

THE BEHAVIOR OF
SPOTTED ANTBIRDS

BY
EDWIN O. WILLIS

ORNITHOLOGICAL MONOGRAPHS NO. 10

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Above: Male Spotted Antbird BX, who occupied a territory near the center of Barro Colorado Island for at least the years 1960–1971. Below: Mist-netting a male Spotted Antbird. Bands, read up the left leg and down the right, identify this individual as male CWRS (orange-red, white, red, black-yellow).

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TABLE OF CONTENTS

INTRODUCTION	1
Spotted Antbirds and Their Relatives	1
Army Ants	3
Study Areas	3
Methods of Study	4
ACKNOWLEDGMENTS	5
GENERAL BEHAVIOR	6
Calls and Songs	6
Normal Postures and Movements	9
Resting	13
Preening and Head-Scratching	13
Stretching	14
Egestion and Drinking	14
Sunning	15
Bathing	15
Anting	15
Attacks by Arthropods	16
Reactions to Rain	16
Discussion	16
REACTIONS TO DANGER	18
Freezing	18
Chipping and Panicking	19
Chirring and Mobbing	20
Fleeing and Tameness	23
Investigating	24
Reactions of Captives	24
Discussion	24
AGONISTIC BEHAVIOR	29
Submissive and Escape Behavior	29
Aggressive Displays and Attack Behavior	30
Sequences of Agonistic Behavior	34
Discussion	36
REPRODUCTIVE BEHAVIOR	39
Singing and Wandering	39
Chirping and Flirting	39
Courtship Feeding	40
Grooming	42
Pair Formation	44
Copulation	46
The Nest Site and Nest	48
Building the Nest	49
The Eggs and Incubation	51
Growth of the Young	57
Fledglings	59
Distraction Displays and Parental Alarm	63
Development of Young out of the Nest	65

Renesting and Nest Success	67
Breeding Season	70
Discussion	71
WANDERING YOUNG AND TERRITORIAL ADULTS: SPATIAL BEHAVIOR	83
Dominance and Territoriality	87
Territory Size, Densities, and Biomasses	89
Habitat Selection	89
Discussion	90
FORAGING BEHAVIOR	96
Perch Selection	97
Foraging Away from Ants	99
Searching for Army Ants	100
Following the Army Ants	101
Prey and Prey Treatment	103
Numbers at Swarms	106
Competition at Swarms	109
Discussion	116
ASSOCIATION WITH INTERSPECIFIC FLOCKS	123
Other Members of Flocks	126
Competition Among Flocking Birds	133
Discussion	135
SUMMARY	148
GAZETTEER OF LOCALITIES	151
LITERATURE CITED	152
APPENDIX 1	156
APPENDIX 2	158

INTRODUCTION

Spotted Antbirds (*Hylophylax naevioides*, Formicariidae) are common birds of the undergrowth of lowland tropical forests from Honduras to Ecuador. Skutch (1946, 1969), Johnson (1954), and Slud (1960) studied them briefly, but did not investigate them in detail. Since 1960, as part of a study of ant-following birds on Barro Colorado Island in the Panamá Canal Zone (Willis, 1967), I have studied the behavior of Spotted Antbirds. This report details the results of that study.

Spotted Antbirds (frontispiece) are interesting because they are regular members of the two major types of mixed bird flocks that have attracted the attention of naturalists in tropical forests since the time of Bates (1863). These two types of flocks are those that follow army ants (Chapin, 1932; Johnson, 1954) and wandering flocks (Swynnerton, 1915; Winterbottom, 1943, 1949; Davis, 1946; Stanford, 1947; Rand, 1954; Short, 1961; Moynihan, 1962a; McClure, 1967). The flocks around army ants gather primarily to capture insects flushed by the ants, and thus are not very different from aggregations of birds at fruiting trees, garbage dumps, and other concentrated sources of food. Wandering mixed flocks seldom concentrate at local food sources, so that the advantages of flocking are currently unknown. Morse (1967) and others favor various theories that the birds gain food advantages by flocking, but Moynihan (1962a) and others think that flocking somehow reduces predation. Most authors have had little time for careful studies of individual species, and have based their theories on tabulations of all the individuals and species in observed flocks. The study of Spotted Antbirds gives information from a new direction, and suggests new approaches for the study of wandering flocks.

After the present introduction, there are seven sections in this report: these treat general behavior, antipredator behavior, agonistic behavior, reproductive behavior, spatial behavior, foraging behavior, and flocking behavior. There is a discussion at the end of each of these seven sections.

SPOTTED ANTBRIDS AND THEIR RELATIVES

Male Spotted Antbirds (frontispiece) are brightly patterned with white, chestnut, dark gray, and black. The name comes from a necklace of prominent black spots across the chest, between the conspicuously white upper breast and the white to grayish-white belly. The head is dark gray, contrasting slightly with the black throat and bill and with the dark rufous eyes. The back is chestnut, as are two broad and conspicuous bars on the black wings. The lesser coverts are tipped with white speckles, while the dark remiges are tipped or crossed by a third wing bar of buff to chestnut hue. White bases to the central back feathers form a large dorsal patch that is usually concealed, except when

birds dispute. Each brown tail feather has a black subterminal band and a buffy-whitish tip.

The female Spotted Antbird has bright buff to chestnut bands and feather tippings on the blackish wings, but is otherwise more soberly colored than is the male. She is brownish-chestnut above, with a concealed whitish dorsal patch that can be displayed in disputes. The tail has a buffy tip and a brownish-black subterminal band. The head is brown, fading to buffy-whitish on the indistinct superciliary line and lower face and to white on the throat. The whitish underparts are tinged with pale buff, especially on the sides, and there is a more or less obscure necklace or high breast band of brownish spots. The bill and legs are dark gray and the eyes dark whitish gray.

I have seen only one partial albino, a male with much white on the wrist area on Barro Colorado Island on 22 July 1967.

Spotted Antbirds range in Caribbean lowland forests from southeastern Honduras to the lower Magdalena Valley of northern Colombia. Over the Cordillera de Guanacaste of northern Costa Rica (Slud, 1964) and in central Panamá (El Valle) they range onto the Pacific slope. From central Panamá to central Ecuador they occur in most of the forested Pacific lowlands. I have found them as high as 900 m elevation on Cerro Campana in central Panamá, and there are specimens in the United States National Museum from as high as 1,300 m on Cerro Tacarcuna, eastern Panamá.

East of the Andes live two very similar species, the Spot-backed Antbird and the Dot-backed Antbird. (Common names used in this paper are from Meyer de Schauensee, 1966*; the corresponding scientific names, except for species mentioned in papers cited, are given in the index.) The latter is a flycatching, timid little bird of the *várzea*, or periodically flooded woodlands along rivers. It behaves and calls very differently from the Spotted Antbird, despite its similar appearance. The Spot-backed Antbird behaves more like the Spotted Antbird, but flycatches in and near foliage more often and follows army ants less often. (Skutch [1946: 18] reported that an Ecuadorian species of *Hylophylax*, probably the Spot-backed Antbird on geographical and behavioral grounds, is much like the Spotted Antbird.) Since Spot-backed and Dot-backed Antbirds are similar morphologically but occur together without interbreeding, the similar Spotted Antbirds might also fail to interbreed with Spot-backed Antbirds were they to come in contact. Among related antbirds, sympatric species of a genus or subgenus commonly differ as little as these two in behavior or morphology or both. For these reasons,

* While many of these names may not now be truly "common," in the sense of having wide currency, it seems to me that this is to be hoped for and will be promoted by using them.



PLATE 1. Army ants (*Eciton burchelli*). Upper left, a major ("soldier") and a worker. Upper right, a dense swarm of army ants starting to raid. Lower left, army ants carrying prey from the swarm to the bivouac. Lower right, corner of a nomadic bivouac made of bodies of ants and enclosing the queen and larvae.

I shall follow traditional taxonomic practice and regard Spotted and Spotted-backed antbirds as separate species, even though they are closely related.

ARMY ANTS

Rettenmeyer (1963), Schneirla (1957), and Willis (1967) summarize information on the army ants followed by birds. The two important ant species are *Eciton burchelli* and *Labidus praedator*. These ants form wide raiding swarms, flowing by the thousands over the leaf litter and into tangles near or above the ground, in tropical to subtropical forests from México to Argentina. There are many species of birds that follow the ants and snap up arthropods fleeing from the advancing armies. No bird, so far as is known, regularly eats the ants themselves.

Eciton burchelli (Plate 1), brown-and-yellow ants that average almost a centimeter in length, swarm predictably and in the daytime all year long. These large ants flush many large arthropods, such as spiders, roaches, crickets, and katydids. *Labidus praedator*, black ants averaging about five mm long, flush more small prey, such as sowbugs and amphipods. They swarm above ground mainly in rainy weather, and swarm at any hour of day or night. A raid of *L. praedator* is likely to disappear underground after a few hours and leave ant-following birds stranded. Those ant-following birds that follow army ants more than 50 percent of the time usually follow *E. burchelli* rather than the unpredictable *L. praedator*. Birds that follow army ants less persistently—including many migrants as well as the Spotted Antbird—follow both ant species (Willis, 1966a: 211).

There are a few other army ants that birds sometimes follow. *Nomamyrmex esenbecki*, brown-and-yellow ants that resemble *Eciton burchelli*, occasionally form straggling swarms on the leaf litter in Neotropical forests. Five times on Barro Colorado I recorded Spotted Antbirds attending raids of *N. esenbecki*. Once on Barro Colorado I found a pair of Spotted Antbirds at a loose evening swarm of *Eciton mexicanum*, a mainly nocturnal species that looks like a small *E. burchelli*. Once I found Spotted Antbirds at a straggling swarm of an unknown species of *Eciton* on Barro Colorado, and once at a swarm of another unknown species on Buenavista Point near Barro Colorado. Although column-raiding army ants, especially *Eciton hamatum*, are very common on Barro Colorado and in other areas where I have studied Spotted Antbirds, I have never seen Spotted Antbirds show interest in them. The column raiders, the raiders with straggling swarms, and the semi-nocturnal raiders among army ants are unlikely to be important for diurnal ant-following birds.

STUDY AREAS

I studied Spotted Antbirds at several localities in Panamá and Colombia (Appendix 1). All localities but Yuto and Tanandó (Chocó, Colombia)

are characterized by tropical or lower subtropical forests, moderately hot and humid, and have marked dry seasons between December and April. In the Chocó, where there are heavy rains all year, Spotted Antbirds are less common than in the other areas.

Most of my studies have been on Barro Colorado Island, the research station of the Smithsonian Tropical Research Institute in the Panamá Canal Zone. This island is a 15.7 square km hilltop which was isolated from nearby lowland forests when the waters of Gatun Lake rose, between 1911 and 1914, to form the central part of the nearby Panamá Canal. It is covered by forest except at the laboratory clearing. There is a good system of trails, marked at 100-meter intervals by posts, so that one can easily and accurately map the locations of birds seen. In addition, I set up a grid of compass-line trails near the center of the island.

I visited the island as follows: 28 September 1960–25 November 1961; 18 January–18 February and 25 June–1 August 1962; 20 June–31 August 1963; 18 June–1 September 1964; 15 January–5 March and 4 August–11 October 1965; 16 May–31 July 1966; 1 June–16 August 1967; 14 June–1 September 1968; 28 June–27 August 1969; 27 June–7 September 1970; and 17 December 1970–25 January 1971.

The geology of Barro Colorado is discussed by Woodring (1958), and the climate and vegetation by Kaufmann (1962), Willis (1967), and earlier authors. Rainfall averages 2,730 mm a year, rising to a monthly high of 454 mm in November and then dropping sharply, so that only 7.8 percent of the yearly total falls from January to April. Much of the eastern half of the island and some of the western half were in clearings or low second growth in 1923, when the island was set aside as a biological reserve. However, the fairly mature forests in these areas are now rather like the older forests of the island, although somewhat lower and with fewer treefalls and other clutter in the undergrowth. Little light reaches the lower levels of the undergrowth (Allee, 1926: 288–289), and the annual dry season inhibits epiphytes and lush undergrowth, so that the lower layers of the forest are mostly open and uncluttered. Thin saplings and spindly sprouts and palmetto reach upward for light, while buttressed trees and clumps of palms (*Oenocarpus panamensis*) block long vistas, but the forest is not the impenetrable “jungle” one finds in areas recently disturbed by man. Treefalls, dense sapling tangles around rotting old treefalls, and patches of spiny-leaved “wild pineapples” (*Ananas magdalenae*) add a mosaic pattern of dense patches to the lower levels of the forest in some areas.

METHODS OF STUDY

Spotted Antbirds are being studied in much the same way as were Bicolored Antbirds (Willis, 1967). Birds are captured in mist nets set ahead of swarms

of ants or elsewhere in the forest and marked for later recognition with different combinations of colored celluloid bands. In field notes and in this report, single letters represent a band. Bands are read up the left leg and down the right. Thus, the male Spotted Antbird RWBP had a red band below a white one on his left leg and a blue band above a pink one on his right leg. Between 1960 and 1971, I banded 498 Spotted Antbirds on and near the study area on Barro Colorado.

I watch Spotted Antbirds, at and away from swarms of ants, from distances of 5 to 20 m to minimize fear reactions. These birds readily become fairly tame, and forage near one without signs of alarm.

I took still pictures with an Asahi Pentax and a 200 mm Takumar lens, using electronic flash and Kodak High-speed Ektachrome for color pictures and various films, from Plus-X to Tri-X, for black-and-whites. Movies were taken at 24 to 32 frames per second on Tri-X film, using mainly an Arriflex camera and Angenieux lens. I recorded bird calls with a Mohawk "Midgetape 500" recorder at 9.5 cm per second or on a Uher "4000 Report S" at 19 cm per second. To bring birds closer for recordings or experiments during 1961-62, I used the Midgetape and a Victor XT-401 amplifier and speaker (Victor Company of Japan, Ltd.). Calls were analyzed on Kay Electric Company "Sonographs," using the wide-band filter passes.

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I appreciate the support of a Woodrow Wilson traveling fellowship, predoctoral fellowships from the National Science Foundation, postdoctoral fellowships from the Frank M. Chapman Fund of the American Museum of Natural History, and a Sigma Xi research grant. The staff and facilities of the Smithsonian Tropical Research Institute, Panamá Canal Zone, and of the Compañía Minera Chocó-Pacífico, Colombia, were welcome and welcoming. George Cox, Gordon Orians, Dennis Paulson, Susan Smith, and others provided vigorous criticism for the manuscript, which is not to say that they approve all of its present positions and conclusions. I appreciate the help of Richard Stallcup in the 1964 observations and of Stephen Kistler in the 1970 observations. My wife, Yoshika Oniki, helped with observations and in many other ways.

GENERAL BEHAVIOR

CALLS AND SONGS

Spotted Antbirds are very like Bicolored Antbirds (Willis, 1967) in calls, so I shall use the same terms for the calls of both. Spotted Antbirds apparently lack keening, grunting, and growling calls. Male and female Spotted Antbirds have similar calls and songs.

Chirring.—A sharp rattle or buzz, *chi'i'i'i*, is the usual reaction of Spotted Antbirds to disturbing large animals, such as humans (Figure 1, f). The nine oscillations in the graphed chirr last 0.23 second and range from 1,500 to 6,500 Hertz in frequency (abbreviation Hz = cps). The main energy of the call rises from about 4,000 Hz to 4,500 at the third oscillation, then drops gradually to 3,500. Concurrently, the oscillations speed up to 40 per second at the third and slow to 30 per second by the end. The faint high-frequency clicks terminating each oscillation may be clicking of the bill. The call remarkably resembles the chirring (Figure 1, g) of the Dot-winged Antwren, a bird that does not follow army ants but which associates with Spotted Antbirds in interspecific flocks. The chirring of the Dot-winged Antwren is somewhat low and slow, ranging from 1,500 to 5,500 Hz and with about 30 oscillations per second throughout; it lasts 0.28 second for nine or so oscillations.

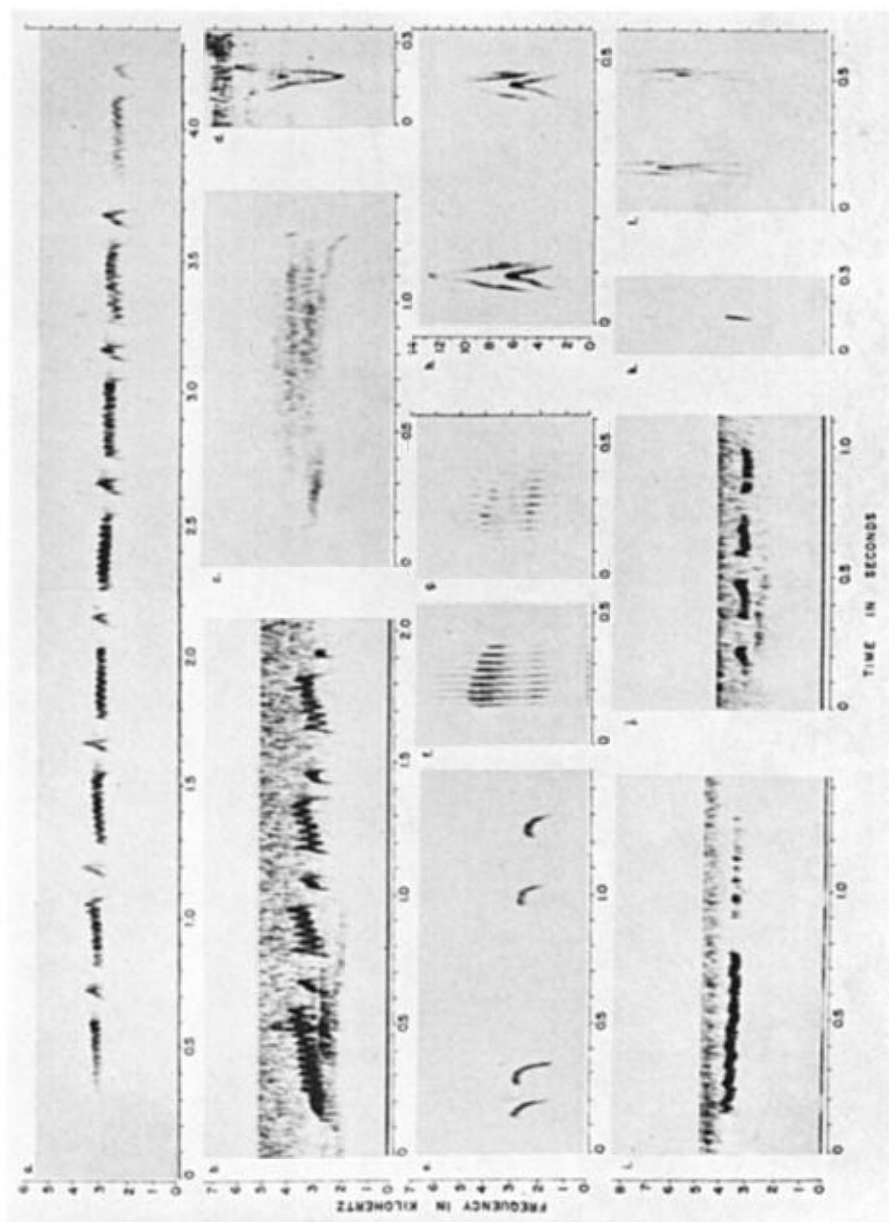
Chipping.—A loud, sharp *peep!* or series of several such notes (Figure 1, h, k, l) is the usual reaction when a Spotted Antbird is very excited, as when a hawk flies up. Two chips (l), graphed at half speed in h to show high frequencies, are simple inverted-V cries 0.05 second long and 0.35 second apart. The main harmonic rises with one brief lag from about 2,500 Hz to 6,500, then drops evenly to 2,500.

A presumed chip (k) of a fledgling in the hand lacks a descending part; it is about 0.02 second long and rises from about 2,700 to 3,800 Hz, with a harmonic at about 7 kHz.

Singing.—For my definition of song see discussion on p. 72. The characteristic "peety weety" song (Eisenmann, 1952) goes *beeeeeeee, tipee, tipeeti, peeti, peeti* or the like (Figure 1, a). After the long (0.5 second) initial note, short (0.05 second) *ti* notes alternate with quavering *peeee*

→

Figure 1. Wide-band sonograms of calls of Spotted Antbirds (one call of Dot-winged Antwren), from tapes at 9.5 and 19 cm/sec. a, Loud-song of a male. b, Faint-song of a female calling fledglings, printed heavily so insect noise shows in background. c, Snarl. d, Bugling, with insect noises above 6 kHz. e, Four chirps. f, Chirring of Spotted Antbird. g, Chirring of Dot-winged Antwren. h, Two chips, at half speed. i, Loud-peeping of fledgling (*peeee, jeeee*), with insect noise above 4 kHz. j, Faint-peeping of fledgling (*piet wiet wiet wiet*), with insect noises in background. k, Chip of fledgling, in hand. l, Same two chips as in h, played at normal speed.



whistles (0.3 second) at about four notes per second. In a typical whistle there are 10 or so oscillations of a few hundred Hz about an average frequency of some 3 kHz. Each simple *ti* cry rises from about 2,500 to 3,500 Hz, with a brief middle lag, and drops evenly to about 2,800 Hz. Up to 10 or 15 *beeeti* phrases are in the loudest songs; "faint-songs" (Figure 1, b) are softer and seldom go over five such phrases. In comparison with the "loud-song" above, the faint-song illustrated shows shorter whistles with stronger oscillations and a more strongly rising frequency. "Serpentine-songs" are faint-songs repeated again and again, punctuated by series of chirping or *peup* notes, such as *beeee tipee tipeeti, peup-peup-peup-peup, bee tipeeti, peup, peup-peup-peup*. Birds serpentine-sing mainly when about to feed mates or young; faint-songs and loud-songs go between mates or from parents to young; loud-songs are used by opposing birds, too. Faint-songs and serpentine-songs are very variable. Songs of females often seem weaker than songs of males, but I have not found dependable ways to tell the sex of a bird from its song alone.

Chirping.—Both male and female utter faint *peup* notes (Figure 1, e) when near each other. In copulation, the chirps of the male deepen to a *pip, pip, pip* series. One female gave a faint *meu* or *meuhhh* hiss during copulation, perhaps a different note or perhaps faint snarling. A chirp curves down from about 2,800 to 1,200 Hz over 0.08 second, and has a faint descending overtone from 3,500 to 2,200 Hz as an apostrophe at the end.

Snarling.—A long, hissing *wrieeeeeeehhhh!* (Figure 1, c) is hurled at an opponent when a bird performs the agonistic display of challenging. The first part (0.2 second) of the snarl drops quickly from 3,500 to 3,000 Hz and stays there while oscillating at 75 per second; the partly overlapping second part (0.95 second) explodes in hissing complex noise, with multiple oscillations at about the same rate, between 2,500 and 5,000 Hz; the third part (0.02 second) is a short whistle that drops from 2,500 to 2,000 Hz and has a harmonic about 4 kHz. The complete snarl here is 1.12 seconds long.

Bugling.—A sharp *twit!* or *chwit!* note (Figure 1, d) is often the first call when a bird jerks upright to start a series of snarling challenges. It apparently is homologous with bugling in *Gymnopathys* and *Rhegmatorhina* (Willis, 1967, 1968, 1969a), but is much shorter—about 0.15 second. The sinuous whistle drops from some 5,500 to 2,000 Hz via a brief lag about 4,500 Hz, rises to over 6,000 Hz and quickly drops below 4,500 Hz. An overtone is at 4,000 Hz for its low point; further details are not visible because the recording is faint and its sonogram blends with background noise.

Hissing and Snapping.—A bird darting past another in a supplanting often gives a hissing *dzihht!* or *chihhht!* or *szapp!* The note often ends with a sharp snap of the bill, but separate snapping is rare.

