicates that Plain-brown Woodcreepers have the kind of territoriality found in the European Cuckoo, some lizards, and

some mammals. Females occupy exclusive territories, while the settled males have more or less separate ranges completely overlapping those of the females. The spacing system should be investigated further in an area where Plain-brown Woodcreepers are more abundant and easily studied, as on Trinidad.

There were 2.8 females and 1.8 males per square kilometer on the study area in 1960–1971. (Each female had an area of about 36 hectares.) At 41 grams per bird, this is a biomass of 138.6 grams per square kilometer or 1.9 grams per hectare. Possibly there were 1 or 2 wandering birds per square kilometer in May each year, or an additional 0.6 grams per hectare, for a total of 2.5 grams per hectare. The total population of Barro Colorado Island in May, at the low point of the annual cycle, would be about 90 birds. In December there would be somewhat over twice as many birds, or 180–200 birds (5 grams per hectare).

SEXUAL BEHAVIOR

Sexual behavior seems to grow directly out of agonistic behavior in this species. Pair bonds and courtship are certainly brief and rudimentary in nature.

Males chased by females in seemingly normal agonistic encounters sometimes growl or give soft rattlets, and allow tailgating or a pecking duel rather than flee to a distance. Gradually the two birds begin to associate in their chasing and to ignore trespassing birds. There are persistent chases during this period, but the two birds frequently alight close together and wait several seconds before resuming pursuit. The two may peck and spar back and forth before resuming a chase. Presumably the process involves an increasing tendency for the female to stay rather than attack the male when he approaches her, but these preliminary stages are difficult to distinguish from agonistic behavior. Occasional reverses of chases, in which the pursuer becomes the pursued, are the first clear sign that sexual behavior is involved and not just agonistic or parental chasing.

Over the course of a few days other elements enter the feuding. The chases become slower and more fluttery; there may be bursts of wingbeats so that the two undulate in flight. The male consistently alights below the female. Growling notes become more frequent than rattlets. Growling, whether by pursued or pursuer, is sometimes accompanied by fluffing of the throat, breast, and crown to a degree far surpassing the normal state among rattleting birds. At times the feathers of the breast part from those of the lower abdomen. The male may hitch up after the female at each stop, even though she pecks down at him and chases him off at times.

In the final days of the pair association, one bird consistently hitches up to the other and nibbles more and more vigorously into its lower back.

"Nibbling" is often accompanied by vigorous growling from either bird, at times speeding into a rattle. The throat of the chased bird is sleeked, but the chasing bird fluffs its throat as it growls. The chased bird often takes wing and is pursued by the other. The chased bird may jab downward repeatedly at the insistent other one, or hitch upward; but the chasing bird quickly follows the chased one. The chaser swings back and forth below the other when it jabs at him, then moves quickly in to nibble its back when it returns to the standard posture. Eventually it stays still for the nibbling. The male eventually nibbles her rump, then moves upward nibbling the female's back more and more rapidly and deeply. She gapes slightly and flattens herself against the vertical trunk as the male hitches up on her back and clings to her slightly spread wings. The male flutters rapidly as the tails of both birds are shifted off and on the perch rapidly. The female seems to rest on the side of her tail while the spread tail of the male remains on the trunk. Copulations I have observed were brief, generally less than a second, as both birds seemed to have difficulty copulating in this vertical position. In one case the male hitched up above the female after copulation, then hitched down past her and repeated the process of growling, nibbling, and copulation. He chased her to new perches and attempted or completed several more copulations during the course of the day.

On one occasion a female alighted just above an unbanded bird. As it growled faintly and gaped slightly, she looked down and gaped as she hitched down under it until she wedged up its breast with her tail. It gaped and finally started nibbling before she looked down and chased it off in a fluttering aerial flight.