Whimpering.—A bird persistently supplanted by a dominant rival gives

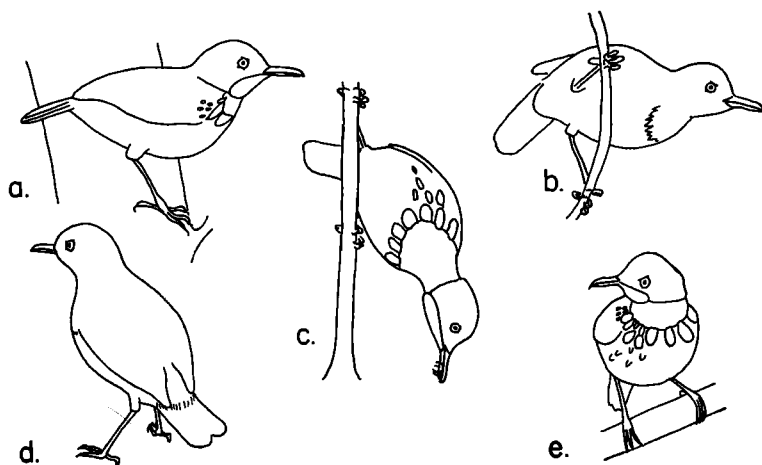


Figure 2. Spotted Antbirds. a, Male, somewhat sleeked in freezing pose, on sloping sapling (from photograph). b, Female, somewhat in the panicking pose, perched near ground (from field sketch). c, Male lunging to peck at the ground (from field sketch). d, Female stands on ground and looks about for prey that escaped (from field sketch). e, Male looks about (from photograph).

faint peeping notes, *pt pee-pee-pee* or the like. Adult, dominant males and others often give this note in the hand when banded or recaptured.

Peeping.—Young birds peep in several ways. “Loud-peeping” (Figure 1, i) is often a loud, two-note *peeee, jeeee!* the last note at a lower pitch. The illustrated loud-peep descends throughout from about 3,600 to 3,400 Hz, is about 1.13 seconds long (first note 0.62, gap 0.13, second note 0.38), and oscillates slightly at about 14 per second. Loud-peeping resembles the song of the Ruddy-tailed Flycatcher. “Faint-peeping” varies greatly, from a sibilant *piet-wiet-wiet-wiet-wiet* that becomes like the song of the adult as the young bird grows, to a soft *pee, pee-pee-pee* (Figure 1, j) or a long, soft *chieeh, chieeh* like a faint version of loud-peeping. At times there are faint *wd* grunts between faint-peeps as a kind of “serpentine-peeping.” The illustrated faint-peeping has slight irregular oscillations between 3,000 and 3,500 Hz; perhaps the oscillatory mechanism is not under full control at this age.

Squeaking.—Young squeak *scraihh* series when fed.

Screaming.—In the hand, birds occasionally scream sharply. One female gave a short *waiiaihh!* scream when supplanted by a Gray-headed Tanager.

NORMAL POSTURES AND MOVEMENTS

To describe the postures or poses of an animal, it is convenient and instructive to depict a “normal” or “standard” posture, in which the animal is “just standing,” and to specify the movements of feathers and other parts of



Figure 3. Spotted Antbird male watching me from inclined perch when I squeaked near nest from which young had disappeared.

the body that produce special poses (Orians and Christman, 1968: 5–6; Willis, 1967: 16). The standard posture for an undisturbed Spotted Antbird (Figure 2, a, e) is much like that for a Bicolored Antbird (Willis, 1967: 16).

Like the Bicolored Antbird, the Spotted Antbird is adept at clinging to slender vertical or inclined saplings (Figure 3). Both cling by flexing the upper leg, extending the lower leg, and angling toe II on the lower foot some 20 to 40 degrees above the closely appressed toes III and IV. The body is thereby tilted or rolled toward the perch (Figure 2, b).

“Flicking” the tail, or lowering it below the line of the body and jerking it suddenly back to near that line, is one of the most characteristic movements of Spotted Antbirds. Among antbirds, *Hylophylax* and related genera flick the tail, while antbirds of *Myrmeciza* and related genera “pound” the tail emphatically downward and raise it slowly (Willis, 1967: 39). As is discussed under “reactions to danger” and at other places, these tail movements usually indicate that the observer or other factors are disturbing or exciting the birds, for tame ones that are inactive or preening rarely flick or pound the tail.



Figure 4. Spotted Antbirds jumping from nests. Male (above) is just opening wings; female (below) is jumping downward rather than flying.

The small Spotted Antbird (weighing 15 to 22 g) hops along limbs more easily and frequently than does the Bicolored Antbird (25 to 35 g). Both species readily yaw and pitch on a horizontal perch or around a vertical perch, pivot or reverse on or along a perch, and hop from perch to perch or on the

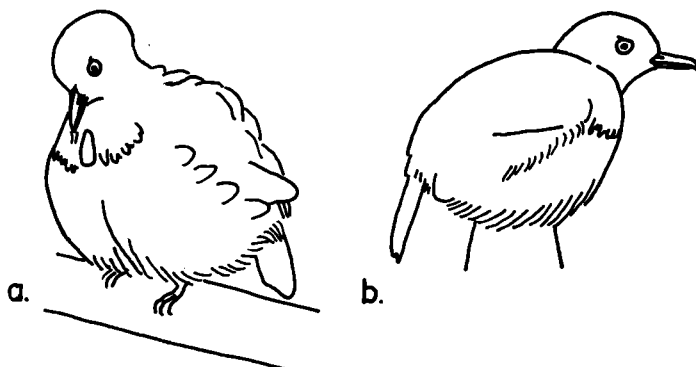


Figure 5. Preening (a) and resting (b) female Spotted Antbirds, from field sketches.

ground. They do so in such stereotyped ways and after such distinct pauses that they sometimes remind one of clockwork toys.

Despite its small size, the Spotted Antbird generally jumps like the Bicolored Antbird to start flight. Figure 4 shows birds jumping from a nest. The first part of the flight is often a parabolic arc, or an arc like that of a projectile, followed by a more or less straight course to the next perch. The male (Figure 4, above) is starting to open his wings on a parabolic jump. Crippled or young birds flutter to start flight rather than jump strongly. Flight is fluttery, slow, direct, and generally much like that of Bicolored Antbirds. However, Spotted Antbirds hover and maneuver through dense tangles more easily than do the larger birds. If frightened, a Spotted Antbird flies as rapidly as a flushed quail. An alighting bird brakes with its wings as well as with its legs. Control, not speed, seems the keynote of its flight.

A traveling Spotted Antbird generally flies 1–20 m at a time, at 1–2 m above the ground, inside the forest. One rarely sees longer flights, higher traveling, and movements outside the forest or across clearings or large streams. I only once saw a bird cross the laboratory clearing on Barro Colorado, although several pairs have territories around the clearing and come up to the bamboos and other vegetation within a meter or two of the edge. The one crossing was in 1971, when bamboos had grown up to provide a shaded passage. In general they avoid sunlit areas; even sunflecks rarely strike them. On Cerro Campana, I once saw them in open woods from which all undergrowth had been cleared; these birds were following army ants near a house.

A travelling bird alights easily on each vertical sapling along its course, looks about from the clinging posture, swings like a gate (pitches) around the perch, and flies to the next perch. Unlike Bicolored Antbirds, which seldom forage as they travel, wandering Spotted Antbirds often forage by

TABLE 1
RECORDS OF PREENING HEIGHTS FOR SPOTTED ANTBIRDS

	Height in Meters											Total
	0.1	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9	1.0	2	
Number of Records	0	6	13	17	18	9	10	7	5	0	8	93

cocking or rotating their heads to study the ground or by darting for prey. A wanderer seldom moves far in one direction unless going to a nest; usually it circles or winds about in an area. At times sharp chipping notes or songs mark its course.

RESTING

A resting Spotted Antbird (Figure 5, b) generally sits on a horizontal perch near the ground in or near moderately dense cover, especially in the tangled limbs of fallen trees or in dense lianas or under a palm clump (*Oenocarpus panamensis*). The relatively open undergrowth where the antbirds forage is less likely to be used for resting, although short periods of resting sometimes interrupt foraging. Besides flexing the legs to sit, the resting antbird fluffs the ventral feathers and back feathers until they cover the feet and sometimes the wings, closes and lowers the tail, and raises and retracts the neck so the head nestles on the shoulders. It looks around, but seldom cocks the head as if looking at the ground for prey. Commonly preening interrupts resting.

PREENING AND HEAD-SCRATCHING

Preening Spotted Antbirds generally take horizontal perches, 1–3 cm in diameter and 0.2–0.9 m above the ground (Table 1) in the edges of tree-

TABLE 2
PERCH ANGLES FOR SPOTTED ANTBIRDS

Angles	Foraging Away from Ants		Foraging with Ants		Preening	
	Records	Percent	Records	Percent	Records	Percent
0– 20°	91	27.1	593	30.1	61	67.0
20– 40°	39	11.6	306	15.6	18	19.8
40– 60°	46	13.7	268	13.6	10	11.0
60– 80°	53	15.8	163	8.3	1	1.1
80–100°	106	31.6	628	31.9	1	1.1
100–120°	1	0.2	8	0.4		
120–140°			2	0.1		
Total	336	100.0	1968	100.0	91	100.0

falls and tangles of lianas or palm clumps. Vertical perches are seldom used (Table 2), even though foraging from vertical perches is a major adaptation in this and related genera.

To preen (Figure 5, a), a Spotted Antbird fluffs or elevates feathers of the region involved, pokes the head into that region, and with a twist of the head runs each feather from base to tip between the mandibles. As well as preening feathers, the bird nibbles at the bases of feathers. At times the bird flashes one wing far out and peers under it ("underwing-looking"). Occasionally one shakes the head or body during a preening session; the latter activity is more common during bathing. In general, the preening activities resemble those of Bicolored Antbirds and other small passerines.

After dissecting prey, and periodically during preening or other situations, a Spotted Antbird sometimes wipes the bill energetically. It strops the bill rapidly from base to tip on the perch or a nearby surface, in much the same way as does a Bicolored Antbird.

Champing or mandibulation, opening and closing the beak rapidly several times, is occasional after preening, dissecting food, and in some other situations, such as the active looking about after a supplanting.

I recorded Spotted Antbirds scratching the head by passing the foot under the wing only twice. Normally this and other antbirds lower one wing and scratch the head over it. I specifically recorded scratching over the wing 48 times for Spotted Antbirds, and saw scratching over the wing many other times without recording the events. Often the head is fluffed, especially the crown of the head. Once I noted that the tail was lifted as the bird scratched over the wing.

Mutual grooming, when a bird grooms its mate or young, is described under reproductive behavior.

STRETCHING

After a Spotted Antbird rests or preens for several minutes, it is likely to perform a stereotyped stretch or two before returning to foraging or other activities. These stretches, common to Spotted and Bicolored Antbirds and many other birds, include yawning or the "bill-stretch," full side-stretches (of wing, tail, and leg on one side), half-flexes (of the partly flexed wings above the back), and toe-standing. Perhaps these stretches are "negative afterimages" of resting postures, in that muscles compressed during resting are extended and vice versa.

EGESTION AND DRINKING

Foraging behavior is considered later, in a discussion of the relations of Spotted Antbirds to army ants and to other birds.

At times Spotted Antbirds regurgitate fragments of insect exoskeletons,

although the fragments never seem to be compacted into pellets. The excreta are white and rather fluid, and are dropped rather frequently. There are no strong behavior patterns associated with elimination, except for slight flexion of the legs and opening the tail coverts so the feathers and legs are not soiled.

Spotted Antbirds rarely drink, except that they sometimes nibble the drops of water at the tips of leaves after rains.

SUNNING

One female Spotted Antbird "sunned" for a minute. She hopped onto a sun-lit twig, half-sat with her feathers fluffed down to the perch, and spread the wing on the side toward the sun as she turned her face toward the sun on that side. Her bill was open, her crown and head somewhat fluffed. The shaded eye opened and closed as if she were sleepy, but the eye toward the sun was opened. Ordinarily Spotted Antbirds avoid sunflecks as if photophobic, so sunning is probably an uncommon activity.

BATHING

Occasionally a Spotted Antbird bathes in a shallow pool, either as a break in foraging during the day or, more commonly, as one of the last activities of the day, between 17:00 and 18:00. One pair chirped and faint-sang at 17:20 as they moved slowly to a little creek, looked down at several pools and bathed briefly in them, then flew down to the shallow edges of two pools about 0.7 m apart. After hopping into water about to their midlegs, they sat and fluttered briefly. Then they waited and looked about, half-sitting with wings loose and their tails spread, before ducking their heads and foreparts and fluttering busily. Drops cascaded down their backs as they rose. Their tails were half in the water. The female flew up and shook her plumage, then dropped to her puddle for more dips of the body and foreparts. The two finally moved to low perches in a nearby treefall, where they preened quietly as I left at 17:35. Other bathing birds also broke bathing into short segments by flying to perches near the pools briefly; perhaps some did so because I disturbed them. Shaking the body is very frequent after bathing but infrequent at other times in this species.

ANTING

Spotted Antbirds "ant" much as do Bicolored Antbirds (Willis, 1967). The Spotted Antbird holds the prey in the tip of the beak and chews it between sessions of poking the prey into feathers under the tail and wings. To stroke the prey under the tail, the antbird stands very high on the legs and lowers the slightly spread tail until it touches the legs or fills the space between them. It may be that the bird is stroking the prey on the remiges and rectrices

themselves, but the stroking seemed to pass through the under tail coverts or flank feathers. Out of 11 Spotted Antbirds recorded anting with 14 prey items, 5 birds ate 7 prey items. On two of the occasions, male Spotted Antbirds anted and then fed the prey to their mates. The fate of 5 items was not recorded. One bird anted with 4 small prey, eating 3 of them, then preened. One item was definitely an ant, but I was unable to identify others.

ATTACKS BY ARTHROPODS

Spotted Antbirds occasionally hop violently ("jitter") from one foot to the other when army ants attack their toes, but such events are rare. Many Spotted Antbirds forage away from the most active parts of an ant swarm, because larger birds drive them to the periphery. The ants, most numerous and aggressive at the swarm center, are not likely to attack peripheral birds very often. I have rarely seen a Spotted Antbird peck and throw away an attacking army ant or shake one foot at an attacking ant, but these actions are so widespread among related antbirds that the Spotted Antbird probably does them whenever necessary.

Mosquitoes elicit head-shaking, flitting the wings, and twitching the tail from side to side from Spotted Antbirds, much as in Bicolored Antbirds. I have not seen a mosquito get blood from any antbird.

Bird ticks occasionally attach near the corners of the gape and swell up with blood. Wandering immature birds seem more prone to have ticks than do settled breeding birds, suggesting that the latter encounter fewer ticks or remove them more effectively.

REACTIONS TO RAIN

Spotted Antbirds generally wait under leaves or other shelter during heavy rains, but move about readily during medium to light rains. They forage little during medium to heavy rains. Free-moving birds rarely seem to have any problems with wet feathers, even though the feathers of birds captured in mist nets during rains quickly become sodden. A small bird like this can easily find local places protected by overhead leaves, as the rainfall pattern near the forest floor is notably irregular. At times a Spotted Antbird shakes its body or head to throw off a raindrop or spray.

DISCUSSION

Such adverse (i.e., entropy-increasing) and small influences as stiffness, desiccation, rain, cold, dishevelment, dirt and external parasites seem to trouble free-living Spotted Antbirds relatively little in their normal environment in the shaded forest undergrowth. Still, maintenance behavior against these adverse influences occupies some time and energy, and birds unable to spend

enough time, such as immatures chased about by adult birds, quickly become disheveled.

Temperatures in the forest undergrowth (Allee, 1926: 280) are well below the body temperatures (42.0°C ; $n = 34$; Y. Oniki, MS) of Spotted Antbirds, especially at night or during rains. The fluffing during resting and preening is probably a heat-conserving activity, as is sitting so that the feet are covered. Sitting may also require less muscular effort. The rather sparse and loose feathering of antbirds, compared with northern forest birds, noticeable when one prepares study skins, probably is enough to conserve heat without requiring an inordinate amount of plumage care or feather replacement at the molt. I doubt that heat itself is much of a factor, except a permissive one, in the evolution of sparse feathering. Some tropical seabirds and birds of clearings have thick feather coats, so that the latter can protect against radiant heat. Intense tropical heat, rare in the forest interior, might occasionally stress the thinly-feathered antbirds if they did not avoid sunlit clearings or open areas so assiduously. Spotted Antbirds never seemed overheated enough to show gaping, panting, gular flutter, ruffling the feathers, or sleeking. Birds released from mist nets sometimes opened the beak and panted rapidly, as did birds persistently chased, but these reactions were short-lived and may have been related to fright rather than to overheating.

Avoidance of sunflecks and clearings, and the rarity of sunning, are probably reactions to light rather than to heat. Gordon Orians (pers. comm.) has pointed out that antbirds of the forest undergrowth have very large eyes compared with birds of the forest edge, and that they may have difficulty seeing in bright light. Timidity in well-lighted open situations may be due to problems in detecting predators.

Normal behavior patterns probably protect free-moving Spotted Antbirds against heavy tropical rains rather well. Water conservation is probably not a problem for Spotted Antbirds, because they live in a constantly humid environment at moderate temperatures and eat very juicy prey. Their fluid excreta suggest that eliminating water and nitrogen are not problems.

Preening and resting birds generally take horizontal perches, but foraging ones take vertical perches as well. Spotted Antbirds are specially adapted to cling to vertical perches, but it must take less energy to stay on a horizontal perch if a bird has a choice. The light-seeking undergrowth of deep tropical forests is vertically oriented to a degree that northerners can scarcely imagine; a foraging bird, especially one over army ants, will seldom have a horizontal perch to stand on unless it takes the ground, where it will rarely have a good vantage point and probably would be attacked by ants. Probably foraging Spotted Antbirds have to take vertical perches, but preening ones can hunt for horizontal ones that are easier to stand on.

Anting is generally considered a kind of maintenance behavior, one that consists of the use of insect secretions and other things because they are stimulating (Whitaker, 1957), kill mites (Dubunin, *vide* Kelso and Nice, 1963), or soothe areas of molting feathers (Potter, 1970). In Spotted Antbirds and many other tropical species I have studied, anting seems to be a way of treating objectionable prey. Spotted Antbirds sometimes eat such prey after anting, while Plain-brown Woodcreepers commonly do so. Possibly anting may have secondary value in plumage care in both of these species.

Normally antbirds preen off or shake off dirt and water and external parasites rather well. The head is a site that ticks and feather lice occupy rather frequently, however. Perhaps the relative frequency of grooming the head in mutual grooming is correlated with difficulty in grooming the head. The wing is another place where mites and bird lice stay in many birds; perhaps the pattern of underwing-looking is a reaction to parasites.

REACTIONS TO DANGER

Reactions to large predators are a kind of maintenance behavior, related to reactions to small parasites, but distinctive and prevalent enough to be considered separately. When a possible predator appears, a Spotted Antbird may freeze, panic, or mob. Later reactions are fleeing, tameness, and investigating.

FREEZING

If danger is distant or uncertain, the Spotted Antbird sometimes crouches and freezes. Related antbirds sometimes "keen" (Willis, 1967: 13) when they freeze, but I never noted this call for Spotted Antbirds. At times a freezing Spotted Antbird gives a faint, long note, which seems almost a "snarl." Compared with the standard posture, the body feathers of a freezing Spotted Antbird are compressed. The head is up but the front of the body is down, indicating femoral flexing (as in Willis, 1967, "flexing" means closing the angle proximal to the part cited and "extending" means opening the angle proximal to the part cited) and head extending; the neck is retracted. The only movements are blinking the eyes unless signs of panic such as head-turning and wing-flitting or tail-flicking begin.

Spotted Antbirds flushed off nests or travelling through the forest sometimes alternate freezing with sudden movement in an alternating pattern that makes them difficult to follow.

On one occasion freezing was a reaction to my movement. Once it was a reaction to an outburst of chipping from Ocellated and Bicolored antbirds, once a reaction to keening from Ocellated Antbirds, and once a reaction to loud alarm calls ("stieking") of Plain-brown Woodcreepers. Compared with

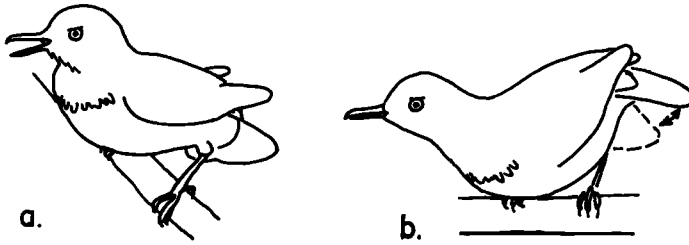


Figure 6. Mobbing (a) and panicking (b) female Spotted Antbirds, from field sketches.

Bicolored Antbirds, Spotted Antbirds freeze very infrequently. They more often start chipping and panicking, which they do on the slightest pretext.

CHIPPING AND PANICKING

At times a Spotted Antbird starts chipping *peep!*, one or more times in each series, loudly and emphatically. Often it is more or less in a posture or display (Figure 6, b) that I call "panicking." The bird jerks its head one way and then the other. The body and head are sleeked, and the wingtips scissor together. The bird flits the wings briefly as it flicks the more or less spread tail very sharply. I am not certain what movements produce flitting; it may simply be a brief carpal extension, but a quick flexion of humerus and midarm may contribute.

The panicking bird seems high on its legs, but the body angles downward to the horizontal or below. Probably some joints of each leg are extended and others flexed to produce this posture; the foot and tarsus are apparently extended, the femur and tibiotarsus flexed (see definition three paragraphs above).

Often the flicking and flitting lead to pivoting back and forth or reversing to mirror-image positions as the bird looks at the object of alarm with one eye and then the other. These sharp movements lead to sudden flights from perch to perch and to cover if danger persists or if other ant-following birds panic or call in alarm. The Spotted Antbird chips loudly as it flees to a treefall, palm clump, liana tangle, or other cover. It continues the display and calling in cover. If danger is not so close, the bird becomes hyperactive at foraging. It sallies sharply for prey with *peep!* notes, darts from perch to perch, and in general acts as if mixing the activities of panicking and foraging.

Spotted Antbirds seem very excitable, very prone to panic and chip rather than use freezing or mobbing. While other antbirds are chirring and mobbing the observer, the Spotted Antbird quickly turns to panicking and chipping. While other antbirds are freezing at a distant hawk, the Spotted Antbird chips loudly.

Bicolored and Ocellated antbirds, the dominant and well-fed species at swarms, sometimes react to the chipping of Spotted Antbirds and stieking of Plain-brown Woodcreepers (another subordinate bird that calls and panics readily) by keening and freezing, chipping or panicking, or fleeing to cover. Some subordinate and poorly fed Bicolored Antbirds continue to forage as they chip and panic, as do the Spotted Antbirds and woodcreepers. Often the dominant birds continue to hide and preen in cover rather than over the ants after the general panic is over, and at such times the subordinate birds forage very busily.

At times a Spotted Antbird chips when a Bicolored or Ocellated Antbird or other large bird supplants it. I specifically recorded *peep!* calls from Spotted Antbirds supplanted by Bicolored Antbirds on 18 occasions, by other Spotted Antbirds 6 times, by Gray-headed Tanagers (5), Plain-brown Woodcreepers (2), Ocellated Antbirds (2), Great Rufous Motmot (2), White-whiskered Puffbird (1), and Chestnut-backed Antbird (1). Twice a Spotted Antbird displaced by a coati (*Nasua narica*) gave chipping calls, and once a fall by a nearby marmoset (*Saguinus Geoffroyi*) caused chipping.

Chipping was a reaction of Spotted Antbirds to hawks (Double-toothed Kites, three times; Common Black Hawk, once) and to alarm notes of other birds (Plain-brown Woodcreeper stieking, twice; the *ah, rrrrr!* of a Slaty Antshrike, once). Once the chatter of a flushed Black-throated Trogon caused chipping. On many occasions I seemed the cause of their chipping and panicking, but chirring and mobbing were generally their first reactions to me.

CHIRRING AND MOBBING

I recorded chirring at a passing brocket (*Mazama americana*) twice and to a running coati once, but the other prolonged chirring reactions were to me and other humans. Birds away from other birds are especially likely to chirr persistently when the observer passes. Bicolored and other antbirds chirr at passing cats, tayras (*Eira barbara*), and other ground predators, but Spotted Antbirds tend to go into chipping and panicking much more readily in such situations. One Spotted Antbird started flitting and flicking when a squirrel (*Sciurus granatensis*) approached. Others flitted and flicked and were silent when I approached.

The mobbing display or behavior pattern is rather similar to that of Bicolored Antbirds, but is even more likely to be confusingly combined with panicking behavior. Tail-spreading and -flicking are probably characteristic of both patterns of behavior, but wing-flitting is more likely to be a sign of panicking than of mobbing. Birds that chirr without adding chipping flit very little. My earlier statement (Willis, 1967: 40) that Bicolored Antbirds flick the tail more during mobbing than during panicking is probably incorrect; recent studies suggest that Spotted and Bicolored antbirds flick the tail

strongly both in mobbing and in panicking. A Spotted Antbird combining mobbing and panicking often turns the head one way and then the other or pivots, reverses, and darts from perch to perch or to behind cover, but mobbing birds tend to hold a perch and direct the conspicuous white breast and both eyes toward the observer.

The mobbing bird tilts the body upward (Figure 6, a) and splays the legs, suggesting that mobbing differs from panicking in extension rather than flexion of the femora. I now rather doubt statements (Willis, 1967: 38, 41) that panicking Bicolored Antbirds splay the legs; more likely panicking Bicolored and Spotted antbirds flex or adduct the femora and hence bring the legs toward the center line. Probably both Bicolored and Spotted antbirds flex the tibiotarsi and extend the tarsi and the feet in panicking and mobbing, but the feet seem to be flexed more in mobbing.

Instead of scissoring the wingtips together as in panicking, the mobbing bird generally spreads the tips of the wings. I am not sure whether this represents active carpal extension or is a passive carpal extension caused by humeral extension.

As in Bicolored Antbirds, the neck is ordinarily flexed to the body and lifted during mobbing, in contrast to the neck extending (lengthening) and neck lowering during panicking. The head is often flexed on the neck during mobbing, but is extended if panic enters the display.

I am not certain what feather movements are associated with mobbing in Spotted Antbirds. Probably head-fluffing and throat-fluffing are used, as in mobbing in Bicolored Antbirds. The body feathers are probably somewhat spread for mobbing, as this would make the bird look bigger and more ferocious to a mammal; possibly the body is inflated, too. However, sleeking of both body and head starts as soon as a bird mixes panicking with its mobbing.

Birds with nests or young out of the nest chirr and mob the observer very strongly and persistently. These birds show little panicking, and probably would be the best ones to observe for future studies of mobbing in antbirds.

In northern latitudes and brushy or dense habitats, birds often approach and call when one makes a squeaking or hissing sound. Usually tropical birds, especially ones of forests, flee at such sounds rather than approach. However, Spotted Antbirds with young out of the nest sometimes appear and chirr when one tries squeaking, as Richard Stallcup (pers. comm.) has also noted on Barro Colorado. One male near a just-robbed nest that had had nestlings in it came up and chirred repeatedly whenever I squeaked; he gave faint "snarling" also (Figure 7).

Certain individual Spotted Antbirds are especially prone to chirr and mob the observer. Male YBXR, who occupied a territory near the summit of



Figure 7. Above, Spotted Antbird male mobbing or investigating me when I squeaked near nest from which young had disappeared. Below, male ending investigation.

Barro Colorado and saw me every year from 1960 to 1966, always chirred and fled in panic when I appeared. He habituated to my following very slowly, and seemed to be as wild at each new meeting as the first time I saw him. His son and grandson also chirred and mobbed very readily. Most other

Spotted Antbirds I have encountered repeatedly ignore me or chirr only briefly, even when I appear for the first time in several months.

FLEEING AND TAMENESS

Quite often Spotted Antbirds flee and disappear after mobbing or panicking, especially if they are in open undergrowth and are not with army ants or with a flock of birds. To read the bands on their legs, I sometimes had to chase them about for half an hour to an hour before I could come within 20 m of them. They can disappear surprisingly well behind an isolated tree trunk or two, and change directions so frequently that they can be difficult to follow. They hide in treefalls and in dense patches of saplings, behind or under palm clumps, or in tangles of lianas, and circle in these thickets when one tries to drive them out. Infrequently (more often if one sets a low mist net!) a persistently chased bird flies higher and higher in the undergrowth as it doubles back and forth until it is 5 to 15 m above the ground like an antwren. Poorly flying fledglings do this regularly. Fleeing birds are commonly sleeked and flick the somewhat spread tails, probably as low-intensity panicking; they chip or are silent rather than chirr in many cases, unless young or nests are nearby. At times one flees until it reaches an antwren flock (see below).

Spotted Antbirds often become tame. They are usually among the first birds to return to a swarm of ants and resume foraging after the observer appears, although one usually has to wait 5 to 15 minutes. Subordinate Bicolored Antbirds also return quickly, suggesting that low status on the peck order is directly correlated with tameness.

While Spotted Antbirds habituate to the observer rather rapidly, they never become as tame as do individual Bicolored Antbirds. The latter habituate to the observer very slowly, but with frequent contact become so tame that they forage within three m. Perhaps Spotted Antbirds did not become this tame because I seldom observed an individual as long or as frequently as I did individual Bicolored Antbirds. Spotted Antbirds are likely to be driven away from swarms by the larger Bicolored Antbirds, or to wander about the outskirts away from the swarm and me. Moreover, each Spotted Antbird has a smaller home range than does a given Bicolored Antbird, and is encountered less often as I follow a swarm of ants about through the forest. However, even Spotted Antbirds that I have observed repeatedly over the years tend to flick and flit or move away, if I try to observe them from closer than five m, more often than do Bicolored Antbirds I have seen equally often.

Tame birds usually are rather fluffed when I approach. At times the head is fluffed, as in tame Bicolored Antbirds. The tail is closed and down, or jiggles in slight flicks. These movements probably are low-intensity signs of mobbing rather than a distinct "tameness" display.

INVESTIGATING

Infrequently, Spotted Antbirds fly toward the observer after (Figure 7, upper) or during a mobbing session or as he watches tame birds quietly. Young birds are more likely to "investigate." The investigating bird peers with one eye and then the other. It extends the head on the neck, extends the neck, and lowers the neck on the body. The bird tilts forward, suggesting that the femora are flexed. Probably some other segments of the legs and wings are flexed or extended more than in the standard posture, but the fluffing of the body hides most such movements. Moreover, I was usually uncertain which leg and wing movements were those of mobbing or panicking and which were ones of investigating. Commonly the investigating bird approaches and retreats (Figure 7, lower) repeatedly, suggesting ambivalent "approach-avoidance" behavior as in chaffinches, *Fringilla coelebs*, and other birds (Rowell, 1961: 59).

REACTIONS OF CAPTIVES

In mist nets or in the hand, a Spotted Antbird kicks, opening its feet at the same time, and immediately flutters its wings or attempts to flutter them. Sometimes it escapes and flies off. If not, it tries kick-fluttering again and again, sometimes with a chip or two. As one removes it, it sometimes whimpers. In the hand it may start pecking or hanging on and twisting with the sharp, hooked bill; but it is not as persistent at this as are the larger antbirds, perhaps because its small bill cannot hurt an enemy much. If one frees the tail and wings, they are spread as the antbird pecks. The back is sometimes spread so that the white patch shows. At times the pecking bird snarls faintly. There may be a brief scream, but Spotted Antbirds are not persistent screamers. Pecking attacks may be related to the display of challenging, and whimpering to the display of cringing, displays described in the section on agonistic behavior.

DISCUSSION

Spotted Antbirds have at least two main types of aggressive reactions to danger from large animals—attack or "cornered rage" (as in the hand) and mobbing—and three main types of escape reactions—passive freezing and active panicking and escape. Two other behavior patterns, tameness and investigating, are probably useful when danger of capture is slight. Some of these patterns are similar to ones that psychologists and neurophysiologists have studied in rats and other mammals: stimulation of the basal nucleus of the amygdala gives rage and ablation gives tameness (Beritoff, 1965); fleeing to avoid a shock (the CAR, or conditioned avoidance response) depends on the cingulate gyrus, and freezing (?) to avoid a shock (CER, or conditioned emotional response) depends on the septum (reviewed in McCleary and

Moore, 1965). Ablation and stimulation experiments suggest that rage, freezing, and fleeing have connections upward to the cortex and downward to the hypothalamus (Brown and Hunsperger, 1963), and that rage areas are medial to escape areas. Åkerman (1966b: 341ff.) reports similar results for pigeons (*Columba livia*): medial stimulation from hypothalamic to sub-cortical (archistriatal) regions gives complete sequences of defensive calling and fighting, while more lateral sites give sequences in which fleeing consistently follows freezing. Mobbing and investigating seem to be unstudied, perhaps because these patterns depend on complex cortical centers more than on lower ones. The observations on Spotted and other antbirds suggest a diversity of predator-related behavior patterns, which could be based on distinct neural regions like those that control some pigeon and mammalian patterns or which could be linked (as freezing to fleeing) in part.

Many ethologists have suggested that conflicting "drives" or "tendencies," such as attack and escape, are major components of behavior patterns or displays (Hinde, 1969: 381; Marler, 1956; Moynihan, 1955; Stokes, 1962; Tinbergen, 1959). One should always question widely accepted hypotheses, however, if there are alternatives. I question the hypothesis of evolution of behavior by means of conflicting drives, because I think the hypothesis of simple ritualization of unitary drives has not been disproven.

The hypothesis of conflicting drives, when it suggests the evolutionary origin of a display, is comparable to the theory that a species arises when two other species hybridize; the hypothesis of unitary drives is rather like the theory that species evolve by divergent evolution. The question in both speciation and the evolution of displays is whether hybridization or divergent evolution is more important as a source, because both patterns of evolution probably occur. According to evolutionary theories, a hybrid animal or display can perhaps outcompete parental types in new or intermediate or changeable environments, especially if competition or danger is not extreme. The mobbing-panicking ambivalence in Spotted Antbirds may be appropriate to a new situation, where the human approaches rather than wanders past such a small bird as big mammals should do. In normal predator reactions, however, ambivalent behavior seems likely to be selected against unless variable behavior confuses the predator. The reaction to a significant predator should be definite, quick, and appropriate rather than ambivalent. Therefore, it seems more likely that predator-related behavior patterns evolve through divergence than by hybridization or Hegelian "thesis plus antithesis gives synthesis."

The hypothesis of conflicting drives also suggests the neurophysiological origin of such displays as mobbing; it says two inputs are necessary for a given output. Preliminary neurophysiological work (Åkerman, 1966b: 344) suggests that protective behavior comes from single brain areas different from

those for defensive threat and aggressive threat; there seems to be no evidence that stimulation of two centers is necessary to produce ordinary predator-avoidance sequences, and hence no evidence that the hypothesis of conflicting drives is correct there.

Given the present state of knowledge, it is almost as difficult to suggest ecological causes for particular predator-related behavior patterns as it is to suggest physiological causes. It is uncertain, for instance, why freezing is rare in Spotted Antbirds but moderately frequent in Bicolored Antbirds. Perhaps Spotted Antbirds freeze infrequently because they usually forage in open undergrowth, near but not in cover, and move about rather actively whenever larger birds exclude them from the best and safest sites at swarms of ants. Freezing would be maladaptive if the predator is likely to have seen the prey moving about. If so, the even more active and less frequently skulking antwrens should show freezing less frequently than do Spotted Antbirds.

Panicking and chipping are unusually frequent in Spotted Antbirds. The chipping of lone birds traveling to nests is particularly difficult to explain. Alarm calls, according to usual theories, warn others of the same species, particularly mates and young. It is possible, however, that sharp and easily located alarm calls also tell the predator that "this is an alarmed bird, one that will be difficult to catch." Keening sounds, present in species related to Spotted Antbirds and in many other species, are probably difficult to locate (Marler, 1955) and warn others of the same species with little risk to the caller. Chipping calls, by contrast, are short and sharp and have plenty of cues (high frequencies for location by differences in wave form at the two ears, plus sudden or staccato on-off for location by time of arrival at the two ears) for localization by any listening predator. I suspect a waiting predator is less likely to attack a bird that chips and shows panicking behavior as it travels through the forest. It may also be that the suddenness and irregular movements of chipping and panicking startle or confuse or irritate a potential predator, in the way the sudden sounds and zigzag flights of Common Snipe startle human hunters. If so, hyperactive and conspicuous chipping could be selected for.

The tendency of pairs of Spotted Antbirds to forage moderate distances apart, rather than together as do pairs of Bicolored Antbirds, may also explain why the latter use ventriloquial keening moderately often in danger situations but the former generally use the easily located chipping. The mate may need to locate the caller if the two are far apart, but keening would not specify the location of the caller. Foraging separately is often necessary for pairs of a subordinate species in poor foraging zones around swarms of ants, while pairs of a dominant species can get food near each other at the rich central zones.

At swarms of army ants, the niches of Spotted Antbirds and Plain-brown Woodcreepers may have something to do with their frequent and at times seemingly hysterical panicking. Larger dominant birds, mainly Bicolored and Ocellated antbirds, take the best and safest foraging sites and leave peripheral and unsafe sites to the Spotted Antbird and the woodcreeper. Being at the edge, the first line against potential predators, would by itself favor quick panicking. Moreover, the dominant birds tend to desert a swarm and let the subordinate ones forage during and after a general panic. Otherwise the dominant birds tend to preempt a swarm of ants by remaining over it even when preening or resting. Selection might favor those subordinate birds that are prone to call the alarm quickly and persistently, even to such things as falling leaves, if they thereby gain a little foraging time at the center of swarms of ants. The usefulness of premature panicking would be limited by habituation of the dominant species, which might ignore the alarm notes of subordinate species that cried "wolf" too often. Bicolored and Ocellated antbirds do ignore many of the isolated *peep* calls of Spotted Antbirds; it takes a nearby or repeated series from the latter to start the first two in their own chipping panics, although they look up or freeze briefly at nearly every chip of a Spotted Antbird.

There are thus at least four likely functions of hyperactive panicking and calling in Spotted Antbirds: warning or teaching others of the species; warning a predator; confusing it; and scaring off dominant competitors.

Mobbing behavior probably has similar functions in Spotted and Bicolored antbirds: irritating or distracting the predatory animal that is near a foraging site or offspring so that it moves away; and warning or teaching other birds of the species: I have elsewhere suggested that chirring mimics the growls of carnivores, and that such harsh bird calls are unpleasant to humans because our ancestors had to live and hunt among birds that could scare away our prey (Willis, 1967: 41). Chirring is relatively easy to locate, even if the high frequencies that allow location by differences in intensity at the two ears are lacking. Mobbing behavior seems to be threatening rather than escape behavior, even when the birds dart to cover or hide behind tree trunks or other vegetation. It is generally directed at predators that are not likely to catch an alarmed adult, such as slow-moving mammals. Rarely other species of antbirds (Willis, 1969a: 369) chirr at slow-moving or waiting hawks; probably chirring is not a "ground-predator" call but a general "disturbance" call. Hawks are generally more dangerous than simply disturbing, of course, and antbirds generally react to them by chipping and panicking rather than by mobbing and chirring.

There are several possible causes for the relative lack of reaction to squeaking noises in Spotted Antbirds and other birds of the undergrowth of tropical

forests. Probably it would be dangerous for a slow-flying bird of the open undergrowth to approach such noises, for forest-falcons and other hawks sometimes approach such noises (N. G. Smith [1969] and Dennis Paulson, pers. comm.). Approach to squeaking seems characteristic of birds of dense cover, birds that have plenty of places to escape. These birds are also more likely to gain by approaching, for they can seldom see predation or learn predators from a distance as can birds of more open habitats. It may also be that birds of bushy or northern habitats, with their larger broods (Lack, 1968: 166–168), tend to mob or approach noises that sound like their own young; such actions might distract a predator that has caught one young, thus protecting others. Robert Ricklefs (pers. comm.) has found that tropical birds of species with broods of four defend their young more vigorously than do ones of species with broods of three or two. Experimental studies, plus comparative analyses of responses to squeaking in different birds and age classes at different seasons, are needed to determine whether such responses serve to protect young, allow learning, or perform some other function.

Other kinds of curiosity also seem more characteristic of birds of dense habitats than of tropical birds of the forest interior. Spotted Antbirds are relatively incurious, tending to flee rather than approach in almost every situation. Only young approach readily. Possibly birds of dense vegetation can afford to investigate an intruder with little danger, given that investigating has some advantage. Hermit Hummingbirds, especially the tiny species of dense undergrowth (*Phaethornis ruber*, *Phaethornis longuemareus*) investigate humans readily inside the forest; they are able to fly away quite rapidly, of course. It may be that taking a close look allows a bird to see if an animal is a predator by allowing it to make an attempt in a situation where the bird has a very good chance to escape.

Probably the relatively constant moderate tameness of Spotted Antbirds, as contrasted with the initial wildness and later lack of fear of Bicolored Antbirds, is related to various features of their ecologies. The Spotted Antbird is small, and probably is less likely to be prey for a large mammal than is the Bicolored Antbird. The even larger Ocellated Antbird is much more wary than is the Bicolored Antbird. However, elsewhere in the class Aves large birds are not always more timid than small ones, so that there may be other reasons for differences in tameness in the three antbirds. The Spotted Antbird nests above the ground rather than in holes in stumps like the Bicolored Antbird, hence is less likely to be trapped in a nest by a mammal or have a mammal rob its nest. The Spotted Antbird is low on the peck order when larger birds are around a swarm of ants, but can get prey if it forages near the observer when wary larger birds retreat. (Subordinate individual Bicolored Antbirds, and the similarly subordinate Lunulated

Antbirds of the upper Amazon—Willis, 1968: 137—also forage near the observer and become tame readily.) However, the Spotted Antbird is a facultative ant-follower and can wander widely around a swarm, so that it need not stay near the observer and become extremely tame the way subordinate Bicolored Antbirds must do. Spotted Antbirds also must forage in rather open sites when large antbirds exclude them from sites near cover, hence must be very alert and wary.

AGONISTIC BEHAVIOR

Agonistic behavior, or the reactions animals show when disputing over space or food or some other resource, includes in Spotted Antbirds submissive displays, escape behavior, aggressive displays, attack behavior, and fighting. In agonistic behavior, as I define the term, the “enemies” are intermediate in size and distance between close but very small or dispersed ones (e.g., ectoparasites) eliciting maintenance behavior and distant but large or very dangerous enemies causing alarm behavior. I realize that some ethologists include a much wider range of displays, such as mobbing behavior, fleeing from predators, etc., within their definitions of agonism. However, I prefer to include these activities under “Reactions to Danger,” above.

SUBMISSIVE AND ESCAPE BEHAVIOR

Submissive behavior is rare in Spotted Antbirds. The most characteristic movement of the display, which may be called “cringing” because it is similar to that display in Bicolored Antbirds (Willis, 1967: 47), is ruffling the feathers of the head. The body feathers are often sleeked, but at times the subordinate bird fluffs the ventral feathers. Generally the white area on the breast is small, almost concealed despite the fluffing. The tail is closed and droops weakly below the normal for the standard posture. The bird may crouch, or flex the legs so that the body is close to the perch. At times the head is down and retracted somewhat, unless the bird is foraging.

At the instant the dominant bird supplants it, the submissive bird may give a weak whimpering call. Sometimes the subordinate whimpers each time it changes perches, even though not attacked. Wandering independent immatures whimper more readily than do young birds or adults, which generally flee without calling or flee giving aggressive displays or displays rather like panicking: One immature female fluttered the tips of her wings as she whimpered.

Escape behavior is well developed in Spotted Antbirds. As a subordinate bird wanders about in a more or less submissive posture, it looks upward or extends the neck upward, peering about as if foraging actively. One bird extended the head up three times as if pecking atop an imaginary leaf (Figure

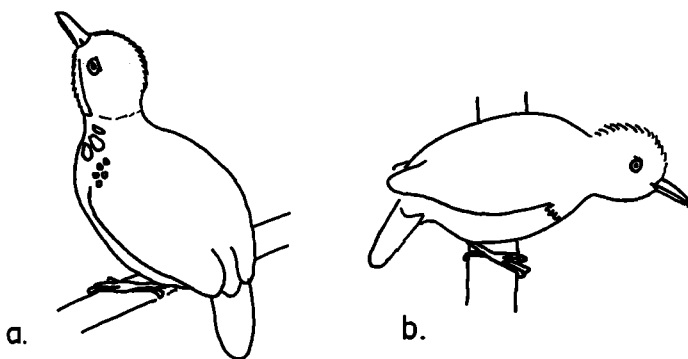


Figure 8. Subordinate Spotted Antbirds, from field sketches. a, First-year male repeatedly pecks in the air over his head when chased by resident male. b, First-year female takes head-down-and-fluffed posture after pursuit by resident female.

8, a). A subordinate bird changes perches very often. It tends to move upward or peripherally if attacked, much as any Spotted Antbird does if larger birds exclude it from a swarm of ants. At times subordinate birds moved over and foraged near me as soon as dominant birds attacked. They may flit the wings and flick the tail, two signs of high but unspecific arousal or excitement. A subordinate bird flips or pivots one way and then the other, or reverses on its perch. Usually it keeps its back toward a dominant bird.

As the dominant bird darts past in a supplanting attack (see under "Wandering Young and Territorial Adults," below), the subordinate bird quickly yaws or pitches or flutters off to the side. If attacked in flight, it evades the direct course of the dominant bird by dropping to a perch or fluttering to one side or the other. The subordinate bird flutters rather conspicuously on the tips of its wings in flight, suggesting that there is some restriction of flight by flexion of the inner segments of the wing, as in "cringe-flying" in Bicolored Antbirds (Willis, 1967: 49). However, I have not noted such extreme mixtures of submissive behavior and flight for subordinate Spotted Antbirds, though they often seem rather fluffed and have retracted necks and feet in flight. The whimpering call is often given in flight, at the moment the dominant bird darts past.

AGGRESSIVE DISPLAYS AND ATTACK BEHAVIOR

The basic aggressive display may be called "challenging," because it is very similar to the display of challenging in Bicolored Antbirds. However, Spotted Antbirds usually exhibit challenging at two "typical intensities" (Morris, 1957) rather than performing many intermediate displays. One kind of challenging is usually associated with bugling, the other kind with

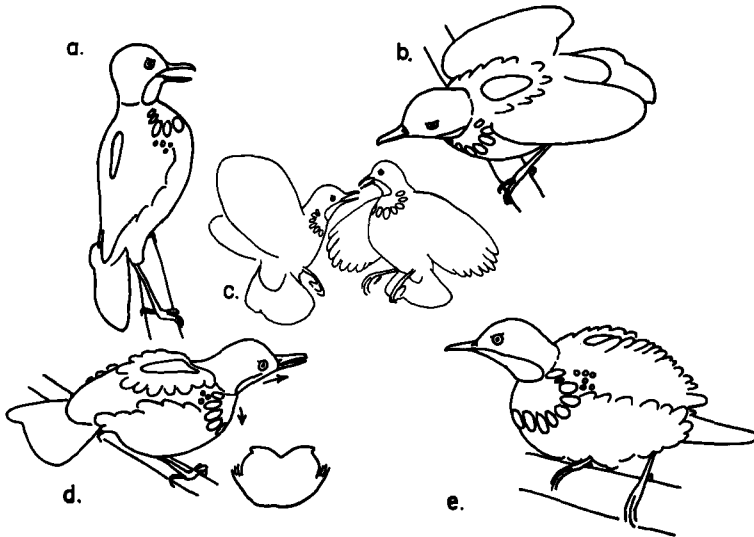


Figure 9. Challenging and fighting among Spotted Antbirds, from field sketches. a, Male in high-challenging posture. b, Male low-challenges at other male below and to his left. c, Two males flutter downward pecking at each other. d, Typical low-challenging posture, showing forward movement of head and downward display of white chest (arrows) and a cross-section of the body (at right, below) to indicate fluffing of the belly feathers and parting of back feathers. e, Male in extremely fluffed low-challenging pose, confronting another challenging male.

snarling. The first kind of challenging is probably an extreme or intense form of the second kind, in which muscles contracted for the second kind are contracted more strongly. It may be called "high-challenging," in contrast to "low-challenging" for the display associated with snarling. The two kinds intergrade, but intermediate displays are not common.