On a few occasions wandering females were persistently nibbled by unbanded birds even though each female snapped down at the other bird or chased it off. On another occasion a female with young birds was persistently nibbled by an unbanded bird, although fluttering and pecking aerial duels were the result. Once a wandering young bird, independent less than two weeks, nibbled the back of another bird. Perhaps a male may attempt nibbling and copulation as soon as a bird it approaches fails to flee or attack, whether or not male or female are settled or in the appropriate stage of the nesting cycle. This may explain occasional cases where one bird nibbled another and the second nibbled back before there was a fluttering chase. However, female PSPM was observed to nibble the back of male RYBX in one pairing sequence, and to be the recipient of nibbling from an unbanded bird on another occasion, so the sex roles in nibbling must be reversed occasionally.

Most observations of sexual behavior were for unbanded birds, so that I do not know how many days the birds of a pair consort with each other or

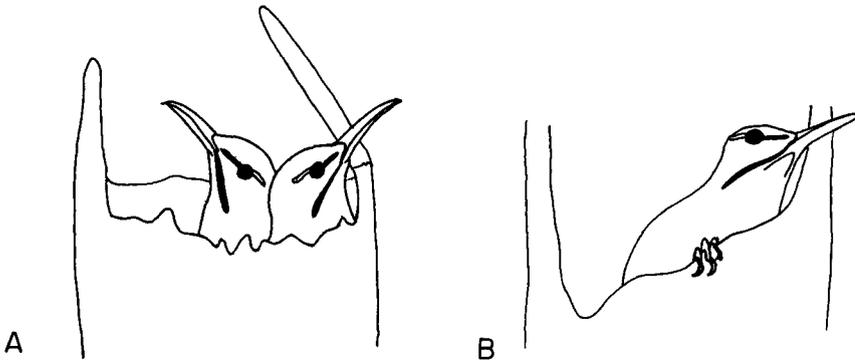


FIG. 11. A, "cavity-sitting" by two woodcreepers. B, female BXRБ peers snakelike from the top of her nest cavity before leaving it and the single nestling. From field sketches.

whether the female accepts more than one male. Observations of another behavior pattern, "cavity-sitting," suggest that the interest of the male may extend somewhat beyond copulation. One bird flies to a cavity in the top of a pole-sized stub, peers down into it and around, then turns and backs down inside repeatedly. At times a second bird flies up and joins it in hitching up and down inside the cavity (Fig. 11,A). Growling sounds emerge as if a bumblebee is boring into the wood. After a minute or two of their jack-in-the-box behavior one bird and then the other emerge and fly off. It may be that copulations occur during cavity-sitting, for one wandering young female was mounted by an unbanded bird as both cavity-sat, despite much pecking when he first nibbled her back.

Male RYBX and female PSPM went through a sequence on 5 July 1966 in a way that suggested he was showing her a nest-hole. He gave a series of growls at a hole in a big stub; she flew up beside him and he hitched sideways, then flew off; she hitched up and flitted as she peered in several holes. Later he gave a rattlet as she hitched up to him. Both looked about, then she nibbled his back a few times. He flew off after looking down at her.

NESTING

A bird brought food to and carried a fecal sac away from a northwest-facing hole 4 m up in a stub 0.2 m in diameter in a new agricultural clearing in the forest at Tres Esquinas, Colombia, at 10:04 on 20 April 1962. One carried food to and a fecal sac away from a cavity in the top of a stub 0.2 m in diameter and 5.5 m tall, 25 m out in a manioc field in forest at Maloquinha, Brasil, at 18:02 on 25 February 1966. Pinto (1953) records an

incubating female collected at a nest with a single white egg 2 m up in the trunk of a tree, 1 January 1924. Snow and Snow (1964) record dates of laying in nests in Trinidad from May to "September" (= early October). The latter record represents a young bird prematurely out of the nest on 10 November (D. W. Snow, in litt.). I noted adults still feeding grown young out of different nests on Trinidad on 4 and 15 December 1961, so that the nesting season extends later than the Snows indicate in their article and is essentially the whole rainy season.

Five nests the Snows located (their three other records are of birds carrying food to sites not exactly located) ranged from 1 to 9 m above the ground, in tree holes, the open tops of a bamboo stake and of a broken *Bactris* palm, and in a hollow tree branch. Two eggs were in each of three nests, two young in a fourth; none were successful (the fifth nest, high, was not revisited). Four of the nests were in forest and one near a house.