High-challenging is the first and very evanescent response to a new intruder. It involves, besides bugling, a sudden jerk into an upright pose (Figure 9, a). The "rule of angles" (Willis, 1967: 54), that angles between the longitudinal axis of the body and its limbs, head, feathers, etc., are opened for proximal parts and closed for peripheral parts in aggressive display (and vice versa for submissive display) is followed in nearly every movement of high-challenging. In other words, the ends of the limbs and the head (with bill closed) tend to be flexed, while the inner portions of the limbs and the posterior neck are extended for aggressive display. The head is sleeked and the body feathers expanded, so that the white bases of the back feathers are spread into a conspicuous white patch. Probably the bird inflates the body as well as fluffs the feathers. The tail is widely spread, and jerked to the line of the body. I have never seen a Spotted Antbird spread its wings for high-

challenging, but the femora and other joints of the legs are extended. At the same time, the phalanges are flexed and grasp the perch strongly. As the neck is extended, the head is flexed to bring it to horizontal. The eyes are apparently converged as the bird stares at the opponent binocularly, but the movement is not as noticeable as in the larger and bare-faced Bicolored Antbird.

High-challenging seldom lasts more than the first second the challenger sees an intruder. Bugling is rarely repeated even once before the bird drops down into a very spread low-challenging pose and snarls repeatedly at the other. At times high-challenging is repeated briefly as punctuation in a long sequence of low-challenges, but low-challenging is the staple aggressive display of Spotted Antbirds.

Basically, low-challenging (Figure 9, b, d, e) presents to the opponent the white back patch and white breast, outlined below by the necklace of spots that gives the species its name. Low-challenging grades at lowest intensity into the standard posture (but white breast and dark tail are slightly spread) and at highest intensities approaches the high-challenging posture. It is thus a graded display, one that ends at times in postures passed through on the way to higher-intensity postures at other times.

At normally high intensities of low-challenging, the whole chest seems to expand or sway toward the opponent as the bird snarls. In part this is a result of actual expansion of the pectoral region during or for sound production, in part a result of fluffing of the chest feathers, and in part a result of a forward and downward swaying of the whole body from the legs. The head stays in place or is extended forward in a slow-motion jab as the body first sways forward and from side to side with the snarl, but the pectoral region of the body goes down as if pushed from above. The depressing of the pectoral region, besides expanding the white chest and dark necklace, presents the white back patch to the opponent as a frame for the dark head, which is sleeked so that it blocks view of the back rather less than would otherwise be the case. Sometimes the head moves to one side during the snarl, thus showing the white back even more conspicuously. The bird may reverse several times, alternating showing the white breast and back to the opponent. At times the snarling bird pivots on the perch, or sways 60 to 90 degrees, as if waving the white breast and back-spot at the opponent. If the opponent is above the low-challenging bird, it angles the body upward so the spots still point at the opponent.

The ventral feathers, including the belly feathers but not the throat feathers, are fluffed out so that they completely cover the lower edges of the wings (Figure 9, d). However, the white spots on the shoulders of the male remain exposed despite dorsal and ventral fluffing. The tail is spread widely and

raised to the line of the body, or to horizontal. Between snarls the tail is flicked, or rather dropped and raised very slowly and regularly. If the tail is down at the start of a snarl, the bird raises it to horizontal very slowly rather than flicking it up. At times the tail is flicked as fast as once a second, but such birds generally start chipping loudly as if going into the display of panicking.

There is some extension of the neck and arching (flexing) of the head on the neck, but not as much as in high-challenging. Since the body angles downward or is level for most low-challenging, some of the joints of the legs must be flexed. Possibly it is the foot that is flexed to bring the bird swaying forward and downward, but it may be that more proximal joints are flexed in contradiction to the "rule of angles." The body feathers are often so fluffed the legs cannot be seen, but the bird is so close to the perch there must be either little extension of the proximal segments of the legs or some flexion. The wings are sometimes crossed at the tips, suggesting either carpal flexion according to the rule of angles or more proximal flexion in contradiction to the rule.

The low-challenging display shows a conspicuous patch on the back and one on the chest to the opponent at the same time. The Guianan Rufous-throated Antbird shows a patch on the back to the opponent by using a similar low-challenging display (Willis, 1967: 50-52). However, in the case of the Rufous-throated Antbird the legs are splayed and at least the central joints of the legs tend to be slightly extended during low challenging. Whether the level position of its body is caused by femoral flexing or by foot flexing is uncertain; if caused by femoral flexing, the rule of angles is contradicted for a species very close to the Bicolored Antbirds for which it was first proposed.

Attacking Spotted Antbirds generally darted past the opponent so rapidly I could not see any sign of "challenge-flying" as in Bicolored Antbirds. However, the attacker sometimes gave a *twit!* as it flew at the other, suggesting that challenging may be mixed with flying to the attack. Normally the attacker gives a hiss or hiss and snap as it passes the trespasser. Beforehand, the attacker commonly compresses the body to close to the standard pose, or pivots one way and then the other as it stares binocularly at the opponent. There is also commonly a pause in the snarling and displaying for several seconds after an attack. Probably the attack behavior tends to replace challenging display in most cases, rather than the two mixing.

Often the attacking Spotted Antbird flies long distances, up to 10 or 20 m, in supplanting an opponent. Since the attacker goes past the opponent several m in many cases, the opponent often just hops a few cm at the attack. The attacker may then do several more long supplanting flights, forcing the

opponent to skip about and stop foraging or move farther and farther from the ants. The attacking flight seems more a display than a functional supplanting in these cases. However, stroboscopic photography will be necessary to see whether the attacker actually shows certain movements of challenging as well as normal flight movements.

SEQUENCES OF AGONISTIC BEHAVIOR

A moment after a trespassing nonterritorial bird appears at a swarm or elsewhere, a resident bird high-challenges briefly and then low-challenges repeatedly. At the first snarls, the trespasser ruffs its head, flits and flicks, and forages busily as it circles evasively. At times the resident jerks into a high-challenging pose without calling, or darts over and supplants the trespasser once or twice. Then it follows the trespasser about with snarls and occasional supplantings. If the birds are at a swarm of ants, the trespasser may return repeatedly but is driven off each time it returns; it has to forage in poorer peripheral zones. Its feathers become disarranged, for it has little chance to preen. Often I encountered a trespasser wandering forlornly back near the ant bivouac or up to 100 m from the swarm itself. Such birds sometimes moved in as I arrived and foraged actively for a few minutes during the commotion caused by my arrival, but were expelled when the residents returned.

Sometimes subordinate birds open the white back and go into weak low-challenging poses, with or without snarling, before they go into submissive displays or escape behavior.

After a time a resident bird supplants a trespasser without snarling or challenging, but even in the nonbreeding months of December to April there is seldom as much tolerance of a trespasser as in Bicolored Antbirds. Usually the trespasser must move out of sight of the resident bird to avoid occasional supplantings from distances of 5 to 20 m. However, quiet trespassers are not pursued far, and sometimes forage at different forks of an ant swarm or behind cover.

Feuding territorial Spotted Antbird males commonly open a sequence of agonistic displays with reciprocal high-challenges, then drop into low-challenges and snarl at each other repeatedly. At times a bird jerks up into high-challenges, with or without bugling notes, between low-challenges. If two or more territorial Spotted Antbirds feud and neither gives way, white-backed and challenging birds swirl about like snowflakes. Some of the feuding birds repeat their snarls so intensely and rapidly and puff out so strongly that one expects them to explode at any moment. A bird may snarl as rapidly as once per two or three seconds, although the usual rate is one every five seconds or so. One bird hisses as it supplants another, both snarl back and forth, and the first bird supplants the second again. (Johnson [1954:

56] mistook white-backed feuding for "courting" behavior.) Submissive behavior, especially whimpering as the victor attacks, sometimes occurs briefly as the defeated bird flees. Outbreaks of chipping or songs sometimes end the dispute.

Usually one female disputes with another and one male with another in feuds, but at times there are supplantings between the sexes. Once an excited male supplanted his own mate during a dispute. Females generally display and attack each other less strongly than do males of the same or similar age classes, but otherwise dispute and sing across territorial boundaries much as do males.

Fights and reverse supplantings are rare, even in the most heated and prolonged disputes between rival Spotted Antbirds. I saw three brief scuffles when birds tried to supplant trespassers and the latter fought back. Once two males did a fluttering fight down from four m above the ground, pecking at each other but not touching (Figure 9, c). On another occasion a fight on the ground ended in a dominance reversal, the male from one side gaining dominance at a spot near his territory and thus incorporating it into his area.

Normally birds at or near territorial boundaries challenge each other briefly or flit their wings, flick their spread tails, and drift apart to sing back and forth. The strongest displays and attacks come from a male well within his territory, especially if a trespasser gives aggressive or threat displays over a swarm of ants.

Agonistic displays seldom last long away from swarms or after one pair deserts. However, pairs or individuals sometimes sing back and forth very loudly for several minutes. Distant songs of a trespasser often start the resident male moving toward it. In one case where I was very close to a resident pair when a distant bird sang, I noted that the resident male mixed *twit!* notes with his chirping to his mate, but did not go into the high-challenging pose that normally accompanies the note. Both of the pair moved toward the other bird, and a feud was soon going. Young birds that sing quickly attract adult birds, which drive them off.

When I use recorded songs to look for pairs, the white-backed male often comes up rapidly and silently, spread tail flicking, and looks about; he starts loud-singing after the tape recording stops. If the playback continues, he flies over the recorder and looks down with faint snarls but stays in weak low-challenging poses rather than going into strong display. He pivots one way and then the other, flits the wings and flicks the tail, darts from one perch to another, and in general seems agitated although wary of both the observer and the recorder. The female may appear and sing if he starts loud songs, but she is generally less excited and responsive. Recorded songs never attracted a female when her mate was absent.

During prolonged disputes there are often activities other than simple agonistic behavior. Commonly, if the observer is close, one or more birds may burst into chirring even if they had been ignoring him before the dispute. At other times, especially in prolonged disputes, one or more birds burst into persistent chipping, flitting, and flicking as if panicking. At times a dominant bird went into chipping hysteria when a subordinate bird stayed instead of fleeing. Sudden attacks on and pounding of insects by the antbirds seemed more violent and conspicuous when these activities interrupted disputes than when they occurred while the birds were foraging uninterruptedly. Once a dominant male regurgitated insect fragments before he attacked a subordinate bird. A dominant female did the same on another occasion. One dominant male scratched over the wing after an outburst upon the arrival of a new female. The latter stopped chipping and started chirping to him.

Subordinate birds often billwipe, flit the wings and flick the closed tail, point the bill toward the toes while rotating the head on the neck so one eye is toward the other bird ("toe-looking"), and perform other activities. One dominant bird, white-backed, approached an opponent but then closed the back patch and billwiped; a minute later the first bird started challenging displays. Another dominant male, faced with a subordinate that was busily eating prey and ignoring him (except for chipping notes) went into a low-challenging display and gave a faint bugle, then started chipping and reversing, looked down at the trespasser, and flew ahead to the ants as the trespasser retreated. Energetic preening sessions often interrupt disputes.

Foraging often interrupts prolonged disputes over swarms of ants, sometimes in a periodic manner that suggests the bout structure of many animal activities (Marler and Hamilton, 1966: 153). The dominant bird grabs an insect and flails it energetically, while the other bird moves off and forages for a time. A period of silent foraging ends in another snarling and supplanting outburst. Periods of foraging, challenging outbursts, and chases may follow each other all morning if the trespasser does not desert.

DISCUSSION

For over a decade, Tinbergen and other ethologists have suggested that threat and appeasement behavior (i.e., aggressive and submissive displays), as contrasted to fighting and fleeing and attacking, arise mainly when the animal faces stimuli that evoke attack and escape behavior at the same time. For support, Tinbergen (1959: 34) notes that a gull on its territory commonly attacks without display and the trespasser flees without display, while two gulls at a boundary commonly display strongly. Neither Spotted Antbirds nor Bicolored Antbirds (Willis, 1967: 97) show this kind of behavior. At the boundary, there is very little cringing or challenging display and much dis-

placement behavior in Bicolored Antbirds. Song disputes are more common at the boundary in Spotted Antbirds. Challenging occurs at boundaries in Spotted Antbirds but is strongest when the trespasser is well inside the territory, and cringing is strongest from the trespasser when it stays rather than fleeing.

One of Tinbergen's students, Blurton Jones (1968: 147), found that captive Great Tits (*Parus major*) do react with some types of threat to alarming and attack-provoking stimuli presented at the same time. This favors the theory that conflicting tendencies of attack and escape produce threat. However, Blurton Jones' birds also threatened to attack-provoking stimuli alone, especially if distracting food in another corner of the cage or wire screens prevented simple attack. He proposes that anything that interferes with the attack of an attack-provoking stimulus may elicit threat to it. Escape tendency is thus not necessary to threat, even if it is one of several things that can interfere with attack and make more advantageous the alternate behavior of threat.

Neurophysiological evidence also raises doubts as to the necessity of escape tendencies in threat behavior. Von Holst and von St. Paul (1963) and Akerman (1966a) found that single-electrode stimulation of "threat" sites in chicken and pigeon brains induced attacking and threat behavior. Concurrent stimulation of sites that induce escape behavior interfered with threat. Possibly the neurophysiologists found only output pathways of attack and escape rather than the input pathways suggested by Tinbergen's theory. However, their evidence taken at face value suggests that threat is part of attack pathways and that escape interferes with it.

Whether threat is a substitute for attack as Blurton Jones suggests, or whether it is part of attack as the neurophysiological evidence suggests, one no longer has to accept Tinbergen's early theory that escape must balance attack to give threat. Threat need not occur only at places where attack tendencies equal escape tendencies, as at the boundary between territories; it can occur anywhere that it is more advantageous than simple attack would be. This allows one to see Tinbergen's observations on gulls and mine on antbirds as complementary rather than discordant. Perhaps gulls attack in the center of their territories because they have small and safe territories from which they can chase intruders with little effort or danger. Antbirds might threaten vigorously and attack for short distances because chasing for long distances consumes time and energy in a large territory and is dangerous in the tropical forest, yet a challenger near the center of a large territory or a swarm of ants could usurp much of the territory or swarm. At the boundaries, gulls perhaps threaten because small changes are relatively important in a small territory but attacks are prevented by dangerously strong resistance. Bicolored Antbirds

do not threaten, and Spotted Antbirds only threaten a little before briefly singing back and forth, because small changes in a large territory would not be enough to offset the risks of predation and loss of time and energy involved in boundary disputes. Moreover, gulls set up territories rapidly while antbirds hold territories for long periods; the latter situation probably requires less threat per unit time and reduces the rewards of persistent agonistic behavior. The gull and antbird studies add to experimental evidence that threat is an activity that can be used where it is ecologically advantageous, rather than one that is necessarily linked to boundaries or to other places where escape tendencies balance attack tendencies.

Some of the behavior patterns of Spotted Antbirds at boundaries and in intervals between disputes, especially preening and billwiping and perhaps even unusually conspicuous foraging, fall in the class of "displacement activities." These activities commonly arise when a bird is changing from one activity to another, and hence seem more likely to be due to "conflicts" of two or more stimuli or tendencies than does normal agonistic behavior.

There is currently much discussion whether such activities are actually relevant in situations where they seem dilemma-generated or out of context. Many ethologists feel that some displays were originally displacement activities; if so, there should be displacement activities that are in the process of becoming displays. Evolutionarily, it seems unlikely that displacement activities will be favored unless they become relevant to communication or to some other function. Kruijt (1964) and others suggest that they may actually be relevant in such agonistic encounters, in the sense that different displacement activities may be performed at different frequencies by subordinate and dominant birds and thus communicate agonistic arousal or status. Smith (1966: 16) suggests that in flycatchers certain activities and calls communicate tendency to take wing or not to take wing and thus are relevant even though they often seem out of place.

For Spotted Antbirds, I have the general impression that dominant birds are more likely to go into chipping and hysterical flitting-flicking or into mobbing, and subordinate ones to perform billwiping, preening, toe-looking, and the like. These activities could be part of the general spectrum of agonistic displays or on the way to incorporation in that spectrum. I have described most of these activities elsewhere because they are primarily used in other contexts. Toe-looking, the only exception, is a very infrequent and indistinct pattern in Spotted Antbirds. It is better developed in species of antbirds that display bright-colored bare faces by it, often as an "eyespot-display" reaction to the observer in mobbing or investigating (Willis, 1969*b*: 378).

Tinbergen's original theory (1940) that displacement activities arise from high arousal or a central excitatory state, combined with van Iersel and Bol's (1958: 85) theory that two effectively equal activities mutually inhibit

each other and permit the appearance of a third (the "disinhibition" hypothesis), may help considerably in explaining the hysterical chipping that appears when two Spotted Antbirds terminate a vigorous dispute and move apart or resume feeding. As a fight ends, a combatant presumably changes from attack motivation to some other motivation, such as flight or feeding; and at the moment when the old and new motivations are equal a third motivation, such as for chipping, may temporarily be released, or disinhibited, if the bird is excited enough or has the third motivation anyway.

REPRODUCTIVE BEHAVIOR

Courtship behavior, behavior used in pair formation or in maintaining the pair bond between mates, involves four main activities in Spotted Antbirds: wandering and loud-singing; chirping and "flirting"; courtship feeding; and mutual grooming. Pair formation will be discussed after the description of these main activities.

SINGING AND WANDERING

A male or female that has lost its mate, or a young male that has successfully settled in an area by challenging and singing at neighboring males until they recognize his claim, sings rather loudly and frequently as it travels about its area. Young females and males, by contrast, wander without singing. A male or female also sings loudly if one captures its mate in a mist net or if the mate disappears for some time. If the birds of the pair are incubating or caring for young, there is almost never such behavior. Infrequently, but more often than do mated birds, an unmated bird wanders far off its territory (in Figure 19, for instance, male YBXR wandered far from his territory only during 1965, soon after he had lost his mate), but at such times it sings little. Neighboring birds react with loud-singing, and song or challenging duels may send the wanderer back to its own area.

CHIRPING AND FLIRTING

The first reaction of a lone male to a new female or vice versa is usually a bugle or a snarl and brief challenging, with white back showing. Then the unmated male or female starts chirping and ruffling the head as it moves near the newcomer, rather than chasing it off. Soon the male alternates series of faint-songs with his chirps as "serpentine-singing," and the female answers with chirps. The body seems somewhat fluffed and the legs splayed. Together, chirping or serpentine-singing and the new posture may be called the display of "flirting."

Flirting and foraging alternate as the unmated bird stays near the new one or wanders near it. Flirting rarely seems to interfere with foraging. Brief

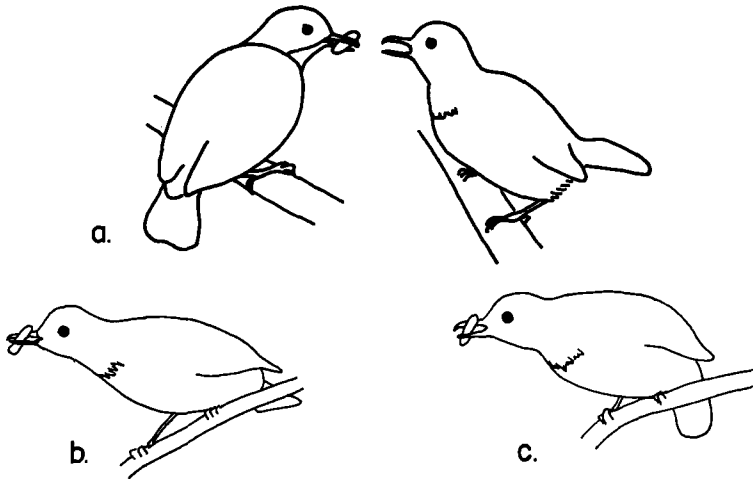


Figure 10. Courtship feedings by Spotted Antbirds, from field sketches. a, Male feeds female, who squats and raises tail as she gapes. b, Female chewing prey after feeding, in crouched posture with neck rather extended and tail up. c, Female chewing prey, her tail down.

snarls and other signs of agonistic behavior quickly disappear. The male rather often does "displacement activities," such as toe-looking and billwiping, but none seem ritualized. Rather frequent flicking the tail and flitting the wings also suggest generalized excitement rather than definite courtship displays.

COURTSHIP FEEDING

As in Bicolored and other antbirds I have studied, the male Spotted Antbird feeds the female. After chewing and preparing prey, he starts rapid chirping and serpentine-singing. The male wanders about, chewing the prey. When the female answers with a brief faint-song or chirping or he sees her, he flies toward her. If the female is distant, she sings loudly in answer to his loud-songs. In one case a single song from the female was enough to bring the male to her through the forest from at least 50 m away. As he flutters up and feeds her, his serpentine-songs run into a very rapid series of chirps at about five per second. Her chirps, if any, come at two per second or less. At times the watching female darts to the male as soon as he starts chirping or serpentine-singing with food in his beak. One female looked at her mate as he captured prey, then looked at the rocks below her again; only when he gave three chirps did she dart to him for the feeding.

Both birds tend to extend the legs for a feeding, but the toes are not clamped. The legs are splayed. The female gapes as she stretches toward the male. During the feeding, the male has his head somewhat ruffed, but his

body is sleeked. The female ruffs her head as she takes the food, but she is rather sleeked (Figure 10). Her tail rises to the horizontal and is slightly spread. Both birds may flit the wings if the feeding is slow or difficult. Both birds stretch their necks in passing the food, or the female may grab it as the male recoils slightly.

There are sometimes signs of hesitancy or agonistic behavior during a feeding. One unmated male snarled and challenged the mate of a neighboring male while that male was elsewhere with a fledgling. The unmated male tried to feed her twice, but his attacks with white back patch showing at the last moments drove her away both times. In his abortive attempts to feed her, he gave chirping notes that graded to chipping ones, and made agitated flitting and flicking and back-and-forth movements. Once a male pecked at a female after feeding her, and she fluttered away. One female pecked so rapidly that the male fluttered away; a second, less violent peck gained her the food. On one occasion, mates had a tug-of-war back and forth before the male let the female take the food. On another the female tried to cling near him and peck it from his beak; he flew off 2 m and she fluffed and sat down; when he fluttered off and serpentine-sang she merely sat and gave a few faint-songs. On still another occasion the female hopped repeatedly toward her mate, who sidestepped each time; he was giving some faint snarls with his chirps, perhaps because I was near. At times one or both birds have the white back showing.

Normally the female crouches, head down, and eats the prey as the male flutters away after a feeding. She may hop away from him before eating, especially if she sidled to him and stretched his way rather than allowing his approach to within one or two body widths. She may flutter off, her crest still raised, and wipe her beak after the feeding. In one case she froze, head low and extended on the neck, as he flitted beside her; she ate the prey only when he left, then lifted her head and fluffed her body to the normal resting pose.

After a feeding, the male sometimes sits near the female or nibbles at her beak. Grooming followed such feeding-sitting on some occasions. The two birds sometimes stand near each other for a moment, facing in the same or different directions. Both or one may champ the beak or flit the wings and flick the tail.

Frequent courtship feeding is the rule as a male gains a new mate and in the days before a nesting. If there are no competitors at a swarm of ants, the male feeds the female so frequently that she scarcely forages for herself. She rests and preens in cover near the swarm while he works actively. At times the female is so well fed that she will scarcely take food. In one such case, a male chirped rapidly as he flew up to the resting female, but she sat and looked at him. Finally she accepted the food, a cricket, lackadaisically as he fluttered

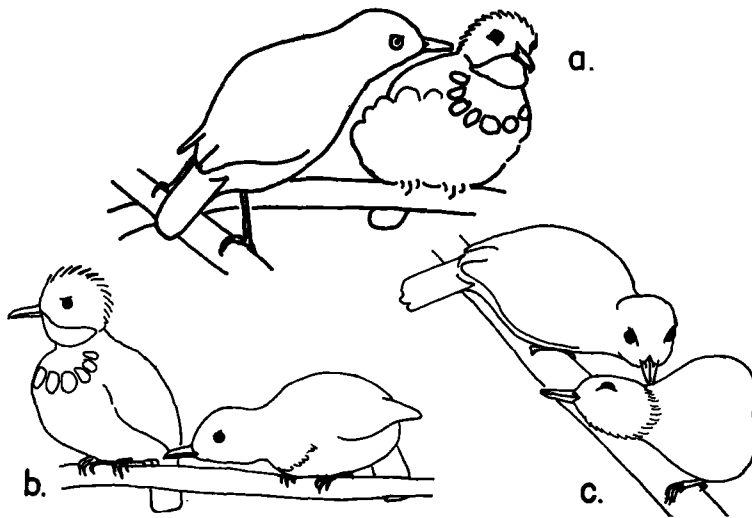


Figure 11. Mutual grooming by Spotted Antbirds, from field sketches. a, Female stretches to preen male, who tilts and ruffs his head. b, Female nibbles bands of male, but he still ruffs the head. c, Female preening her female offspring, who tilts the head very strongly.

the tips of his wings and chirped rapidly. As he returned to the ants, she shook off and ate a leg of the cricket, but the body fell to the ground; she looked down at it but did not go down and pick it up. On another occasion, a female dropped the prey four times and the male flew down, got it, and gave it to her again until she finally ate it on the fifth attempt. However, there are usually competing larger antbirds at swarms of ants, so that the female Spotted Antbird ordinarily has to forage for herself more than do female Bicolored or Ocellated Antbirds similarly close to nesting.