One nest on Barro Colorado was 3.5 m in a cavity in the top of a 0.2 m diameter stub in open forest. The nest-cup, a few dead leaves with a rhizomorph lining 0.5 m down inside the stub, held two small and downy young with areas of bare orange skin at 13:50 on 3 June 1966. They were probably two days old. One young left the nest about 16:30 on 25 June, so the nestling period was 23–25 days.

I watched from a blind 38 hours on 12 days, mainly in the afternoons because morning visits on 7 and 11 June (7.5 hours) showed no different patterns. Only female BXRFB fed the young. She brooded them only during rain on 6 June and between 09:27 and 10:28 on 7 June; perhaps even small young are often allowed to cool off despite the longer developmental period lack of heat would require. Her visits with food were very irregular, from 4 to 162 minutes apart (mean, 46.0, $n = 39$). On 6 and 7 June the average interval was 87 minutes, then 48 minutes on 10–11 June, 30 minutes on 14–16 June, 40 minutes on 18–20 June, 54 minutes for 21–23 June, and 39 minutes for 25 June.

On nine occasions she brought variously colored cicadas, which probably were not taken over ants. Other prey were a lizard (*Anolis limifrons*), a lizard or a frog, a roach, and orthopterans (2), and several mangled insect abdomens. Usually she held the prey lengthwise inside her open bill, but the lizard projected back past her face and the roach was held in the bill tip. Prey was seldom less than the exposed bill length (25 mm). She was not known to follow ants during the nestling period, although other females feeding young in undiscovered nests have been known to do so.

She occasionally sang at a distance, but approached quietly otherwise. She often froze on a nearby sapling or the nest pole for a minute or two, looking about, before hitching to the nest edge and looking about again. If I

approached the nest as she did, she stieked and fled with wing-flitting, hitching up distant trees. Once a Chestnut-mandibled Toucan flew down and scared her away as it peered in the nest before I drove it off with difficulty. She froze or hitched behind the nest-stub at each whirr of toucan wings overhead, but on other days had ignored their sounds.

To feed, she looked inside and flipped head-first into the cavity. Once, returning in rain to brood without food, she backed tail first into the cavity. She sometimes gave faint rattlets as she looked in or went inside, and continued them if the young did not take the food. To rechew food, she sometimes reappeared at the nest entrance or flew off, then returned. Often she appeared at the nest entrance after a feeding and craned her neck about slowly like a snake (Fig. 11,B) for several minutes. At times her throat feathers were ruffed. Often she champed her bill, especially one day when toucans were flying overhead. Once she pecked and tossed a large ant (*Paraponera clavipes*) walking nearby. After peering, she often hopped to the inside top of the stub and waited before flying off, or flew off directly. A few times she flew off directly before waiting at the entrance.

She normally flew off directly when carrying a fecal sac, which she did on 12 of 26 visits between 14 and 24 June, but only three of 16 times 6 to 11 June and on one of five on 25 June. Presumably she ate most fecal sacs before emerging until the young were about two weeks old, and ignored fecal sacs on the last day.

The young gave a few hissing answers to her rattlets on 10 June and thereafter. On 16 June it gave a weak song inside the nest about three minutes before the female arrived. On 25 June, but not as late as 24 June evening, the young came to the nest entrance except during a rain. It seemed as big as the female, but had a rather short bill, a tail one quarter the normal length, and three-quarters-open remiges showing bare bases. It gave a rattly song once, but preened and looked about silently most of the time the female was away. It gaped widely for feedings and after one feeding. At 15:51 she watched as it flapped one wing out to climb up on the nest entrance after a feeding, then tapped twice on the nearby trunk with her bill. Both watched and waited as marmosets passed overhead, and it hissed at her a few times. She pecked into its open gape before leaving 16:08, and it gave squeaky rattlets as it looked after her. Later it fluttered atop the nest-stub. At 08:34 the next morning the female looked in the empty nest; at 09:14 she sang and rattled when I shook a nearby vine on which there was a snake (*Pseustes poecilonota*), discovered by scolding antwrens of a forest flock.