I have never seen courtship feeding after incubation starts or before two fledglings are starting to feed themselves, at about 30 days out of the nest. If there is only one fledgling, cared for by the female, the male occasionally feeds his mate soon after the fledgling leaves (see below).

GROOMING

Flirting or courtship-feeding birds, especially ones mated a long time, occasionally come up to each other and start mutual grooming or "allopreening" (Cullen, 1963) when they meet in preening or nesting situations rather than foraging situations. Typically one bird hops or flutters up beside the other, which immediately ruffs the head and arches it on the neck (i.e., raises the neck on the body, flexes the joints of the neck or retracts the head, and flexes the head on the neck) so the bill points somewhat downward. In this

“invitation-to-grooming” posture the head may be angled away from the mate, which begins to peck and nibble at its bill or at feathers of the crown or face and throat as if removing and eating tiny particles. The head is normally the only part of the body groomed. Once a female pecked at the undertail coverts of her mate, who flew off. Bands on the legs sometimes get pecks (Figure 11, b). Often one or both birds champ the beak busily between nibbling sessions.

Rather frozen stances are characteristic of birds being groomed. Commonly the bird being groomed is sitting or sits more closely each time the groomer nibbles it. The groomed bird may sit with tail and head down, like a towel frozen over a clothesline. At other times it has its body fluffed out and the tail down and closed, in the posture normal for self-preening. It often tilts the head more and more at each peck of the groomer, freezing in each new position like a man in a barber's chair. Oddly, the groomed bird freezes its head in position and ruffs the crown whether the mate is pecking its head or some other part of the body.

Once a female sidestepped, reversed, and ruffed her head as the male flew to a position beside her. He looked about, chirped repeatedly, and hopped to preen only a centimeter from her. She looked down, her head fluffing diminishing slowly. When he fluttered 0.5 meter away, she twice scratched her head over the wing, did a right side stretch, and started preening again as if suddenly released from forced immobility.

The bird doing the grooming extends the joints of the legs and stretches the neck and head (extends the head on the neck, extends the joints of the neck, and lowers the neck on the body). Often the head angles upward from the neck rather strongly. Since the body of the groomer is angled upward, the femora are probably extended. The legs of the groomer are splayed, another indication that the femora are extended. The other joints of the legs often seem to be extended, but I am uncertain whether the feet and phalanges are normally flexed or extended. The groomer ruffs the crown up and down, but the body stays rather sleeked and the back patch seldom shows. If the groomer is also sitting and loafing, the body is fluffed as is normal during resting. The tail is closed and down as in the standard posture.

At times one bird grooms the other then is groomed in return. The invitation-to-groom posture sometimes comes from the approaching bird rather than from the sitting bird. Grooming does not always follow the invitation posture. Once both birds went into the head-ruffed, neck-arched grooming posture and froze, so that neither groomed the other. Once a female ruffed her head and hopped to a position beside her mate, but she flew off when he continued to preen.

As is sometimes the case without grooming, the two may sit and preen (autopreen) next to each other after or before grooming. At times the two were so close that one of the pair hit the other with the tail when it reversed

directions. On one occasion the female did a full right stretch and bumped the male off his perch with her wing. More often, however, one bird hops a few centimeters away from the other before preening, and preening birds are farther apart than grooming birds. Some field notes follow.

In one typical sequence, the pair ignored the peeping of their nearly grown juvenile as the adult female twice flew up to the distance of one body width or less from the male. The two stood together each time, preening a little. The second time the female turned and nibbled at the head of the male. She then jabbed strongly, but he just ruffed his head and pointed his bill down, freezing with head somewhat tilted away from her and lowered. When she, in her lower and half-sitting position, stopped nibbling his lower face he returned to a normal pose, then nibbled her head a few times. She started preening the wing toward him, brushing him almost every time she extended it. He started to preen, but after taking a few blows of her wing he flutter-hopped over her to her right side. They stood facing different directions instead of the same way after he hopped back closer, to one body width from her. Both resumed preening; but the male had gained little, because his mate now preened her right wing, hitting him with it as often as she had been hitting him with her left wing before.

At times the male or female hops over the back of the other, which ducks the body and ruffs the head. Both chirp frequently during such leaps and during grooming.

Occasionally a bird grooms a young bird, so the behavior pattern is not limited to courtship. Once I saw mutual grooming between mates after I flushed a male off the nest, but in general there is no grooming when birds have eggs or nestlings to care for.

PAIR FORMATION

Pairs were always formed when one member was on territory. No wandering bird held a mate, although wandering males chirp and feed females at times and occasionally travel with them for a few days.

A territorial male that has lost his mate or is waiting for his first mate sings persistently and loudly, then flirts with and feeds any trespassing female. Pair formation is accomplished by a few days of repeated courtship feeding, flirting, and association of the two birds.

Normally the new mate is a wandering young female, six to twelve months old, or a wandering old female that has lost her mate and deserted his territory. In several cases, females under six months old chirped and were fed by unmated males actively seeking mates, but did not form permanent pair bonds. Once a male seeking a mate pushed such a young female off her perch with his breast as he chirped rapidly, but she scarcely reacted except to eat his gift. In general, females under six months of age act like juveniles when courted.

A female that loses her mate generally wanders off the territory in a few days unless she pairs quickly with a wandering male. One such female flirted

with a wandering male by serpentine-singing and flying near him when he captured an insect.

Mated birds sometimes court birds of the opposite sex to which they are not mated. Males whose mates are on the nest generally challenge and chase trespassing females the first few minutes, but chirp and forage near them if they evade attacks and persistently chirp nearby. Once a trespassing mated female managed to steal a spider from a serpentine-singing neighboring mated male. In another case, two males exchanged mates. A male that has lost his mate occasionally steals the mate of one of his neighbors. In all such cases, the male presumably courts an already mated bird.

There was no case of polygyny or of a wandering female displacing an adult mated female, presumably because the mated female normally drives any new female away or because a male with a mate is usually antagonistic. One immature female repeatedly tried to take food from a mated male, but he jumped into more and more upright and challenging poses each time she grabbed; he did not attack her, but flew over and fed his own mate. Another wandering female chirped at a challenging male and kept coming to him, but the resident female challenged and started the resident male's challenges anew; both drove off the wandering female.

A mated female may tolerate a trespassing male rather readily, as long as neither her mate nor his mate is present. In fact, a trespassing male often seems dominant if the resident female is alone. She keeps out of his way, and the two chirp back and forth as do pairing birds. Even wandering males, without mates or territories, sometimes take the best sites at swarms of ants and restrict resident females to poorer sites. One preening resident male went into an upright pose but did not call when a wandering male came up and displaced the resident female. The resident male then returned to preening, leaving his mate to shift for herself as the wandering male took the best foraging sites.

A wandering male often uses chirping or serpentine-singing when he moves in near a resident or wandering female. Wandering females often chirp as they move in near resident or wandering males. At times the wandering males or females are driven away, but often the chirping causes the aggressor to compress the body feathers and return to foraging or even start chirping.

After a few days of pair formation, the paired birds wander together unless incubation or other duties interrupt. At times the two forage 10 to 30 m apart. If disturbed by a human or a hawk, a member of a pair is likely to chirp or sing until the mate answers with similar notes or faint-songs; then the two move together. The two may loud-sing to each other as they wander separately in the morning as if looking for a swarm of ants, and in the evening as they wander before bathing or roosting. If they are close together, they chirp or faint-sing now and then. If one bird finds a swarm, it stops singing

and the other circles in to it, singing until there is an answer from the foraging bird. Both chirp as the mate moves in and forages nearby. One female fluttered the tips of her wings briefly, like a young bird, as she flew to the limb beside her mate. At times the male starts rapid chirping or amorous serpentine-singing as the female approaches, even though he does not have food for her.

At times there are faint snarls among the chirping notes when the pair work less than a meter apart, but supplantings are rare. One male chipped and snarled at a new mate for a minute after she had panicked and chipped; when she chirped, he gradually subsided, looked about, and scratched his head over his wing; later he fed her. The male of a pair with young in the nest chirped faintly and frequently and uttered *beeee'tree* serpentine-songs as both foraged busily; he supplanted her twice in sallies to the ground. She ruffed her head and froze on the first supplanting. Later they perched a body width apart and chirped busily, both in ruffed-headed and slow-moving poses as in grooming behavior. One other male supplanted his mate when she did a sallying catch four m above the ground. She froze, flitting her wings and flicking her tail. Finally she started tentative chirps and he chirped back. Periodic snarls and supplantings are more common if the two have other mates.

One female flitted her wings and snarled faintly as her mate worked 0.6 m from her. Flitting the wings and flicking the tail are often reactions to a mate within 0.3 m, although in Hediger's terms (1950: 111) Spotted Antbirds are almost "contact" birds compared to antagonistic "distance" birds like Bicolored Antbirds. The latter supplant mates closer than a meter away, and preen more than a body width apart, but Spotted Antbirds tolerate the mates so readily it is difficult to tell whether males or females are dominant.

In the few cases where a Spotted Antbird did retreat as its mate came up, the male was always the displacer or supplanter. Normally the female and male wander more than a meter apart when foraging, so that the two seldom go for the same prey item or compete for the same perch.

COPULATION

Courtship feeding always precedes copulation in Spotted Antbirds. After a number of courtship feedings in the course of a few days, the female no longer flees with the food as soon as she grabs it from the male's beak. As she chews it with head down beside the male, he tries a quick hop to her back. He is chirping rapidly, as he has been since he gave her the food. At first she hops away or leaves whenever he tries to hop on her. His chirps come less and less rapidly. He looks at her, then returns to foraging. Later she squats, with legs splayed and the feathers of the belly lowered, even as she takes the food (Figure 10, a). Finally she stays, and copulation ensues.

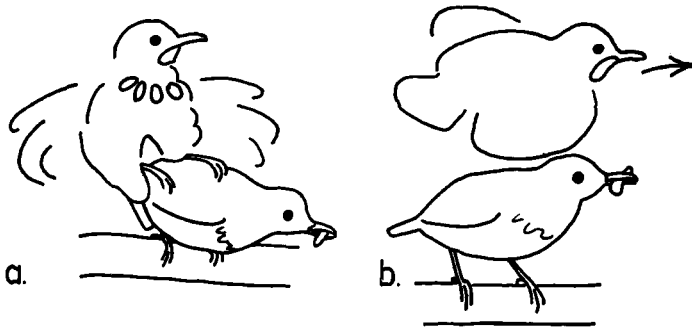


Figure 12. Copulation by Spotted Antbirds, from field sketches. a, Male flutters wings as female holds food that he gave her. b, Male flutters off as female rises, food still in her beak.

The female crouches on the limb and holds her head low, the food still in her beak. The male balances on her back, sitting on his somewhat diverging tarsi and on his under-tail coverts (Figure 12, a). At first he shifts the feet back and forth. His feet are at the sides of her back, just behind and above the insertions of her wings, apparently grasping her back feathers. He is in a somewhat upright position, his head and body rather strongly fluffed. He has the neck very strongly retracted, the head arched on the neck, and the neck lifted on the body. These three movements, at lesser intensity, are characteristic of nearly all the courtship encounters in this species. As his tail goes to one side of hers, he tilts backward so that the cloacae come into contact. His ventral apterium is open, as he is fluffed very strongly, and apparently is inflated also. He usually flutters the wings rapidly and regularly, perhaps for balance. The fluttering is somewhat peculiar, suggesting that certain joints of the wings are extended or flexed more than in normal flight. If the wings are flexed in the same way as the legs, the carpal and perhaps ulnar sections should be extended and the humeral section flexed, but this is uncertain. Most of the display of the wings is in the distal sections, however.

As the two copulate, the chirps of the male deepen and slow to a *pip-pip-pip* series at three or four notes per second.

After copulation, the fluffed male (Figure 12, b) sometimes flutters off to a perch nearby. His flight is still fluttery, suggesting some flexion of sections of the wing as a holdover from the copulatory activities. The female, still crouched, finishes chewing and gulping the prey. At other times the female slips out from under the male, sometimes so rapidly copulation was probably not complete. In one such case the female did not rotate her tail so his tail could go past hers, though he sat on her back and fluttered his wings for 10 seconds as he moved his tail one way and then the other. In another incomplete

copulation, the male did not flutter his wings; after the female slipped out from under him he wiped his beak. The male often perches, fluffed and head retracted, on the perch the female was on. She works intently with the food and ignores him. Preening sessions sometimes follow copulation. The male is more likely to resume foraging and the female to preen.

THE NEST SITE AND NEST

Spotted Antbirds serpentine-sing and wander, flicking the spread tail frequently, when searching for nest sites. At times one alights on the edge of an old nest and looks down into it. One male fed his mate and then went to an old nest and sat in it several times, turning one way and then the other. Another male, apparently unmated, also visited an old nest and flicked his tail as he looked down into it; he gave serpentine-songs, then chirped, but soon rejoined the bird flock he had been with. One female visited an old Slaty Antshrike nest and pecked at loose strands, perhaps searching for nest material. Skutch (1946: 18–19) has noted that other antbirds are interested in old nests, and that their visits to nests of other species may lead to ornithologists' mistaking ownership of antbird nests.

One pair with a successful nest (young left 10 August 1969) had small young in the same nest 13 October but lost them by 21 October, then laid eggs there April 29–May 1, 1970, but lost young between 20 and 27 May (observations courtesy of Robin Foster). One pair nested in exactly the same site as had a completely different pair the preceding year. Thus, old nests or nest sites may be used at times.

Usually the bulky, leaf-decorated nest cup (Figure 13) is suspended between two small diverging or parallel twigs of a slender sapling. Although the vertical sapling is normally not strongly incorporated into the side of the nest, the nest is only rarely placed in a fork or between twigs more than a few centimeters out from some vertical support. Perhaps horizontal twigs farther out bend too much with the weight of the nest, especially the thin and weak twigs one usually finds low in the forest.

Nests are usually in fairly sparse undergrowth, with clear views in every direction. However, at times the nest is near patches of shrubs or near a sharp slope of a gully or stream, so that visibility is blocked on one or two sides or the nest is hard to see against the ground.

The nest of the Spotted Antbird is, next to the nest of the common Slaty Antshrike, one of those most frequently seen in the undergrowth on Barro Colorado. The former nest is a thick and bulky cup of rhizomorphs ("fungal horsehair") with pendent or plastered dead leaves. It is rather irregular outside, and looks more like a pile of debris than does the thin and neat cup of the antshrike. Perhaps the pendants and plastered leaves help conceal the nest of the Spotted Antbird somewhat, but it is rather conspicuous to a



Figure 13. Nest of Spotted Antbird.

human. Internally, it is a neat cup lined with black rhizomorphs. Much of the body of the nest is made of black rhizomorphs and other slender strands. Three nests that Skutch (1946: 19) found on Barro Colorado were rather similar, although one nest was composed mainly of slender pistillate inflorescences of *Myriocarpa izabalensis* (Urticaceae) and included few rhizomorphs. He records one nest as having an inner diameter of about 6.3 cm and a depth of 7.0 cm.

The 120 nests I had located by 1 September 1970 were 0.3 to 1.7 m above the ground; the median height (for 113 nests, counted as 115 because one was used three times) was 0.7 m, or somewhat above the usual foraging height. The mean height for these 115 nestings was 0.78 m; the mode was 0.6 m (20 nestings). Four of the five nests above 1.4 m were on steep ground or above gullies.

BUILDING THE NEST

Both male and female build the nest. The male did more work than did the female at the nine nests at which I watched construction, by 48 visits to 16 (3 to 1). At several nests only the male visited during the brief periods I watched. At one nest where I watched construction from a blind on 10 July 1966, the ratio during 113 minutes of watching was 21 visits by the male to 10 by the female. Skutch (1946: 19) recorded 19 visits by the male and 13 by the female during two hours he watched from a blind. He noted that the male seemed more active in shaping the nest. The female generally is more disturbed than the male when one watches without a blind. But both birds chip, flick their tails and flit the wings, and hesitate before going to the nest if the observer is in plain sight. Some birds started faint snarls as they flitted and flicked near me and the nest. From behind a tree at the above-

mentioned nest on 9 July 1966 I watched both the nest and the birds attending a passing ant swarm and the female made only 4 visits to the male's 11. Probably the ratio of visits by the male to those by the more timid female is more likely to be 2 to 1 or less rather than 3 to 1 when the birds are not disturbed.

The one pair watched from a blind generally worked without alarm notes, but the male often approached with a series of chipping notes. Alarm calls of a distant Black-striped Woodcreeper and Plain-brown Woodcreeper caused the female to crouch on the nest and look up nervously. Later the male chipped as he approached and left and was excited because of the continuing alarm calls of a Black-striped Woodcreeper. However, as the woodcreeper continued calling the pair worked even more quietly than before. After the woodcreeper had stopped, the female Spotted Antbird gave a few chipping notes as she worked. Other birds, watched without a blind, sometimes chipped as they worked on the nests.

A female Chestnut-backed Antbird, "pounding" her tail (see p. 10), flew to a point below the nest and stared up at the male Spotted Antbird as he worked there. She hopped up the sapling and pecked at the male; he spread out his body and wings and fluttered the wings as he pecked back. She dropped to the ground as her mate came up; both pounded their tails as the male Spotted Antbird froze on the nest. The female then hopped up again and drove the male Spotted Antbird off the nest in a fluttering fight. Four minutes later the pair of Chestnut-backed Antbirds, now 5–7 m from the nest and foraging, ignored the returning male Spotted Antbird. As is discussed later, antagonism of Chestnut-backed to Spotted Antbirds both at and away from swarms is probably related to foraging competition, as the Chestnut-backed Antbird uses different nest sites (Skutch, 1969).

Usually birds building a nest tug and flutter as they pull off rhizomorphs and other thin strands from trunks, limbs, and rotting logs 1–50 m from the nest. At times skeletonized dead leaves, some so decayed that only the midribs are left, are pulled from piles of trash near or on the ground. The birds seldom visit the ground or move above 2 m from it. Ordinarily few leaves or strands, sometimes only one or two, are carried at a time. Once, however, a male carried a large tuft of rhizomorphs and left part of it on a nearby pile of debris while he took part to the nest. Then he returned, picked up the rest of the rhizomorphs, and took them to the nest.

At the nest I watched from a blind (08:30–09:46, 16 July 1966), the 16 intervals between 17 arrivals of the male with material varied from 2 to 9 minutes and averaged 4.7 minutes; the 9 intervals between 10 arrivals for the female varied from 1 to 13 minutes and averaged 6.0 minutes. The 26 total intervals between visits of male and female varied from 30 seconds to 9 minutes and averaged 2.8 minutes.

Often one member of this pair arrived with material as the other worked on the nest. At such times, as when they wandered near each other looking for material, the male serpentine-sang or chirped faintly; the female often chirped. At times the male serpentine-sang or faint-sang to the female's faint-songs as he worked on the nest and she hunted for material 1–30 m away. When one bird first arrived as the other sat on the nest, he or she chirped a few times or silently waited a few seconds until the bird on the nest left. At times the arriving bird hopped up the stem of the sapling or waited nearby, but generally it alighted on one or the other of the two horizontal twigs supporting the nest. In these cases the arriving bird always alighted distally to the bird on the nest, generally within a centimeter or two of it, as it quickly finished work. Once, eight minutes after the attack by the female Chestnut-backed Antbird, the male Spotted Antbird gave faint snarls from the nest as his mate came up; the pair of Chestnut-backed Antbirds were still nearby. Otherwise there was no sign of antagonism between the members of the pair of Spotted Antbirds.

Usually the arriving bird deposited its strands on one or across both of the twigs supporting the nest as soon as it alighted or as soon as it hopped in to the nest when its mate departed. Then the bird looked about briefly, pecked at or tugged at the strand just deposited, pulled it around the stem or one or both twigs, and departed. Pulling and pushing strands with the bill from above seemed the main method of construction at this stage. At times the bird deposited material and left within a few seconds. Later in the hour I watched, as a thin cup or cupped platform of rhizomorphs and a few skeletonized leaves began to take shape, the female sat directly in the nest and pressed her body down into it. She apparently kicked at the same time, thus enlarging the inside of the cup and tangling the strands. Earlier in the morning the male arranging material had squatted on the south twig, but not on the nest itself, which was then a slight bridge or saddle between the twigs. As he half-sat and pulled material one way and then the other with his bill, he flicked his closed tail as if excited. He first stepped into the nest and did sit-kicking in the nest several times at 08:39. The morning before, this nest had consisted of just a few strands on each of the separate twigs supporting the nest.

THE EGGS AND INCUBATION

This nest received the first egg 15 July and the second 17 July. In this and several other nests little new material was added during the two or three days before the first egg was laid. However, I flushed the male off this nest at 07:45 on 13 July and at 08:18 on 14 July, when a new strand was over the nest cup, so there is some addition even on the days before the egg is laid.

In one nest, barely started on 30 June, the first egg was in the nest on 6 July and the second on 8 July. At three other nests, two days intervened between the laying of the first and second eggs. Probably nest construction and the following less active period generally take about a week, and eggs are laid two days apart. The Bicolored Antbird and Slaty Antshrike also lay eggs two days apart, suggesting that this may be regular among antbirds.

In two cases for which data are available, female Spotted Antbirds visited nests and laid eggs between 07:15 and 08:18 and between 07:30 and 09:00.

The two eggs are whitish, streaked and splotched very heavily with dusky brown to chestnut. I had observed 84 such clutches by 1971; two eggs in one other clutch were stained chestnut all over. Four other nests I found, on which pairs were incubating, held only one egg each. In most cases there were two young in nests which contained young birds, but in several cases there was only one young bird. In cases where only one egg or young was present the original clutch may have been two, and one egg or young lost. Skutch (1946: 19) reported two clutches of two eggs each from Barro Colorado, mottled with umber on whitish; a set he measured were 23.0×15.1 and 23.0×15.9 mm in dimensions. Four eggs I measured were slightly smaller, averaging 20.9×15.0 mm. These four eggs weighed less (average, 2.15 g) than did 6 eggs (average, 2.6 g) not so measured.

Both sexes incubate, as is usual in the Formicariidae (Skutch, 1969: 182). Both males and females have vascularized, bare brood patches. Regular incubation begins when the second egg is laid. I have not seen birds on nests when only the first egg is present, but there may be occasional incubation. In one case young hatched a day apart, suggesting that the first egg may have been incubated alone for some time; however, the last egg at this nest hatched after 16 days, a rather long incubation period. Often one egg in a nest will be wet from rain. At times, however, even two eggs may be wet from rain if both birds happen to be off the nest when rains hit; apparently they do not attempt to return rapidly.

Judging from birds observed at ant swarms and flushed off nests, each bird incubates one to four hours at a stretch. The male incubates for an hour or two in the early morning, after the female has incubated all night. Only the female is at a swarm of ants before about 08:50 to 09:30 if the pair is incubating. The female then stays on the nest an hour or two. The male often incubates the rest of the morning. In the afternoon the birds alternate. The female usually has three or four sessions during the day, totalling about four to six hours (midmorning, midday, midafternoon, late afternoon) and the male four or five, totalling about six to eight hours (early and late morning, early and middle and late afternoon). Skutch (1946: 20) found a similar pattern at a nest he watched from one noon to the next, but only two sessions by the male and three by the female; the male was on 338 minutes (47.0 per-

cent), the female on for 327 (45.5 percent), and neither on for 54 (7.5 percent). The female was on at night. At that nest, the male arrived with excited chipping notes for both incubation periods and the female gave sharp chipping notes after she settled on the nest one time; otherwise they were silent. The male left the nest, chipping, for eight minutes during one session.

I watched from a blind at one nest after flushing the male off at 14:24. The female came up with loud chipping at 14:54 and continued loud calls even as she flew to the south twig supporting the nest. She looked in, flicking her closed tail, and hopped on at 14:55. She continued loud calls as she settled, then was quiet. Except for ruffling her head and looking about, turning her head through a small angle each time, she was quiet until the chipping notes of the passing male were heard at 15:44. Then she looked about actively, hopped up and over the edge of the nest, and fluttered away low and silently northeast toward the male.

Incubation, from the laying of the last egg to the hatching of the second young, required 15 days at this nest and at one other, but 16 days at a third nest. Skutch (1946: 20) predicted a 15-day incubation period for Spotted Antbirds, based on his knowledge of the incubation periods of other antbirds.

I watched from 07:40 to 15:41 on the day of hatching (1 August) at the above nest. The male, on the nest when I arrived, stayed low for 10 minutes after I arrived. At 08:18 and 08:34, after much looking around, he rose and poked down in the nest. From 09:02 to 09:05 and 09:14 to 09:15 he rose and looked beneath himself several times, champing his bill and ruffling his head each time. At 09:15 he rose again, grabbed half of an eggshell, and fluttered off eastward with it. One tiny blackish young was in the other half of the eggshell. At 09:20 the male came back, calling *peep-peep-peep!* repeatedly; he flew to the nest and half-sat, flicking his closed tail as he pecked down into the nest. At 09:22 he flew off silently; at 09:26 he returned silently to a vertical stem nearby, then flew to the twig by the nest and started a chirping series. He stopped and froze as a coatimundi passed 15 m to the northeast. Finally he looked down and pecked in the nest a few times, twitched the wings apart a few times, fluffed out his underparts gradually, looked about, looked down, and at 09:30 hopped down on the nest. When the female arrived at 09:36, they chirped faintly and he flew off past her. She came silently to the edge of the nest, looked down with tail closed and down, pecked into the nest, and a minute later flew off with the other half of the eggshell. Back she came to the nest edge, looked and pecked down a bit, then fluffed out her underparts and shifted her wings back and forth and hopped down on the nest. She took a long time to settle, and her head was rather fluffed. After looking about very actively and giving faint snarls twice, perhaps at my movements in the blind, she suddenly (09:57) hopped out of the nest and grabbed a sowbug from the ground below. She seemed to eat it, but on her return she pecked down into the nest several times. She fluffed the belly feathers, flitted the wings a few times from her hunched position, and hopped on. She looked about more actively than she had when incubating eggs on 27 July. At 10:18 she rose and poked under her, then settled. At 10:26 she rose as if pushed; 10:36, she rose, looked under her, picked up half of the second eggshell, and flew low off northeast with it; 10:40, the returning male, calling *peep-peep!* loudly, took food to the nest; 10:45, the female, chirping, replaced him at the nest edge and fed the young. She flew

off to a point near him. He sallied to the ground, took the young more food at 10:48, and hopped on the nest to brood until the female arrived at 10:55 with still more food.

At this nest, therefore, the two young hatched about an hour apart, and both parents carried the eggshell halves away. The young were fed less than two hours after hatching. The detailed notes continue.

From 10:43 to 15:41 there were 17 feedings, 8 by the female and 9 by the male. The 16 intervals between feedings varied from 2 to 76 minutes and averaged 18.2 minutes; eight intervals for the male varied from 5 to 83 minutes and averaged 36.5 minutes; seven intervals for the female varied from 10 to 110 minutes and averaged 40.3 minutes. The male also brought food at 12:02, but dropped it below the nest; when tossing leaves there brought nothing, he left and returned at 12:11 with another prey item. Three times the male left the nest after feedings, at 10:43 and 12:47 and 13:28; the female left the nest after the 10:45 feeding only. At other visits the feeding bird fluffed out and hopped down to brood the young.

The male brooded five times, 3 to 41 minutes at a time (average, 21.6 minutes) and was on the nest when I left; he brooded or was feeding young 116 minutes and was away 174 minutes between 10:45 and 15:35. His eight periods away from the nest varied from 2 to 76 minutes (the latter was the time he returned after 67 minutes but dropped the prey). The female's seven periods away from the nest varied from 1 to 44 minutes. She brooded seven times, 1 to 66 minutes at a time (mean, 20 minutes); she brooded or was feeding young 148 minutes and was away 142 minutes. One parent or the other was thus at the nest 264 out of 290 minutes, or 91 percent of the time, between 10:45 and 15:35 on the day of hatching. Skutch (1946), as has been noted, found that the two parents incubate 92 percent of the time. Except for two times (12:47 and 13:28) when the male left directly after a feeding and the one time (10:45) when the female did so, the feeding parent stayed and brooded until the other parent arrived.

Several times the male gave a series of chipping notes as he approached the nest, but at other times he arrived quietly or gave faint chirps or faint-songs to the female. He sometimes chipped near the nest, but was silent on it or gave faint chirps as he bent down to the young. She gave faint chirps or faint-songs to him when he arrived as she brooded, or she departed silently past him. She chirped or faint-sang or was quiet as she arrived. He was silent or chirped faintly as he left past her. Neither was noisy on the nest bush, although the male twice continued chipping until he was a few centimeters from the nest bush. Once the female gave a faint snarl at a Slaty Antshrike foraging past. Usually the parents arrived low, sapling to sapling near the ground, and circled somewhat before they came in to the nest bush and then flew or hopped up to the nest.

The prey fed the young was mostly very small, less than 5 mm long; some items seemed to be sowbugs. The parent half-sat and lowered its closed tail as it hunched over the nest from the twig supporting its south edge. At times a few chirps preceded the feeding, which was always rapid. The parent then champed the beak and looked about. At times it poked or pecked down at the young, but I saw no sign of eating or otherwise disposing of fecal sacs. A minute or two after arriving, it either flew off silently or spread the ventral feathers gradually, rearranged the wings, and hopped down to settle over the young.

Feeding and brooding behavior of adults at two other nests on the day of hatching were generally similar. The adults generally brooded young after widely spaced feedings. Other detailed notes follow.

At one nest I watched from 16:00 to 17:20 (24 July 1961) and took flash pictures of a pair feeding young in Day 4 (i.e., hatched somewhat over four days earlier). This pair approached and fed the young silently, and did not stay to brood. The male gave a few chirps as he departed past the incoming female on one visit. They approached the nest by short flutters, flew up to it from below, and dropped near the ground on leaving. Seven intervals between eight feedings by the female varied from 1 to 39 minutes (average, 9.3); she fed the young five times between 17:03 and 17:13 and was foraging very close to the nest. Four intervals between five feedings by the male varied from 1 to 21 minutes (average, 10). Twelve intervals for both parents ranged from 1 to 24 minutes (average, 5.5). Once the prey was a 2-cm caterpillar; the female had to rechew it after placing it in a young gape. The female carried away a fecal sac after this feeding, at 16:13; the male carried away fecal sacs after feedings at 16:37 and 16:50.

Feedings and broodings at five of six other nests watched by myself and Yoshika Oniki in 1969 and at one nest watched by Stephen Kistler in 1970 were similar. (At the sixth nest in 1969 the pair were very disturbed, either by my blind or by snakes [see below], and feedings were irregular; 9 intervals between visits of both parents when the two young were in Days 2 and 3 averaged 34.5 minutes. Then one young disappeared, and 5 intervals between visits to the single young on Days 4 and 5 [before it disappeared] averaged 18.7 minutes.) At the six normal nests, feeding rates increased greatly after Day 0, but decreased somewhat on the last day in the nest: the average for 19 intervals between feedings of two young by both parents was 18.0 minutes on Day 0, the day of hatching; 43 such intervals averaged 11.0 minutes on Days 4 and 5; 67 such intervals averaged 12.5 minutes on Days 6 and 7; 88 intervals averaged 5.6 minutes on Days 8 and 9; and 38 intervals averaged 9.4 minutes on Days 10 and 11.

High feeding rates on Days 8 and 9, and occasionally on Day 4 (see above), were always associated with parents' foraging near the nest. Parents normally stayed near the nest on Days 8 or 9 to Day 11, and occasionally did so on other days. They did not always feed young rapidly when staying near the nest, however.

We recorded 185 feedings by males and 108 by females from Day 0 to Day 11. Females feed the young as assiduously as males (44 by males/47 females) until young are in Day 5, but then become less active (141 males/61 females) from Day 6 to Day 11. However, one female fed as much as the male on Day 9, and the female always resumes full activity as soon as the first young leaves and she has to feed either the one in the nest or the one outside of it by herself.

There was little daytime brooding at the six normal nests, except once during a period of rainy weather. The last brooding recorded was for three minutes when young in one nest were at Day 8. There was fairly regular daytime brooding at the disturbed nest in 1969 when young were in Day 2, part-time brooding on Days 3 and 4, regular brooding on Day 5, and none



Figure 14. Female Spotted Antbird waiting for possible fecal sac after feeding nestlings. This nest was used three times in 1969–1970, only the first time successfully.

on Day 6. Flushing parents off other nests also suggests that brooding decreases rapidly after the first few days, concurrently with the above-noted increase in feeding rates (primarily because of an increase in feeding by the male). Females regularly brood at night; one arrived at 18:08 when young were in Day 6.

During the first hours after the young hatched, no fecal sacs were removed (none in 22 visits at three nests). On Days 1 and 2, fecal sacs were eaten before the parent brooded young on three of eight visits. At one nest, only one fecal sac was carried away in 11 feedings on Day 11, just before one young left. On Days 3 to 11 at other nests, however, fecal sacs were carried away by a parent, its neck unusually extended, after 38 of 137 feedings, or 27.8 percent. One female carried a sac to a perch 13 m away and shook her head after dropping the sac. Often the parent waits a few seconds after a feeding, champing the beak and pecking down into the nest, if no fecal sac appears (Figure 14). For other views of attentive behavior see Plate 2.

I watched at one nest between 08:43–13:45 on 22 August and 05:45–07:13 on 23 August for the departure of two young. The male started chirring and chipping near my blind at 08:58, attracting the female to give faint snarls. Then they chirped until 09:12, which started loud *peeee!* notes from one young in the nest. At 09:15 one parent moved to the palmettos under the nest, the young fluttered and hopped up on the nest edge, and immediately fluttered to the ground and away along it. Its *peeee!* notes alternated with the serpentine-songs of the male that was leading it away. The female



PLATE 2. Spotted Antbirds at the nest. Above, male looks at young after a feeding.
Below, female starts to carry fecal sac away.

stayed and foraged within 30 m of the nest the rest of the observation period. She alone fed the young remaining in the nest, and the calls of the male came only from near a treefall some 50 m to the east.

The young in the nest gave some faint-peeping notes. The flutter of wings from the female's arrival at a low perch nearby often started it to utter a noisy squeaking. After feeding it sometimes gave faint-peeps and preened a little. Once when the female stayed three minutes on the nest edge the young peeped and preened busily, then gaped and squeaked into her face.

From 11:02–11:20 a Keel-billed Toucan foraging near the nest and later the treefall caused repeated chipping from both birds. There was no feeding between 11:02 and 11:27, the longest interval until feeding slowed to three times per hour about noon. The female at times chirred when I moved abruptly in the blind, which was fairly thin. On my passing at 17:50, she chirred rapidly except during the few seconds I passed the nest.

The next morning I arrived in the dark. The brooding female slipped off the nest in the semi-darkness at 06:15, and fed the young every 2.9 minutes (10 intervals) from 06:31 to 07:01. Only once did she carry a fecal sac away. The young preened actively, gave some peeping, squeaked and gaped before rapid feedings, and at 06:47 tried several times to flutter up on the nest edge as the female approached. At 07:01 she stayed below the nest after feeding; the young tried several times to hop on the nest edge, succeeded, and at once leaped to the ground below her. A few minutes later it was 0.1 m up on a low twig there; the female chirred rapidly as I caught and weighed it.

Thus the young left separately without any practice at fluttering in the nest, and only one parent fed the young remaining in the nest. This also occurred at two other nests; at one nest the male stayed with the remaining young and at the other nest the female did so.

Excepting the above-mentioned rapid sequence, 30 intervals between feedings of the one young remaining in the nest by a single parent averaged 10.7 minutes (with the rapid sequence, 40 intervals averaged 9.5 minutes). This is barely longer than the average interval for two parents feeding two young in the nest on Days 10 and 11 (38 intervals, 9.4 minutes).

The young that remains in the nest (and probably also the one outside the nest) is fed almost twice as rapidly as it was a few minutes before the first young left. However, the two young in the nest are also fed at this fast rate on Days 8 and 9, two days before they leave.

GROWTH OF THE YOUNG

The young are very small, black, and lack down at hatching, as Skutch (1946: 21) has noted. They weigh up to 2.3 g, probably normally somewhat less than the 1.8–2.4 g of an egg before hatching (Figure 15). By two days and a few hours after hatching (Day 2), the quills of the remiges are appearing; the longest (number 4 from the end) is about 1.0 mm long (Figure 15). The young grasp the nest lining weakly and peep faintly when removed. Their bellies are relatively large and bulky, and the major process going on is plainly assimilation of food.

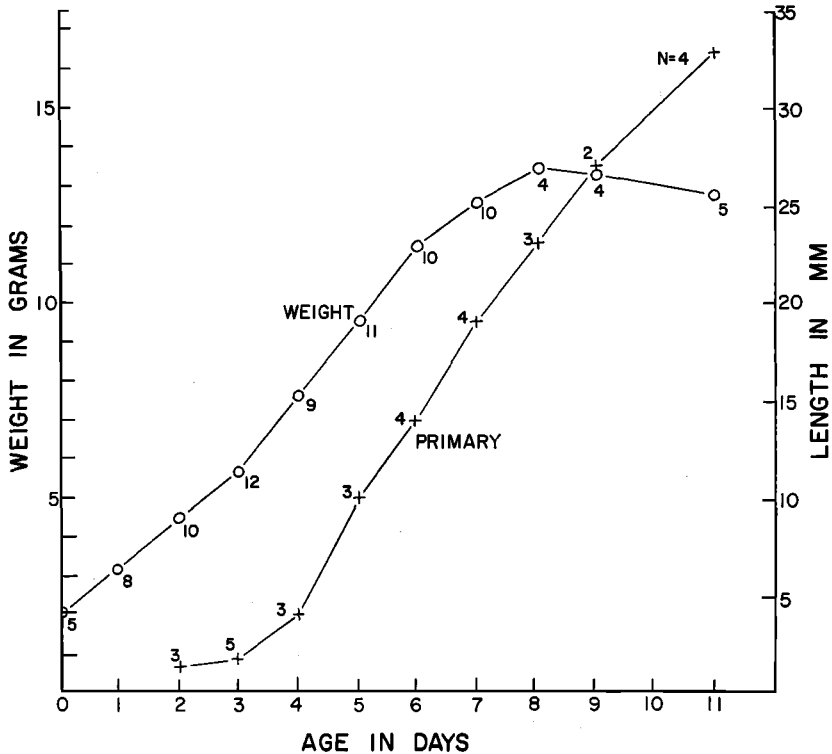


Figure 15. Measurements of the longest primary remex, and weights, for young Spotted Antbirds.

Black pinfeathers are evident on the wing coverts by Day 4, some rusty tips on Day 5, and brushy tips by Day 8. The primaries are opening to brushy tips on Day 8, and have vaned tips along 20 percent of their lengths on Day 10. Long pinfeathers are on the dorsal tract by Day 4, brushy tips on Day 8, and long vaned tips from then on. By Day 8 there are short tips on the ventral feathers. Thus, most of the opening of feathers occurs on Day 8 and thereafter.

On Day 2 the eye slits are starting to appear. By Day 4 the eyes are held partly open, and on Day 7 and later the young usually keep the eyes open when held in the hand. Young gape and squeak to the touch of the hand until Day 5 or 6, but crouch in the nest and huddle in the hand thereafter. On Days 8 and 9 and thereafter they struggle and attempt to jump out of the hand or weighing apparatus. They clutch the nest lining little when removed until Days 5 and 6; by Days 7 and 8 their feet are well developed and clutch the nest lining strongly. Squeaking changes to peeping notes when



Figure 16. Young Spotted Antbirds on Day 4; from the nest in Figure 14.

removed on Days 4 and 5, then to gradually louder *pee-pee-pee-pee* nest-leaving notes from Day 7 on.

As noted above, young squeak noisily as the parent approaches and feeds, peep nest-leaving notes now and then, preen between feedings, and—as indicated by approximately 15 observations—hop out of the nest during or near the end of Day 11 (i.e., on the twelfth solar day in the nest or early in the morning of the thirteenth solar day, just before the young is 12 days old). One other young left late on Day 10, but the disappearance of its nest-mate on or about that time suggests that a predator got one young and the other fled prematurely.

FLEDGLINGS

Soon after it leaves, a young bird can flutter up to 5 or 10 m only a few times in succession, with some loss of elevation, then must hop-flutter rather



Figure 17. Young Spotted Antbird, just out of the nest, on Day 11; from the nest in Figure 14.

weakly over the ground or along a stem. It can cling to a vertical perch soon after leaving, but tires rapidly. It often falls over the perch on alighting. When not being chased, it sits most of the time on a low, slender twig near the ground, attended by one parent. Figures 17 and 18 show such young. The young often is in dense sprouts, treefalls, and similar places where it is difficult to detect unless one triangulates on its faint calls to the attending parents.

A young just out of the nest or sitting on the nest edge is very poorly feathered. The tail is a set of brush-tipped feathers about 1 mm long. Sometimes the rear end of the body twitches, especially the white feathers of the undersides, as the wingtips flit upward as if the fledgling is excited; in the hand one can see that it is flicking its tail. However, many fledglings seem placid on a perch or in the hand, and struggle only to stay on top of the hand or to escape any dorsal touch during the first minutes after capture. Sometimes the young bird gives a faint *pee pee pee pee*. The wings are rather well feathered dorsally, with bright buff or chestnut tips to three rows of wing coverts (the greater primary coverts lack tipping) and on the leading edges of the secondaries and the tips of the inner secondaries. There are no wing coverts under the wing. The remiges are all short, but the vanes are four-fifths or more expanded, so the shafts are bare only at the bases. There

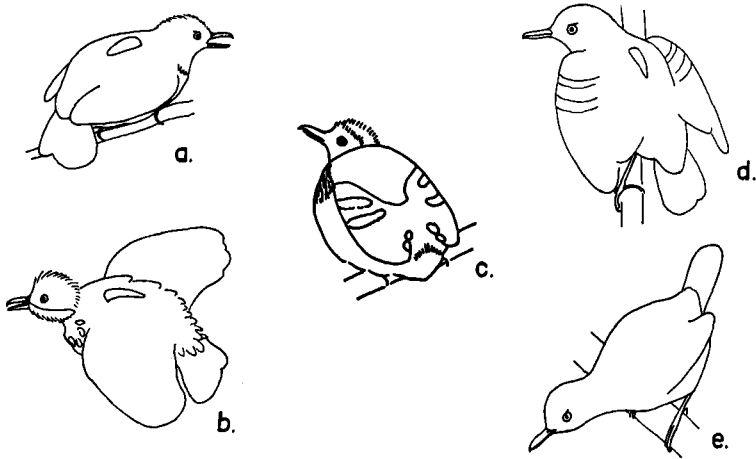


Figure 18. Young Spotted Antbird (c) and distraction displays by parents, from field sketches. a, Female crouches, snarling and showing white back-patch, near a fledgling. b, Male flutters along ground with tail spread and dragging, near fledgling. d, Female takes upright frozen posture after being flushed off nest and eggs. e, Same female in downward frozen posture at another perch a few seconds later.

are enough unsheathed dull chestnut-brown dorsal feathers to cover the back between the wings when the fledgling sits hunched up in its usual waiting posture. The crown of the small head, otherwise rather bare and blackish, is covered with a "crew-cut" patch of dusky, brush-tipped feathers. A few auricular feathers have brush tips, but the face is mostly bare. The bill is blackish, a bit soft and irregular and small; the not-very-prominent gape angles are yellowish-white. The rather loose and downy whitish feathers of the lower breast and along the sides leave the ventral apterium and undertail open and bare. The breast is well covered with brownish-smudged similar feathers. The large bare pinkish shanks and the large feet are slightly smaller than adult size, but are well developed except that the slightly short toes grip weakly. I have not found a way to distinguish the sexes at this age.

As in Bicolored Antbirds, one parent feeds one young and the other parent feeds the other. If one young is lost, its parent infrequently helps the other parent feed the remaining young. However, after a hawk killed one male his mate fed both young birds of the family. If there is only one young bird and the female is feeding it (6 cases), the male sometimes feeds her and she takes the food to the fledgling. If the male is feeding the only young (18 cases), she flirts with him but is not fed until the young is getting food for itself to some extent. The great preponderance of male care of single young perhaps arises from the greater care of nestlings by males in the last few days,

hence, the greater chance that males will lead any single young from nests or take them over later. If there are two young, one parent occasionally appears and chirrs briefly as the observer chases the young of the chirring other parent. Generally the extra parent returns to its own distant young when the attending parent stops calling. At times the male and his young bird are 100 m or more from the female and her young bird, especially during the first few days, when the young are not easily moved. At times there is a permanent exchange of young between parents; in one case a male took over an immature female and the female took over an immature male. However, among families with one young female and one young male I noted no significant tendency for parents to feed young of the opposite sex. In 8 such families males fed the young males while in 11 the females fed the young males. This was true even though older young of the same sex as the attending parent are more likely to elicit snarls, challenging, and supplantings from the parent.

As a fledgling waits quietly, its own parent wanders about foraging. Occasionally it flies to the young bird and feeds it. After capturing food, the parent chews it and starts serpentine-singing. The young bird answers with faint-peeping and starts flicking its tail and looking about even if (or especially if?) it is on one's hand. If the young does not answer, the songs of the wandering parent are louder and louder, and it stops chirping. Eventually the parent wanders past the calling or silent young bird and feeds it or leads it off.

Usually the chirping part of serpentine-singing predominates as the parent flies up and feeds the young, although there is not often a rapid series of chirps as in feeding the mate. The young flutters and squeaks as it extends the neck and head just above the horizontal and gapes at the parent, which often recoils a little. Then the parent inserts the prey into the open gape of the young. The parent watches the gulping young, then flies off.

If the parent is performing "leading behavior," it stays a few meters from the young bird and chirps and serpentine-sings while reversing back and forth and flicking the tail. Soon the young is hopping and fluttering over the ground or among low twigs after the retreating parent. The latter feeds it when they have reached a new hiding place.

At times the parent works a fairly distant swarm of ants and commutes 100 or 200 m to the young bird, but generally the parent works near the young bird even if there is a swarm within 200 m. In some such cases the parents may have failed to discover the swarms, of course. As the young birds grow, they and their parents are more likely to be at any swarms of ants in the neighborhood. Within a few days after leaving the nest the young bird gains the ability to flutter 10 to 15 m repeatedly from one horizontal twig to another without losing much altitude, even if it sometimes has to flutter

and pull itself up on the perches when it alights. At this stage the young can be led rather easily by its parent.

DISTRACTION DISPLAYS AND PARENTAL ALARM

Parents flushed at nests flee and chirr repeatedly. Usually the incubating bird flees long before one reaches the nest, but at times the bird stays on the nest as one passes within a meter or two. At times a flushed bird gives a brief snarl, but most quickly disappear silently after the chirring sequence. A bird flushed off the nest sometimes flutters low over the ground. One female, flushed off eggs, fluttered low and then froze at 0.1 m above the ground for a minute (Figure 18, d); then she fluttered 10 m farther and took an upright, spread-winged pose (Figure 18, e) on a vertical sapling for a minute. The latter pose, but with wings spread upward, was presented to something on the ground near a nest, where snakes twice attempted robbing (see below). In this case the female started giving faint snarls on the nest, the male came up and snarled faintly, and she fluttered off to give the display and snarl faintly. Both birds looked at the ground and snarled faintly. The nest was empty the next day. This pair often gave faint snarls on the nest; two days before the above incident the female gave these notes and then flushed off as a snake (*Pseustes poecilonota*) reached up to rob the nest. (I collected the snake as it reached in.) Once I noted a Spotted Antbird away from any nest giving faint snarls at a vine snake (*Oxybelis* sp.), which is another snake that probably robs nests.