From 11 to 20 July the young and female were with army ants elsewhere in her territory. On 11 July the young had tail and bill three-quarters the normal lengths, and was "playing" by pecking off and dropping bits of moss

(Other young often pecked at leaves and billed them or other bits of debris, as if hungry or playing). It tried fluttery sallies for prey. On 16 July its tail and bill were nearly the adult lengths, and it caught one prey on its own. The female was by now in very worn plumage. (Female GX went into molt when her young were about this age, 14 July 1966). On 19 July she pecked it after it hissed near her, and it fled. On 20 July, however, she lured it away from me with rattlets.

There is no information on incubation except for Pinto's (1953) record of collection of an incubating female. Skutch (1969) records that one bird alone incubates and feeds the young in Tawny-winged Woodcreepers, another species with the attack-and-nibbling type of sexual behavior. Probably the female Plain-brown Woodcreeper also cares for eggs alone, as males lack incubation patches. Male and female do not associate during the period of nesting, as far as I have been able to determine.

Several other broods of young have been seen on Barro Colorado, including other broods of female BXR. The young appeared as early as June and as late as September. One or two fledglings follow one female; no male associates with the group. The young are well grown and fly well before the female brings them to a swarm; the smallest young I have seen, those of female PXR in 1964 and of an unbanded female in 1969, were fully feathered but had small beaks and half-length tails. At times these smaller young stay in one area and the female commutes to them from a swarm. The female more often stays nearby, even if no ants are available nearby. She sticks loudly as a human passes, but the young are silent at this stage.

The young birds forage little at this stage, but they gradually become independent over the next month or two (young were with female RBYM at least 17 August–11 October 1965). When the female catches food and has hammered or chewed it thoroughly, she utters a brief rattlet. If the young is busy preening, the female has to utter several rattlets. The young bird eventually flies up, takes the food in hitching past her, and eats it. The young may gape or flutter the tips of the wings briefly if the female holds the food or moves away at first. At times the young hisses or squeaks as it is fed. Larger, well-flying young hardly give the female a chance to rattle; they follow or chase her with hissing notes and hitch up to her as soon as she captures food. They gape at her head silently or with hisses. At times one nibbles the back of the female. She is forced to flee their hissing pursuit if she is to eat any food herself or even to forage in peace. Occasionally the female chases away larger young or snaps at them when they follow her closely. During feedings there is scarcely any display beyond gaping and squeaking by the young; the parent chucks the food into the open gape and bill-wipes or flies away.

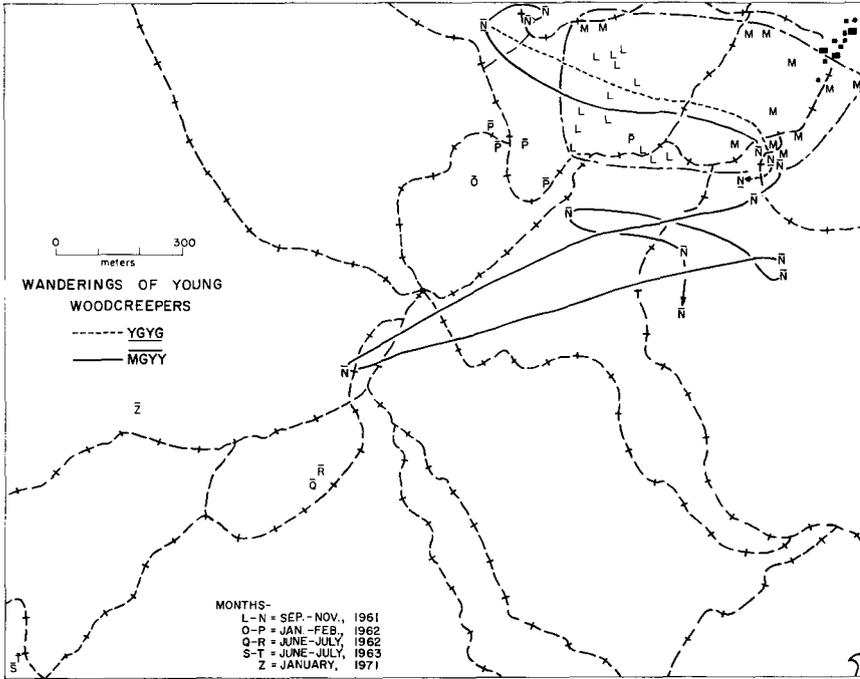


FIG. 12. Wanderings of two young Plain-brown Woodcreepers, the offspring of female RBYM, from September to November, 1961, and in 1962-1964 and 1971. Both young were with the female in her territory (inside the dot-dash line) in September and October, 1961; thereafter, records of YGYG are underlined and of MGYG overlined.

On one occasion a female Plain-brown Woodcreeper called *stiek* loudly nearby when an Ocellated Antbird briefly pounced on her screaming young. Females and juveniles sometimes sing back and forth when separated from each other. When the observer passes a female and her grown young all often start stieking and hide behind trees, and move off through the forest with occasional songs or stiek notes.

Sibling woodcreepers occasionally supplant each other, but they are usually so widely separated around a swarm that there are no chances for arguments at feeding times. In some of the broods I observed, the female fed one sibling frequently while the other was ignored and began to forage at an early age. This suggests that a female may sometimes have difficulty feeding more than one fledgling.

Young birds beginning to forage for themselves peck and pry at debris or even hit it on a perch as if to kill it; they examine epiphytes and nearby trunks actively in a fashion reminiscent of woodcreepers of the genus

Xiphorhynchus. One pecked at army ants (*Eciton burchelli*), and dropped them before fleeing with *stiek* notes. One tried backing down to a leaf-filled cavity as if to bathe or cavity-sit, but missed the cavity. Later the young woodcreepers wait more patiently and sally for prey in adult style.

The few birds banded as young wandered widely after leaving the female and did not associate with her or with each other even if they returned to her home area later (Fig. 12). Occasionally a young bird supplants wandering birds known to be older, although settled birds supplanted young birds in most cases.

DISCUSSION

Of all the birds that follow army ants on Barro Colorado, the Plain-brown Woodcreeper has the simplest and most individualistic social behavior. It is plain in this aspect of behavior as it is in voice and plumage.

Parental bonds involve little interaction between birds, except for persistent following of the parent by young birds. A long nestling period, typical of cavity-nesting birds, perhaps allows young to be relatively independent soon after they leave the nest. However, it seems more likely that having inconspicuous communication may protect young birds in a species that depends to a considerable extent on hiding or fleeing from predators in open vegetation rather than on keeping in or near dense cover.

Care of nests by one parent obviates the need for displays between parents and thus perhaps makes these open-cavity nesting birds even safer. Also, as Smith (1968) has pointed out for chickarees (*Tamiasciurus* spp.), the absence of the male means that there is one less animal to deplete food supplies or frighten prey near the nest. Skutch (1969:407) records that a female Tawny-winged Woodcreeper foraged actively near the nest in the evening; if the Plain-brown Woodcreeper ever does this a male and female caring for the nest together would compete rather strongly. Nesting Plain-brown Woodcreepers apparently do not travel much to distant ant swarms, and probably forage in areas near the nest on rather alert prey, such as lizards and cicadas; two birds might scare such prey more than would one.

The sexual behavior of Plain-brown Woodcreepers also involves little social display or interaction. Most birds with brief pair bonds have well-developed courtship ceremonies, plumage, or voice. Darwinian sexual selection, the necessity for correct recognition of a conspecific bird, and competition between males should lead to hypertrophy of male sexual behavior in such species. It is possible that insectivorous birds cannot develop a lek or similar time-consuming system of strong courtship display because their food is too widely dispersed or unpredictable (Snow, 1962). European Cuckoos, a species with a social system most like that of Plain-brown Wood-

creepers, are also insectivorous. The necessity of not frightening alert prey by having too many birds about, and of not attracting predators, may make it advantageous to Plain-brown Woodcreepers to be retiring and inconspicuous in courtship behavior.