Parent birds normally are quiet near their nests. Supplanting attacks on trespassing Spotted Antbirds often are silent, without the usual snarling. Often the pair simply disappears, leaving a good swarm of army ants to trespassers, if a human is nearby.

If one approaches within 30 m of a fledgling Spotted Antbird or of nestlings 10 or 11 days old, the parent usually comes up and starts chirring rapidly. There is usually tail-flicking, wing-flitting, reversing, and hopping from perch to perch. The throat may be puffed out. Between chirrs, the parent occasionally gives a faint snarl or two. At times the white center of the back shows, another suggestion that the bird is partly in the challenging display as well as in the mobbing display. Chipping and panicking are rare, however. The parent wanders near one in a quite distracting and conspicuous way. Often it moves to the side away from the young bird, or cuts between one and the young if one happens to go toward the young. However, the parent circles about so irregularly that one seldom can find where the young bird is unless he backs well away and waits until the parent starts singing and the young answers. Sometimes the parent starts leading the young away.

If the fledgling is in the hand, it gives faint-peeps and flicks the tail as soon as the parent starts giving faint-songs, but it stays very still if the parent is

chirring. One faint-singing male, which came with a caterpillar in his beak as soon as the fledgling started faint-peeping from my hand, was very agitated. He spread his tail and flicked it, spread his body until his flank feathers were over the wings, and flitted the wings and pivoted back and forth as he gave snarling and chirring notes rapidly. The young bird leap-fluttered his way. When I chased it, the male chirred and fluttered back and forth from one low perch to another between me and the young. He had his wings down and beating stiffly in distraction display at each perch. Once he fluttered along the ground in a more typical distraction display, a "fluttering run." This and several other parents fluttered past their hopping young in a "shielding flight" whenever the fledgling moved. In one particularly beautiful instance, a female knocked her fluttering fledgling from the air and hopped conspicuously away over the ground after "continuing" its flight a meter beyond the point where the nonplussed and frozen fledgling tumbled down. The young stops in such cases, and I generally found myself following the conspicuously fluttering and calling parent.

The "fluttering run," noted also in other parents, involves spreading and tilting the tail one way and then the other as it is depressed to or nearly to the ground. The white back patch is spread, and the wings, slowly beating and partly spread to either side, emphasize it as the bird sits on or flutters along the ground. The body feathers are spread, as are the throat feathers. At times the wings beat in rapid bursts as the parent wheels or crouches on the ground. At other times the parent performs the display from a low perch, or hops up and down onto low perches as if running hurdles as it flutters along the ground. One old male who did an especially good series of fluttering runs also did several "shot-bird" displays, involving a slow forward pitch off a horizontal perch, clinging head down an instant, dropping to the ground 0.4 to 0.6 m below, flopping briefly, and then hopping away flapping the wings. Another male did the same display, showing his white back as he did so. I have noted this display also in Red-throated Ant-Tanagers (Willis, 1961: 499), so it occurs both in songbirds and suboscines. After distraction displays, as the parent hops around, the bends of the wings are held out, the crown feathers go up and down, the tail is flicked, and the wings flit.

When young are a week or two out of the nest, they fly rather well and tend to fly higher and higher, even to 15 to 20 m up in vine-topped trees, if one chases them. The parent stays low in the undergrowth most of the time, except to feed the young after one backs off. At such times the parent flies around chirring, and does not go into distraction displays except for occasional shielding flights. At times I caught both the young and the parent in a net when the parent tried a shielding flight. Once a male flew at and knocked its young off a perch when it was in plain view.

DEVELOPMENT OF YOUNG OUT OF THE NEST

Young Spotted Antbirds grow rapidly and molt into adult plumage during the first seven weeks after leaving the nest. (To get ages for the following accounts, add 11 days if age since hatching is desired and 26 days if age since start of incubation is wanted.) During the first week, the tail grows until it is visible but only about one-third the adult length. The young bird is still below the adult size at the end of the week. The head seems especially small or short-feathered although the dull throat and facial feathers cover the bare areas by Day 7. Downy, brown-smudged feathers cover the breast and dingy whitish ones cover the lower underparts. The young bird hides and waits much of the time, but readily follows the parent if it starts serpentine-singing. After the young has been out of the nest two or three days, it is possible to catch it only by chasing it several hundred m, perch to perch, and shaking it off when it starts taking high perches and freezing there.

During the second week out of the nest the young reaches nearly or fully the adult size, to 17.7 g by Day 10 in one case, although the dull brownish head is still small and ragged. The tail is up to three-fourths the adult length by Day 14. The remiges are well developed, but the wings are still bare of coverts underneath. If the young bird is a male, new, bright chestnut back feathers of the adult plumage are appearing under the brownish feathers of the juvenal plumage. New bluish-gray feather brushes are also appearing among the brownish juvenal feathers on the head. One can tell the juvenile male in the field by his very dark head. The female is also getting new head and back feathers, but these are approximately the same color as the juvenal feathers around them. The chests of both are still an unattractive smudgy brown. The young fly increasingly well, so that one cannot catch them by chasing them. They flick their tails and hop and flutter from perch to perch almost as well as do adults; no longer do they tumble past perches or have great difficulty alighting on vertical or bendable perches. It is very difficult to find or see young between Day 7 and Day 14, because they flee readily with their parents or hide very expertly in dense tangles. I have relatively more observations of older and younger juveniles.

During the third week out of the nest, the young bird reaches full adult size and tail length. At Day 21 the young bird is in full post-juvenal molt. The head is often very ragged and in some birds is juvenal brown, but in most is approaching the color of the adult. Males are getting blue-gray heads and black throats, as in the adult except for dull brown feathers on the crowns and auriculars. They have one or a few new black-tipped white feathers breaking the unattractive smudges across their chests. Their backs are mostly bright chestnut, as in the adults. Females are getting new buff-tipped whitish throat feathers and buff breast feathers. Males and females are now easily dis-

tinguished. Young of this age flee and hide rather readily, especially if their parents are disturbed by the observer. One seldom sees them, except in mist nets.

During the fourth week out of the nest the young are slowly gaining adult plumage. Young and adult females are not easily told apart, except by the indistinct smudgy patching across the breasts of the young females and by their pale gape angles. The smudging on the breast of the young male is more conspicuous among the new spotted black-on-white feathers. Head and back molt are nearly complete by Day 28, although there are some short and dull juvenal feathers breaking the regular outline of the head. The young are flying rather well, and starting to forage clumsily on their own (as early as Day 24 in two cases). They play with small twigs, bits of leaves or whole dead leaves, peck at bumps on branches, etc. Their parents still feed them most of their food, but no longer do they chirr persistently or lead them off from the observer so actively. It is thus relatively easy to see young 22 to 28 days out of the nest.

During the fifth week out of the nest the young bird nearly attains adult plumage. By Day 35 the young male has only a few smudgy brown feathers on his black and white necklace, and the young female can be told from her mother mainly if one looks very carefully for a few dark and smudgy feathers on the breast. However, the young at this age are peeping very freely as they follow their respective parents about, so one can tell them from their parents. At times a parent bird supplants its own young. The young forage by themselves rather well, but readily take food from their parents; probably the adults give them over half of the food that they eat. The young bird is very tame and easy to see; it comes up and peers at the observer, then resumes peeping after the parent.

During the sixth week out of the nest, the young bird loses the last smudgy breast feathers. Except for the slightly swollen and pale angles of the gape, the young bird 42 days out of the nest looks much like the adult. However, it is peeping desperately as it follows its rather antagonistic parent, which frequently supplants it rather than feeds it. Although it is getting most of its own food, it stays near its parents. The latter, if the nesting season has not yet ended, are beginning to seem charmed by each other again. There are male-female grooming sessions when the fledgling is as little as 30 days out of the nest, and at times by 37 days out of the nest the male feeds his mate rather than the young bird. In one case, a male fed his mate and copulated with her when their only juvenile female, in the care of the male, was at Day 29. In another case, a male fed his mate and copulated with her when their only fledgling, a male in the care of the female, was about Day 20. Once a male tried to hop on the back of his juvenile female after a feeding. One male at Cerro Campana tried to do so after feeding a young male! If the male has

been feeding a young male or the female a young female, the young bird is quite often supplanted when it comes up peeping at the adult's serpentine-songs. One such young female left her courting parents and followed a nearby ant swarm into the territory of a neighboring pair at this time. Two other young left their parents about this time, and the young female nine days later was 1,300 m away.

More often the seventh week is the time of the parting of close bonds between young and their parents. The young bird forages for itself even when it stays with its parents. It still peeps frequently, but the parent rarely feeds it. The parent snarls at and supplants a young bird of its own sex. Once a young female snarled back, and her mother promptly supplanted her several times. The young is sometimes tolerated into the eighth week, even in the middle of the breeding season, but by about 56 days out of the nest all young have left their parents. I was not able to check this for young hatched at the end of the breeding season, however; two broods of these young were still peeping with their parents on 23 and 25 November 1961, after at least 52 and 54 days out of the nest.

The various kinds of peeping change little during the period the young bird is growing, but peeping does become more frequent after the young bird is flying well. Until then it is very quiet, except for loud-peeping when the parent sings at a distance or disappears for a long time. When the parent flies up with food or sings nearby, the young bird faint-peeps or serpentine-peeps, and it squeaks as it is fed. During the fourth and fifth weeks, as the parent stops feeding it, the young bird peeps a great deal. When the parent is distant, it loud-peeps; otherwise it faint-peeps. At times the faint-peeping grades into sounds like the adult song when the young bird is five weeks or more in age; one gave songs after being banded. At times younger fledglings give hoarse or faint songs, even at Day 21 or so.

RENESTING AND NEST SUCCESS

One young bird became independent when somewhat over six weeks out of the nest. The other young bird may have stayed longer with the parents, but it was independent when eight weeks out of the nest. The pair started a new nest 5 days later, or 17 days after the first young was independent. There may have been an unsuccessful nest in the interim. Other young became independent at about 50 to 55 days out of the nest, and renestings started up to a week before or after this period. In one case a juvenile female (feeding herself) followed her father and waited, making loud-peeping notes, near the next nest for a week while he incubated, so that renesting started at least two weeks before independence. There were three other cases when a pair had both a nest and a semi-independent fledgling. In one case (the

case of copulation when the female's young was only in Day 20), the fledgling was about 30 days old when the new nest was started.

Granting 35 days for a nesting and 30 to 50 days until the resulting fledglings are independent or semi-independent and a new nest is started, it should be possible for Spotted Antbirds to rear three broods between 15 April and 15 November. One pair did rear two broods, and had at least one unsuccessful nest in between. This pair had young about 15 days out of the nest on 3 June 1961 and independent young by 10 July 1961. The male was feeding his mate on 31 July and 1 August, suggesting that one or more July nestings had failed. They were incubating on 7 and 18 August. On 23 August they were feeding young in the nest. The next nesting began about 30 August, for they had young about two days out of the nest on 5 October. These young were still with them on 23 November.

Normally Spotted Antbirds are lucky to get even one brood of young out of the nest per year, for predators rob nearly all nests. Of 24 nests found before or during egg laying, only 6 reached the hatching date. In 2 of these 6 nests, both eggs failed to hatch (both nests were robbed after more than 16 days of incubation; the incubation period is normally 15 days), and in one nest one egg of two did not hatch (the egg remained in the nest for three days, then disappeared while the growing young remained). The other 18 nests (75 percent) were robbed before hatching. If the two nests showing complete hatching failure are counted as failing in the egg stage, 20 of 24 nests (83 percent) failed in the egg stage. Since I left long before very small nestlings in two nests could leave, young in the third nest disappeared when between three and six days old, and only one of two young left the fourth nest, I have yet to follow a completely successful Spotted Antbird nest from egg laying to fledging. In 8 of the 18 robbed nests, the eggs were taken during the three-day period of egg laying. Two other sets were taken three days after clutch completion, one set between three and six days, and one set on the fourteenth day. The other 8 nests were robbed between egg laying and the fourteenth day of incubation.

If the nest is not robbed before the young hatch, they still have only a moderate chance to survive. Of 19 nests found at or before hatching, one or more young left successfully from 8 (42 percent). If the two above nests in which eggs never hatched are counted, 13 of 21 nests (62 percent) were robbed in the "nestling" period. Only one nest, with addled eggs, was lost in the first three days after the hatching time; otherwise losses were scattered irregularly during the nestling period. Of 12 other broods I found after they were hatched, 8 were successful. Of 16 successful nests, 6 had only one nestling at fledging, and 1 nest that was probably successful added to the 10 to make 11 nests with two young at fledging.

In all, 16 broods of young left 84 nests found at various stages and followed

until success could be determined. Actual nest failure (the percentage of nests in which one or more eggs are laid but from which no young fledge) is higher still, as Mayfield (1961: 255) points out; most of these 16 broods were from nests found only late in nesting. Many nests in which I never found eggs or young (because already destroyed) are not included in the above total of 84. Probably nest failure is lower than the 95 percent of 22 nests found at the start of incubation or before and checked for fledging would indicate; one nestling surviving from each 44 eggs laid would probably not perpetuate this species. Nest failure may be lower than 93 percent (if m is the proportion of nests lost in the egg stage and n is the proportion of hatching nests lost in the nestling stage, the total proportion lost is $m + n [1 - m]$ or $0.83 + 0.58 [0.17] \cong 0.93$). However, nest failure probably averages over 90 percent. Similarly high rates of nest failure are usual for birds of tropical forests (Willis, 1967: 88; Ricklefs, 1969a: 18) and may be usual for mature forested habitats elsewhere (Snow and Snow, 1963: 35).

Nest failures are due to predators, apparently. Snakes are the only known predators. The disturbed nest noted above was almost robbed twice by two different *Pseustes poecilonota*, and was later robbed by an unknown predator. I hit with a rotten stick and chased underground the first large, hissing, spread-gaped snake and collected the second smaller one. I doubt that the first one was seriously damaged, and the fact that it did not return to the nest before the second one suggests that these snakes work by wandering and looking in nests rather than by revisiting nests found earlier. Since my repeated visits to antbird nests have not led to greater mortality than at seldom-visited nests, I suspect that human visits to nests may not attract snake attention unless, perhaps, the snake is watching directly. Also, that two snakes appeared suggests that any routes or home ranges must be wide-ranging or perhaps vagrant or overlapping, as is usual for snakes. *Pseustes poecilonota* is a fairly common, big-gaped snake that readily climbs to the tips of small twigs; it may be a nest-robbing specialist, for the only things I have seen one eat were two nestlings from a nest of Slaty Antshrikes. Since these snakes do not disturb nests, except by pulling out young that grasp the nest linings, and since some destroyed Spotted Antbird nests were rather torn up, or were torn out, or had a hole in the bottom, I suspect other predators also rob antbird nests. Ricklefs (1969a: 39) has shown that species diversity of predators correlates roughly with nest failure, and suggests that many different species rob nests in tropical or mature habitats.

There may be some loss of young the first few days after they leave the nest. Of 17 broods at fledging, 6 consisted of only one nestling; but of 58 broods a week or more out of the nest, 26 consisted of only one fledgling. These data, if taken at face value ($6:17 = X:58$; $X = 20.5$; $26 - 20.5 = 5.5$),

suggest¹ that 5.5 broods of 58 (9.5 percent) had lost one of two fledglings after they left the nest. If so, 0.54 pair of 58.5 pairs ($0.095 \times 0.095 \times [58 + y] = y$; $y = 0.54$) had lost both young by the time I found them. Possibly some 6.58 ($0.54 + 0.54 + 5.5$) young of 117.08, or as many as 5.6 percent, were lost in the first week after fledging. In 15 or so broods watched from the first week to independence, no more young were lost. Even young with broken legs and one with a club foot (swollen and fused-toed, clublike) survived.

If a nest is destroyed, the pair renests immediately. In two cases, building the new nest started about four days after destruction of a set of eggs. I was not able to follow single pairs of Spotted Antbirds throughout a full breeding season. However, no pair has ever been without reproductive activity, either courtship feeding or nesting or caring for fledglings, for more than a few days at any time when it was under observation during the nesting season. From this, from the known nesting periods, and rates of nest destruction, one can estimate that individual females should average eight or nine sets of eggs between mid-April and mid-October. A renesting rate almost as high as this has been determined for ant-tanagers (Willis, 1961: 500) and for Bicolored Antbirds (Willis, 1967: 88).

BREEDING SEASON

On Barro Colorado, the breeding season is the rainy season, from April to November. The earliest nest I found in 1961 had the first egg in it on 18 April. Young approximately 16 days out of the nest on 3 June probably came from eggs laid about 20 to 22 April. Young left a late nest on 23 October; the eggs were probably laid 26 to 28 September. Young 15 days out of the nest on 22 November must have come from eggs laid about 10 to 12 October. I left Barro Colorado on 26 November, and hence could not determine if there were any later nestings. There is no evidence of nesting in the period from mid-November to early April. No dependent young were evident between 15 November 1960 and 3 June 1961, between 18 January and 18 February 1962, between 15 January and 5 March 1965, between 18 December 1970 and 23 January 1971, nor before young left a nest on 27 May 1966. Adults rarely showed signs of courtship behavior before April in 1961 or in the months listed above for 1962, 1965, and 1970–71.

In 1961, the numbers of nests located by month of egg laying, were, from April to October, respectively: 1, 3, 2, 3, 3, 4, and 1. Young left one of the May nests, one of the August nests, and two of the September nests. Counting the young from these four nests, the numbers of flying broods recorded by

¹ These calculations prove, as noted in a letter from the author, to be based on incomplete assumptions. The intricate solution must await his return from Brazil.—Ed.

estimated month of egg laying were 1, 1, 3, 1, 2, 10, and 2 from April to October respectively. I do not know whether more young emerge late in the season every year or not; Bicolored Antbirds were also more successful late in 1961 (Willis, 1967: 88). Since all pairs are nesting more or less constantly from April to mid-November, the greater numbers of young out of the nest late in 1961 indicate that in 1961 early nests failed more consistently than did late nests.

DISCUSSION

Spotted Antbirds, like Bicolored Antbirds but unlike some other species (see Nice, 1943: 174; Åkerman, 1966a: 326; Moynihan, 1955: 86; Wood-Gush, 1956: 141), use agonistic behavior very little in courtship. Preliminary challenging of a potential mate, probably not instantly recognized as an eligible member of the opposite sex, is so brief in the antbirds that it is scarcely more than an initial repelling reaction, rather than a basic part of courtship as are threatening bow-coos in pigeons or "pouncing" in Song Sparrows. The studies of such species as chickens and pigeons have given rise to the widely but usually uncritically accepted "FAM" hypothesis, that courtship results from conflicting tendencies to flee, attack and mate (see Hinde, 1969, and Bastock, 1967, for general reviews).

Spotted Antbirds form permanent pairs only on territory, which suggests that singing, dominance, and other signs of territorial status may be necessary for preliminary stages of courtship. Clearly, agonistic behavior can help each bird get its territory and keep it, drive away competitors for food or for the mate, prevent polygamy and biologically unproductive indulgence and rape (Marler and Hamilton, 1966: 191), and help in many other ways necessary for life and reproduction but peripheral to the actual courtship displays. However, in Spotted Antbirds singing is the only part of courtship that could be considered agonistic behavior. This raises the question of whether singing to mates or young is to some extent "hostile" or agonistic behavior.

Perhaps partly as a reaction against the excesses of early naturalists, who assumed that birds sing only for happiness, scientists sometimes have seemed recently to presume that birds sing out of surliness. Early naturalists may have been partly right, in the sense that "pleasure centers" in the brain probably are part of the physiological system controlling singing (if singing is necessary for survival, such pleasure centers are very likely to evolve); and later scientists may be right in the sense that any pleasure centers probably evolved because singing is an efficient and safe way to ward off rivals, keep a family together in dense undergrowth, attract a potential mate, etc. There is little doubt that singing, especially loud singing associated with calls and movements of the challenging display, helps set up territories and causes flight

or fight reactions in rival Spotted Antbirds. There is also evidence that singing, especially faint songs associated with chirping, helps keep mates and young together. For many other birds singing is an activity that fits both in a chapter on agonistic behavior and in one on reproductive behavior. (Moynihan [1962*b*: 319] has even proposed that song be defined as vocalizations that usually attract conspecific birds of the opposite sex and repel ones of the same sex; but this depends on the situation, for commonly songs attract a hot rival of the same sex and repel members of the opposite sex. I suggest a conventional definition for "song" instead: the so-named (by the first students) major vocalizations of a species, especially its longest or loudest or most musical or far-carrying ones.) Although some may prefer to invoke Occam's Razor to assert that one motivation—say hostility—should stimulate singing or similar vocalizations rather than different motivations in different contexts, I prefer not to assign hostile motivation to courtship song in Spotted Antbirds because challenging seldom is associated with it. Moreover, if it is hostile, the male, who sings less once he gets a mate, and sings more if temporarily separated from her, must be expressing his hostility to her until she arrives! (I am indebted to Lack [1943] for disposing of the possibility that birds sing out of happiness by using similar observations.) It is more likely that song is a long-distance communication of deprivation of a mate, an assertion of presence, etc.; those who invoke hostility should prove it exists in the given situation.

If courtship song is not likely to be hostile in Spotted Antbirds their courtship is essentially an "M" type (Bastock, 1967: 102), in contrast to the "FAM" type of some birds. FAM birds tend toward M displays late in courtship, and occasional elements of aggression and submission appear even in Spotted Antbirds; there is a difference in degree rather than in kind.

The very common display or activity of courtship feeding may have evolved from a flight-fight conflict or from a foraging-mating conflict, but seems more likely to have come from parents transferring attention from fledglings to mates at the start of new nestings. If so, any conflict was probably irrelevant and between parental and mating drives. Birds sometimes bring food to a nest before young hatch, but such instances seem unlikely to lead to courtship feeding. Courtship feeding generally precedes egg laying except in species in which females incubate alone but are fed by males.

The ecological origins of these courtship displays need study as much as do the psychological origins. Courtship displays require expenditure of energy and time and put the displayer in some danger, especially if special colors or structures have evolved to emphasize displays. In Spotted Antbirds and other courtship-feeding species, the male loses food when he gives it to the female. Not only must such disadvantages be offset, there must be such an advantage to the displayers that their genes eventually replace those of non-

displayers. The most likely advantages to displayers are that they can evolve sexual isolation from related species and be sexually selected by or stimulate potential mates.

If there are other species with which a bird can hybridize, and the offspring of such unions survive poorly, the female and to a lesser extent the male must develop the ability to tell its own species. Differences from related species will be selected for, whether differences in plumage (Sibley, 1957: 174) or displays. Displays are probably easier to select for, since changes in morphology inevitably compromise other adaptations, such as those for avoiding predators or for getting food, while displays can be turned on and off. If the species learns the proper displays for a mate, and perhaps even if a change in the neural system (instinct) is required, necessary changes can perhaps be made much faster or more easily than can changes in morphology. Possibly the lack of striking courtship displays in Spotted Antbirds, which have no species similar with them, is evidence for the hypothesis that species without close relatives are unlikely to develop strong courtship displays. The hypothesis needs checking, although Sibley explains the loss of bright male plumages in ducks without sympatric species in this way.

Another factor in the evolution of displays, however, must be the stimulation, attraction, and synchronization of a female and male by displays. Lehrman (1958: 33) has shown experimentally (using injections of hormones) that displays in Ring Doves (*Streptopelia risoria*) stimulate and synchronize the mates. Stimulation and attraction are probably important when mates meet briefly, have a short breeding season, or are limited in available habitat. The shorter the time or the smaller the space in which male and female can be together, the stronger the displays or songs or coloration of the male should be in order to bring the female into readiness to mate in a short time, to attract her to him rather than to another nearby male, and for her to find him in an isolated patch of habitat. (Similar arguments apply for the displays or song or coloration of the female in such birds as jacanas and phalaropes.) The need for synchronization should also lead to strong courtship displays in seasonal or isolated habitats; strong displays, even communal ones, will quickly bring birds into breeding condition.