These birds have not developed the strong or conspicuous aggressive and submissive displays that would seem useful for establishment of dominance. Instead, there are fighting and long chases that seem to waste time and energy. Perhaps quick fights and unpredictable chases may reduce danger to birds that forage in rather open forest midlevels or open lower levels most of the time. Ignoring the opponent until there is a sudden chase makes maximum benefit of the protective coloration until the last moment. Moreover, a defeated bird has plenty of room in which it can forage. Such birds can escape in any direction from a dominant opponent or a predator. Ground-foraging antbirds could trap and hurt each other if they were to use fighting instead of displays. Thus the emphasis on displays instead of fighting in such species as Bicolored Antbirds and the opposite emphasis in these woodcreepers may reflect the ecological limitation of the former species to a narrow zone near the ground and to areas near safe cover. The woodcreepers, by contrast, must be fast at moving to unprotected sites not occupied by antbirds, and must behave inconspicuously or unpredictably in such sites. If so, it would be instructive to determine if the low-foraging woodcreepers on Trinidad, in an area with few competing antbirds or predatory hawks, show a relatively greater use of displays than do the woodcreepers on Barro Colorado. Another factor is that woodcreepers are generally less numerous at swarms than are Bicolored Antbirds; hence woodcreepers may have less need for frequent displays to set up and maintain peck orders. Again, the woodcreepers are very numerous at swarms on Trinidad and may use displays more.

Many patterns of submissive and evasive behavior are also inconspicuous in Plain-brown Woodcreepers, but are rather well developed. It is a bird that seems good at fleeing and hiding, whether from a competitor or from a predator. Submissive calls include rattling, persistent rattling, and to a certain extent growling (which is more often a social call from fledgling to parent or from one sex to another in courtship). There is no clearly aggressive call, while in some antbirds the aggressive calls outnumber the submissive ones. Even song is rare and seldom seems to have an aggressive or territorial function in Plain-brown Woodcreepers.

The poor or inconspicuous development of forms of social behavior in Plain-brown Woodcreepers may have been favored as a result of their foraging behavior under conditions of competition with antbirds. These woodcreepers forage mainly above the ground during periodic probes of ants up trees or slip in and out at open and unsafe places where competing antbirds hesitate

to go. Exploitation of such irregular sources of food at a swarm, in contrast to the regular feast enjoyed by ground-foraging antbirds, must place a selective premium on rapid movement of individuals. Antbirds, which lead mates or young about, have special calls and must be very active to get the mate or young to follow them to another part of a swarm. Not only is time wasted, but other birds of the same or other species quickly home on the calls and antics of the leading bird. Birds that work near the ground, where ants flush food regularly, need seldom use this kind of behavior; but if woodcreepers maintained close pair or parental bonds they would need it every few minutes. It is far better for them to wander individually, quickly move in at available sites as soon as they develop, and keep quiet so few competitors are attracted.

One form of social behavior, stieking and hyperactivity in response to predators, is well developed in Plain-brown Woodcreepers. Single woodcreepers stiek as readily as ones together, and stieking generally causes birds to scatter. Possibly the calling is a communication to the predator ("Here am I, alerted and a difficult catch"), or a call that irritates or disturbs predators; it may also drive off competing antbirds as has been suggested for a similarly subordinate species on Barro Colorado (Willis, 1972). In the past, alarm calls have often been assumed to be altruistic; stieking may also have such a function in Plain-brown Woodcreepers, especially when a family is together. Hamilton (1963) discusses how such "altruism" can evolve in situations where related animals are together.

In contrast to ground-foraging antbirds, Plain-brown Woodcreepers use the same call for terrestrial predators as for aerial predators. Probably there is no reason to develop a separate call for ground predators when a species normally forages well above the ground. Long rattling may represent a type of predator call, perhaps one that irritates or disturbs a predator, but this behavior is also used when a domineering competitor is present.

In contrast to most forms of social behavior, foraging and other types of individual behavior are well developed in Plain-brown Woodcreepers. The woodcreeper is peculiarly specialized in some ways and generalized in others. The woodpeckerlike perching and hitching restrict it in many ways; for instance, these woodcreepers tend to avoid perches below 3 cm in diameter. A bird that perches like a woodpecker is also relatively slow at catching prey below or behind it, and hence is at a disadvantage catching prey near the ground. When better-adapted horizontally-clinging antbirds are present, the woodcreeper scarcely uses the rich and constant source of food on the ground (Willis, 1966). As a result, it is very generalized and opportunistic in its vertical level of foraging. It uses wait-and-flycatch techniques, but moves from the ground to near the tops of forest trees as oppor-

tunities arise. Since the Plain-brown Woodcreeper is a generalist in at least two respects (variety of prey and level of foraging) but a specialist in others (woodpeckerlike perching, wait-and-flycatch techniques, relatively frequent attendance at swarms of army ants), it may be difficult to answer the question (Klopfer, 1962), are tropical avifaunas more diverse because the species have narrower niches? A species may have a niche that is narrow in one or more dimensions but broad in other dimensions. However, the niche of the Plain-brown Woodcreeper is broader on Trinidad, a "peripheral" tropical area with few competing species of ant-following birds, in the sense that the woodcreeper is more abundant there and catches a greater percentage of the total prey items flushed by ants there than in Panamá or Guyana (Willis, 1966).

Perhaps a simple objective way to say if a niche is broad or not is to see if a species captures a greater percentage of the total prey or other resource in a given area than does another species or does the same species in another area. Even though the Plain-brown Woodcreeper "narrows" its foraging niche on Trinidad by foraging mostly near the ground, the ground is such a rich source of food over army ants that the woodcreeper actually gets more prey and thus broadens its niche. It may lose to some extent the ability to forage above the ground, but it is certainly exploiting more of the available food supplies when competing antbirds are absent.

SUMMARY

Plain-brown Woodcreepers usually forage over swarms of army ants and capture arthropods flushed by the ants. The woodcreepers occasionally forage away from ants, at times with the wandering interspecific flocks of the forest interior. They generally wait on vertical perches 1-10 m above the ground and sally like flycatchers to capture orthopterans, roaches, spiders, and other prey from the vegetation or the air. When competing antbirds are absent, the woodcreepers descend and capture prey on the ground more frequently. They use "anting" and "wing-flashing" as foraging techniques; the former behavior pattern apparently wipes harmful secretions off prey and the latter flushes concealed prey.

Alarm behavior, especially fleeing and repetition of a loud call ("stieking") is well developed. In contrast, social behavior is as plain or inconspicuous as are voice and plumage. Agonistic behavior is mainly confined to ignoring conspecific birds, to sudden chasing, and to fighting. Submissive display is better developed but inconspicuous: there is wing-quivering, also a rigid posture during a "rattling" call; aggressive display is rarely seen. The relative lack of display or necessity for inconspicuous displays to avoid predators and competitors may be the reason for an observed high frequency of fighting, which in this species is perhaps not very dysgenic because the birds fight in the relatively open middle levels of the forest where entrapment is difficult.

Settled females occupy exclusive areas, and seldom visit ant swarms outside these areas. Settled males wander widely around the separate centers of their own areas; their mutually overlapping foraging areas overlap with but do not correspond to the foraging areas of females. Settled females apparently dominate settled males occupying the same

regions. There is no permanent pair bond. For a few days at the time of mating an individual female permits a male to come near her without fleeing or attacking. For a time the two squabble vigorously, but the female finally submits to mounting after the male "nibbles" her back repeatedly. "Cavity-sitting," a behavior pattern in which the two birds visit holes in stubs together, suggests that the pair association may extend for a short time beyond copulation. It is possible that the insectivorous niche of the species, and particularly its relatively irregular and marginal source of food, prevent evolution of lek behavior or hypertrophy of male voice or other characters by sexual selection.

Nesting and care of young are tasks of the female. Begging and parental behavior are inconspicuous. "Singing" is used when female and young are widely separated, as it is when adult woodcreepers are alone and wandering away from swarms. A kind of "rattlet" call notifies the young that the female has food. After a month or so the juveniles leave the female and wander separately.

The individuality of these woodcreepers and their relative plainness of plumage, voice, and social behavior may result from their irregularly available and exposed foraging niche. The woodcreeper depends upon irregular sources of food, when ants probe above the ground or when domineering antbirds happen to be absent near the ground. The premium this places upon rapid movement of individuals perhaps precludes development of pair bonds and parental behavior, which would require special calls and displays and thus attract domineering competitors. Moreover, these woodcreepers are adapted for using open sites in the forest midlevels and near the ground in places that antbirds hesitate to go; to use such unsafe sites the woodcreepers apparently depend on inconspicuousness of plumage and behavior, or sudden and unpredictable moves to get prey or chase competitors. They avoid fights with other species, or move in on them quickly or with wing-shivering, perhaps so neither predators nor competitors will be attracted. Individual woodcreepers seem successful at avoiding predation; some on Barro Colorado were over 10 years old.

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APPENDIX: NAMES OF BIRDS IN TEXT

- Antbird, Bare-crowned.—*Gymnocichla nudiceps*
Bicolored.—*Gymnopithys bicolor*
Black-headed.—*Percnostola rufifrons*
Chestnut-backed.—*Myrmeciza exsul*
Harlequin.—*Rhegmatorhina berlepschi*
Lunulated.—*Gymnopithys lunulata*
Ocellated.—*Phaenostictus mcleannani*
Rufous-throated.—*Gymnopithys rufigula*
Scale-backed.—*Hylophylax poecilonota*
Spotted.—*Hylophylax naevioides*
White-plumed.—*Pithys albifrons*
White-throated.—*Gymnopithys salvini*
Antshrike, Slaty.—*Thamnophilus punctatus*
Araçari, Collared.—*Pteroglossus torquatus*
Attila, Bright-rumped.—*Attila spadiceus*
Bare-eye, Black-spotted.—*Phlegopsis nigromaculata*
Reddish-winged.—*Phlegopsis erythroptera*
Crane-Hawk.—*Geranospiza caerulescens*
Creeper, Brown.—*Certhia familiaris*
Cuckoo, European.—*Cuculus canorus*
Squirrel.—*Piaya cayana*
Flycatcher, Acadian.—*Empidonax virescens*
Streaked.—*Myiodynastes maculatus*
Forest-Falcon, Barred.—*Micrastur ruficollis*
Lined.—*Micrastur gilvicolis*
Ground-Cuckoo, Rufous-vented.—*Neomorphus geoffroyi*
Hawk, Semiplumbeous.—*Leucopternis semiplumbea*
White.—*Leucopternis albicollis*
Kite, Double-toothed.—*Harpagus bidentatus*
Gray-headed.—*Leptodon cayanensis*
Hook-billed.—*Chondrohierax uncinatus*
Leafscraper, Scaly-throated.—*Sclerurus guatemalensis*
Mockingbird.—*Mimus polyglottos*
Motmot, Broad-billed.—*Electron platyrinchum*
Rufous.—*Baryphthengus ruficapillus*
Owl, Mottled.—*Ciccaba virgata*
Spectacled.—*Pulsatrix perspicillata*
Puffbird, Black-breasted.—*Notharcus pectoralis*
White-whiskered.—*Malacoptila panamensis*
Sandpiper, Spotted.—*Actitis macularia*
Tanager, Gray-headed.—*Eucometis penicillata*
Thrush, Swainson's.—*Hylocichla ustulata*
Toucan, Chestnut-mandibled.—*Ramphastos swainsonii*
Keel-billed.—*Ramphastos sulfuratus*
Warbler, Canada.—*Wilsonia canadensis*
Woodcreeper, Barred.—*Dendrocolaptes certhia*
Black-banded.—*Dendrocolaptes picumnus*
Black-striped.—*Xiphorhynchus lachrymosus*
Buff-throated.—*Xiphorhynchus guttatus*
Hoffmanns'.—*Dendrocolaptes hoffmannsi*
Plain-brown.—*Dendrocincla fuliginosa*
Red-billed.—*Hylexetastes perrotti*
Ruddy.—*Dendrocincla homochroa*
Spix's.—*Xiphorhynchus spixii*
Tawny-winged.—*Dendrocincla anabatina*
Wedge-billed.—*Glyphorhynchus spirurus*
White-chinned.—*Dendrocincla merula*
Woodpecker, Chestnut.—*Celeus elegans*

DEPARTMENT OF BIOLOGY, PRINCETON UNIVERSITY, PRINCETON, NEW JERSEY
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