The courtship patterns of birds may thus be influenced by the habitats they live in. Verner and Willson (1966: 145) have pointed out that polygamy, with its consequent emphasis on persistent male displaying, arises mainly among marsh and open-country birds in North America. They theorize that the great variation in quality of habitat from one site to another in immature and low habitats makes it possible for some males to preempt such good territories that several females can raise more young in them than they could by spacing themselves out with unmated males on poorer sites. The Spotted Antbird and its relatives represent the other extreme, monogamous birds with

prolonged pair bonds and equal roles of the sexes in caring for offspring, characteristic of forest or mature habitats. In the tropics, the birds that use this system (antbirds, ovenbirds, trogons, puffbirds, etc.) predominate in mature habitats while those that display promiscuity or female care at the nest are often predominant in second-growth or "edge" habitats (tyrannids, icterids, tanagers, etc.) or feed on irregularly distributed nectar or fruits (manakins, hummingbirds, etc.). Parrots and woodpeckers are major exceptions to this rule, since both have irregularly distributed habitats and monogamous systems; but most are large, far-flying birds that can easily and safely move from one patch to the next and thus are not in an environment that is patchy considering their powers of flight.

Differences in pairing systems between forest and savanna birds are known from the same family and genus. In the weaverbirds, genus *Ploceus*, the forest species tend to be territorial and monogamous, and male and female are bright-colored and incubate. Species of savanna tend to be strongly dimorphic and show polygamous and colonial breeding in which the female incubates alone and the male displays conspicuously (Moreau, 1960: 321; Crook, 1964: 104; Lack, 1968: 36). In grouse (Tetraonidae) species of widespread mature habitats (tundra or woodland) tend to be monogamous or solitary-polygynous and have moderate displays, while species of localized habitats (edges of woodland meadows) and grassland tend to be communal, promiscuous, and strong displayers (Scott, 1963: 673).

Orians (1969a) has recently suggested that second-growth and marsh or grassland plants put a large part of their energy into fast growth and quick dispersal of many seeds rather than into biochemical and other protective devices against insects, hence tend to be infested with insects once the insects find them; therefore, second-growth plants have at any one time some abundantly fruiting patches which insects have not yet found and others that are strongly infested. Moreover, greater light intensities in the canopy and in second growth probably lead to great productivities (Pearson, 1971: 50). Either the reproductive parts or the insects are locally superabundant, and produce large local food supplies for birds exploiting them.

Superabundant food supplies both release the male from feeding the young or helping the female at the nest and permit some males to preempt local good sites and get as many females as possible. Strong displays and songs are among the secondary sexual characters that such males can use to drive off other males and attract more than one female each, and the males that do so will leave more offspring. Thus, the FAM mating system, in which the female is impressed by a strong male and there have to be quick and distinctive displays, is perhaps more likely to evolve in ephemeral or seasonal habitats than in climax and constant habitats. In the latter there are many species, each exploiting a sparse and relatively evenly distributed food supply,

and no one area is so much better than another that one male can preempt it or have more females because they do better to go to him than to his poorer bachelor neighbors.

Monogamous systems, especially ones in which the male helps the female at all stages of nesting, will probably be most successful in mature and widely distributed habitats. Monogamous systems make it possible for male and female to share duties of caring for eggs and young, thus partly compensating for a habitat without local food surpluses. The monogamous system does not require conspicuous courtship displays, especially if there are no sympatric closely related species. Sympatric congeners are most characteristic of genera of secondary habitats or patchy habitats, probably because irregularity in time or space allows "fugitive" species (Hutchinson, 1951) to skip about ahead of more efficient congeners as well as favoring the good powers of flight or dispersal mechanisms that make skipping about possible. In mature (homogeneous) habitats, sympatric congeneric species almost always separate out by small differences in habitat or quickly develop morphological differences that cause us to classify them in different genera. The big genera in the tropics are often ones predominantly of second growth and patchy habitats, and show tendencies toward strong displays or care of the nest by the female alone.

In Spotted Antbirds, an important advantage of courtship feeding may be that it helps the female form the eggs and avoid predation during a difficult period. The rarity of courtship feeding at times when the female is not forming eggs, with the exception of the pairing period, suggests that egg-laying and courtship feeding may be linked. Courtship feeding may also indicate to the birds whether it is possible to feed young birds, which will appear in a few weeks (if it is possible to feed a female, it should be possible to feed young); but there is probably so much day-to-day variability depending on whether a swarm of ants is present or not that only general indications would be possible. The two-day period between laying eggs suggests that the female may find it demanding to get food to form the rather large eggs. Presumably smaller eggs could be laid, but at the expense of requiring more food for the young later on and more visits to the nest (Lack, 1968: 190). More visits, besides possibly being more dangerous to the young (Skutch, 1949: 434) probably significantly increase the danger of predation on adults. The sharp chipping notes of Spotted Antbirds visiting nests suggests that they are alarmed, probably justifiably so when one considers that Semiplumbeous Hawks and other sit-and-wait predators would find it easy to capture Spotted Antbirds mainly when they are on the move. The higher rate of feeding nestlings when pairs stay near them may be possible both because predators are less dangerous on short moves and because the birds do not have to spend so much time travelling.

There is no obvious reason why mated Spotted Antbirds groom each other while related antbirds, such as the Bicolored and Ocellated Antbirds, do not. The latter species keep their mates for life with just flirting and courtship feeding. Spotted Antbirds tolerate the mate at very close quarters, perhaps partly because the male and female differ in color and do not provide agonistic stimuli for each other. Perhaps a small antbird, eating common small insects and ordinarily foraging some distance from the mate, can tolerate the mate readily on the few occasions when they near one another, thus predisposing for grooming. However, the Ocellated Antbird tolerates the mate and does not groom. It is possible that Spotted Antbirds more readily pick up head parasites because of their frequent foraging above the ground and through vegetation, hence need grooming more. I have seen more ticks on Spotted Antbirds than on Bicolored and Ocellated Antbirds, but would not vouch for the statistical significance of such rare events. However, I have little doubt but that the even rarer events of predation cause striking behavior patterns in Spotted Antbirds, so that danger or irritation of head parasites or spider webs could easily cause grooming to be favored in evolution.

The Spotted Antbird probably has little trouble finding its simple requirements for nest sites, but the visiting of old nests and the occasional use of the same nest site by the same or different birds suggest that there may be some limitations. The low height probably reduces competition for sites with the lowest nesting individuals of the Slaty Antshrike, as does the tendency to nest close to stems rather than away. However, Spotted Antbirds nest in the next to highest quarter of their usual foraging range and Slaty Antshrikes in the bottom half of their usual foraging range, suggesting that pressures other than interspecific competition are more important—possibly predation or lack of twigs at low and high levels in the forest understory.

The general construction of the Spotted Antbird nest is loose but fairly opaque, probably so the nest resembles trash, while the nest of Slaty Antshrikes is neatly woven but thin and translucent. The low-nesting Red-throated Ant-Tanager, with a trashy nest, and the high-nesting Red-crowned Ant-Tanager, with a thin nest, show an even more striking correspondence between nest type and height of nest (Willis, 1961: 482) than do the antbird and antshrike. Low in the undergrowth the trashlike nests blend with leaves on the ground from the viewpoint of an aerial predator and with piles of debris from that of ground predator. High in the undergrowth, trashlike nests would be silhouetted against green leaves to the eyes of both aerial and ground predators, and the former would see the eggs, so that flycatchers with trashlike nests tend to have roofed nests and to put them at the tips of barely accessible vines or twigs; birds with open nests make them thin or decorate them with green moss so green will show through from both directions and the pale eggs will be less clearly silhouetted from above.

Possibly nests of Spotted Antbirds are not placed in patches of dense undergrowth because some predators on nests or adults could approach unseen or learn to work such patches. Placing nests in scattered patches rather than in the uniform open forest matrix makes it easier for predators to locate the nests if predators specialize. Also, the green leaves of such patches could frame the nest for aerial predators that would overlook it against dark backgrounds.

At the time of building, the birds look for material nearby and move to the nest rather conspicuously and frequently. The female is more disturbed by an observer than is the male, but both chirp and sing and react more strongly to alarm calls of treetop birds than to the observer. Presumably there are no animals, such as brood parasites or predators with long memories, that could cause selection for more caution on the part of the parents; their caution seems mostly for themselves. Looking for material near the nest reduces the energy needed for building as well as dangers from predation, as does concentrating building rather than scattering visits out. Whether looking for material at unevenly distant sites and irregular times is better among birds subjected to brood parasitism is not clear, although one could suggest these or other reasons for irregular searching and building in the numerous species in which it occurs. In any case, the Spotted Antbird is not known to be parasitized by cowbirds or other brood parasites.

The great amount of chirping and flirting during nest building probably helps synchronize the mates, and perhaps helps start hormonal preparations for egg-laying by the female and for incubation, in which both birds must participate. Later there is much less interaction at the nest because then eggs and young might be detected if the pair were conspicuous.

Laying the eggs an hour or two after dawn seems characteristic of antbirds, as opposed to ant-tanagers, which lay eggs at dawn (Willis, 1961: 485). It seems strange that a female would carry a large egg about for a couple of hours, unless she needs food before she can lay or unless it is dangerous to go to the nest when it is still dark in the forest. However, Skutch (1952: 55) notes that flycatchers of open country also lay eggs well after dawn; laying at dawn seems characteristic of some songbirds and hummingbirds, laying later characteristic of shrikes (Susan Smith, pers. comm.) and of suboscines. Is later laying perhaps an adaptation to generally sparse food supply? to difficulties in storing up enough food the evening before? Seed and fruit eaters often can store food up the evening before.

The heavy blotching of eggs of Spotted Antbirds probably helps them blend against the background of dead leaves when seen by an aerial predator. Slaty Antshrikes have almost white eggs; but such eggs are not so conspicuous in a thin nest, and parents incubate them nearly all the time (Yoshika Oniki, pers. comm.), while Spotted Antbirds sometimes leave the nest unguarded

before the mate arrives. (White-flanked Antwrens, which have white eggs in low and thick cup-shaped nests, usually put the nest below an overhanging leaf; they sometimes leave the nest unguarded.)

Possibly Slaty Antshrikes, which are not ant-followers, can be on the nest constantly because they forage near the nest, while Spotted Antbirds often forage a long distance away and at swarms of ants. In such cases, the incubating bird should stay as long as it wants rather than being interrupted so as to cause more long trips. Moreover, the bird on the nest can find an ant swarm that its mate has discovered better by going to the mate off the nest rather than by random search after the mate has come to the nest. Bicolored and Ocellated Antbirds also commonly leave the nest to go to the mate at swarms.

Spotted Antbirds visit the nest slightly more frequently during the day than do their larger relatives, the Bicolored Antbirds; perhaps a smaller bird metabolizes its food stores more rapidly than does a larger one with similar food habits. Skutch (1962: 134) noted how long the incubation sessions of antbirds are considering their size, and suggested that longer periods might result in hunger. Incubation by both sexes allows individuals of this and other antbirds to incubate less than 50 percent of the daylight hours without feeding of incubating mates. Incubation by the female alone is rare in forest-adapted insectivorous birds in the tropics (Willis, 1969*b*), probably because feeding the female or leaving the eggs unguarded would attract predators, while the female could not get enough of her scattered and uncommon food if the male did not help her.

Carrying the eggshells away when the young hatch, rather than eating them as do ant-tanagers (Willis, 1961: 488) or letting them be crushed as do some hummingbirds (Oniki, 1970: 724) is a minor activity but probably has some reason (Tinbergen, 1963: 28). Perhaps hummingbirds, with their thin bills, cannot carry shells away or eat them, and as a consequence have soft whitish nests that allow eggs to be thin-shelled and crush readily after hatching; white eggshells would be conspicuous in a dark nest, such as that of antbirds. It could be that antbird eggshells are too thick or large or too covered with pigments to be eaten, hence have to be carried away. Antbirds with nearly white eggs (Slaty Antshrikes, according to Y. Oniki, pers. comm.) carry the shells away, suggesting that the pigments are not the problem. Antbirds usually dissect insects of the size of eggshells after taking them to the ground, suggesting that they do not have the tongue-bill cooperation or the breadth of bill that allows sequential crushing of an item (as in ant-tanagers eating fruit, Willis, 1960*a*: 163) without slinging it about conspicuously. Perhaps the calcium they could get out of the shells is not scarce enough to be worth attracting the attention of predators by conspicuous shell dissection. This suggests that thick-billed birds nesting in open nests should generally crush

and eat shells, medium-billed ones should carry them away, and thin-billed ones should have soft white-lined nests and crushable eggshells that are left in the nest. However, the soft white nest-linings of goldfinches (*Spinus* spp.) probably have some other basis, although these are small-billed finches specialized for small seeds. Also, shorebirds with rather thin bills commonly carry off eggshells (Sutton, 1968: 502–503).

Chirping and serpentine-singing are associated with feeding the young as well as with feeding the mate; they seem to be general attractive notes in this species. Perhaps it is more correct to speak of flirting as an attracting activity rather than as a courtship activity. Of course, courtship feeding itself is like feeding the young, but serves courtship functions; hence it does seem logical to classify it and flirting and grooming as courtship activities even though they have other functions or are like unrelated activities.

Young are not brooded after the first few days. This releases the parents to forage more and feed the young twice as often at a time when the young need more food, but depends on how fast the young can gain temperature regulation. R. Ricklefs (pers. comm.) notes that putting food energy into early temperature regulation (as down feathers) takes energy away from growth, hence birds that brood their young have faster-growing young. Spotted Antbirds have downless young that grow very rapidly, probably at almost as high a rate as is possible consistent with developing temperature regulation so both parents can forage for them; predation rates probably favor fast growth of young. The lowering of growth in weight the last few days in the nest may represent channeling of energy into feather growth so young can leave the nest and thus avoid predators, but may just reflect loss of water (Ricklefs, 1968: 34) with feather growth.

The high feeding rate of nestlings in Days 8 and 9 is probably facilitated by the parents' foraging close to the nest. They thus reduce travel time. Danger to themselves from predators is also reduced, for the adults can watch for predators near the nest while foraging. Undetected predators could find the nest more easily, however, because of the short parental trips and high feeding rates. Foraging away from the nest probably favors few trips with rare large food items; foraging near the nest favors bringing common small items. The young perhaps do not get as much extra food as the increase in feeding rate would suggest, but may get as much food or more than in previous days. The local population of arthropods near the nest is probably reduced, and this may explain why feeding rates slow on Days 10 and 11 even though parents continue to forage near the nest. At any rate, it would probably not be possible to forage near the nest for the full nesting period without reducing local prey populations or attracting the attention of predators.

Foraging near the nest may be an advantage during the last days the young are in the nest for another reason: young old enough to jump out of the nest

can be rushed out of the nest and led away by the parents if they see a predator approaching. If this is the main reason, the increase in feeding rate may be unimportant. Probably the increase in nest-leaving calls and activity by the young keeps parents close to them.

The sudden increase in feeding rate when one of two young has left the nest, usually due to the sudden increase of feeding by the female, is also interesting. It may be that the low feeding rate of Days 10 and 11 is a result of wariness about predators, for one parent gets food near the nest as fast as two the moment that one young has left the nest. The young that has left the nest is soon off in a safer site with an unexploited food supply, of course. One begins to suspect that the low feeding rate of Days 10 and 11 may encourage young to leave the nest or be necessary because of danger from predators, rather than be caused by lack of food near the nest. At one nest the female soon started feeding two young rapidly on Day 9 when the male, scared away by the observer at the start of observations, deserted them for over an hour. It may be, however, that the female normally forages moderately far from the nest at this time, bringing large prey, and thus is merely avoiding competition with the male rather than withholding food from the young.

Without exact knowledge of weights of food and of distances at which the adults are foraging, plus more data to make sure that these changes in feeding rate are normal, one can say little more. Skutch (1949) suggested that tropical birds are not feeding their young as fast as they can but instead are avoiding going to the nest so rapidly as to attract predators, while Lack (in an addendum to Skutch's article) reiterated his earlier (1947-48) suggestion that birds in general feed their young as fast as they can. The sudden changes in foraging rate by Spotted Antbirds favor Skutch's view, for a doubling of foraging rate is not possible in a system in which young are being fed at a truly maximal rate. However, Lack's general view is correct if Spotted Antbirds are just foraging temporarily near the nest at rates they could not sustain for long without lowering local food supplies drastically. Moreover, the weights of food going to young probably do not differ as much as do the rates of feeding. One cannot yet decide for or against Skutch's or Lack's theses on the basis of data from Spotted Antbirds, but it would be interesting to know if feeding rates are maximal or are slowed by the danger of predation. I suspect they are nearly maximal given the various dangers of predation—i.e., Spotted Antbirds could forage closer to the nest on the average were it not for predators on adults and young, but are feeding the young about as rapidly as is safe.

Probably predation pressures from snakes and other nest-robbers make it adaptive for Spotted Antbirds to leave the nest on Day 11, when they can barely fly. Such young are separated, one with each parent, so a predator is unlikely to get both young at once as it could in the nest. Rates of loss of

fledglings are much lower, even at this stage, than rates of losses of nestlings. Also the parent can lead the young to a new place if predators are searching nearby. Later, when the young fly better, the family reunites.

R. Ricklefs (pers. comm.) has pointed out that in birds the amount of parental alarm and attack is correlated with how much they have to lose; bird species with few eggs tend to defend or display less than birds with more eggs, and there is an increase in defending as the eggs or young develop, up to the point where young are flying well. In other words, the greater the investment of parental energy, the greater is the importance of defending this investment. At their nests Spotted Antbirds perhaps tend to flee and chirr because they have only two eggs or young and would run too much danger to themselves or to the nest without concomitant gain in the probability of young surviving. Once the young is out of the nest, however, the parent has expended much energy on it and also can give the young a fair chance of escaping predation by simple displays that do not put the parent in much danger.

The limited displays of one female near a nest with eggs suggest frozen motions of conflicting behavior patterns, perhaps between incubating and attacking or fleeing. The flitting, flicking, brief intervals of challenging or mobbing, and other agitated activities of a parent when one is near a young bird also suggest conflicting tendencies. There are ethologists (Armstrong, 1949) who feel that distraction displays generally arise from such conflicting tendencies, as well they may evolutionarily. However, the strong distraction displays in Spotted Antbirds are so distinct (the fluttering run, the shielding flight, the shot-bird display, etc.) and ritualized that they seem quick and direct reactions to a situation rather than the hesitant, irrelevant and alternating activities one commonly gets in conflict situations. There should be selection for direct reactions in situations of great danger, not selection for finely graded or irregular responses, unless an irregular response confuses the predator. Only neurophysiological evidence will show whether such displays are caused by conflicting neural inputs.

Fledgling Spotted Antbirds show about the same weekly feathering changes as do the larger Bicolored Antbirds, even though one might expect a small bird to grow and molt and become independent more rapidly than a larger one. Perhaps Bicolored Antbirds, which generally follow the rich food supplies at swarms of ants and are moderately high in the peck order, are better able to support a rapid growth rate once the young are out of the nest than are the Spotted Antbirds, which are subordinate and must go through occasional periods with relatively less food (see the section on foraging behavior). Lack (1968: 289) has suggested that slow growth rates in nesting swifts and others are adaptations for periodic food scarcity, partly because a slow-growing bird can put more of its energy into fat reserves.

Spotted Antbirds renest rapidly if eggs or young are destroyed, but wait almost two months between nests if young are raised to independence from the first nest. R. Ricklefs (1969*b*) has found that birds of northern lands commonly renest nearly as quickly when young are fledged as when they are destroyed, while tropical birds commonly wait longer if young are fledged. He interprets this as a reaction to predation pressures and food availability for young and time available for breeding: in the tropics, with high predation on nests and less restriction on breeding seasons, each young that fledges is valuable and worth a long period of care; in the north, where there is less predation and young can find food with little difficulty, they gain independence while still in juvenal plumage so that parents can raise another brood before the short breeding season ends.

In Spotted and Bicolored antbirds, the dependent period comes to an end as the young gain their first adult plumage and adults become aggressive toward them, while in northern birds the young seem more often to be forsaken despite their juvenal plumage. Perhaps for this reason, northern ornithologists have not emphasized the value of the juvenal characters as nonaggressive stimuli (except Hinde, 1961: 405). Ethologists and psychologists have suggested for years that the big eyes and heads of "babies" elicit nonaggressive behavior in humans. However, these characters have other functions and probably are not evolved specifically to lower parental aggressiveness.

Although such tropical birds as Spotted Antbirds have low clutch sizes compared with birds of higher latitudes, they generally produce many eggs per year because they renest repeatedly and have long breeding seasons. Probably many pairs manage to produce a few young each year, despite low clutch sizes and extremely high rates of nest predation.

The Spotted Antbird stops nesting a month earlier than the Bicolored Antbird, which nests from early April to mid-December. The month of November is the wettest month on Barro Colorado, with an annual average rainfall of 454 mm. Possibly there is too much rain in November for Spotted Antbirds to incubate or feed the young and still get enough food for themselves. Small birds have a proportionately more rapid metabolism than larger ones, and Spotted Antbirds exchange incubation duties and feed the young more often than do Bicolored Antbirds. If excessive rainfall interferes with Spotted Antbirds' getting food, they should be unable to nest and hence rare in regions where rainfall is over 400 mm per month for many months of the year unless the rain falls mainly as occasional deluges or at night. Slud (1964: 221) found fewer in rainy parts of Costa Rica than in a periodically dry region. I found a few at Tanandó and Yuto, up the Atrato River from Quibdó in western Colombia, in a region of about 500 to 900 mm rain per month. The species was absent at similarly rainy El Tigre (4° 57' N lat., 76° 30' W long.), where I spent two weeks. It is much more common to the north, in Antioquia

and Córdoba, in areas of less rainfall. However, the rainfall may be causing an important change in food supply or forest structure rather than interfering directly with the nesting. Usually there are more kinds of professional ant-followers in wet regions, for instance.

It is more likely that the Spotted Antbird stops nesting earlier than does the Bicolored Antbird because the former is low on the interspecific peck order at swarms of ants, or because its food supply tends to fail earlier. In the former case, migrant thrushes at the swarms of ants could be interfering with the nesting of Spotted Antbirds. Although I could easily have overlooked young Spotted Antbirds the first October and November (1960) I was on Barro Colorado, it is also possible that the huge influx of thrushes and other migrants that fall prevented the Spotted Antbirds from raising young successfully. Fledgling Spotted Antbirds were certainly numerous the next October and November, in a year when migrants were poorly represented at swarms. However, the 1961 and 1965 records for Spotted Antbirds indicate strong nesting in September and October, even though the latter is the peak month for migrants at swarms of ants.

The failure of food supply seems a more likely reason for the termination of Spotted Antbird nesting in early November, before the end of the rainy season. Samples of arthropods from the leaf litter on Barro Colorado, taken biweekly in 1961 from late February to mid-November, show a peak of sowbugs early in June and a progressive decline into November. The general pattern of total arthropod numbers is similar. Apparently leaves fall and accumulate on the forest floor during the dry season, leading to a spring and summer "bloom" of arthropods that consume most of the litter by November (Willis, MS). Sowbugs are an important prey item for Spotted Antbirds. The larger antbirds take large prey and such predatory arthropods as spiders, which hide under limbs and treefalls and should be most abundant after the peak of abundance for small prey. However, much more information is needed, especially data on correlations between nesting seasons of Spotted Antbirds and rainfall and insect abundance in other regions.

WANDERING YOUNG AND TERRITORIAL ADULTS: SPATIAL BEHAVIOR

Once a young Spotted Antbird leaves the territory of its parents, it wanders alone except for associating with birds of other species in forest flocks and over swarms of ants. Adult Spotted Antbirds chase it away, and it ignores or evades or chases away other wandering immatures of its own species. Both male and female immatures wander more or less nomadically until they are several months old.

In foraging, nomadic immatures are clumsy for a month or two after leaving their parents. The immatures seem to expend much energy flying

around, chasing prey, and even picking up bits of leaves or twigs. At times they are forced to expend energy because dominant birds restrict them to poor regions at the periphery of ant swarms. However, a wandering immature that is away from ants or away from competitors over ants often seems hyperactive compared with older birds in such situations.

Nomadic immatures are very quiet; they chip and chirr much less readily than do adults. Their chips and chirrs are often falsetto for a month or so. The immatures flee readily from the observer or from a hawk, but seem to be poor or reluctant at performing panicking or mobbing displays. In the mist net, an immature chips or whimpers very infrequently and weakly compared with an adult. The older an immature is, or the less often it has seen the observer, the more likely it is to chirr at him or to flee in a chipping panic rather than to flee silently or to become tame or to investigate.

Agonistic behavior is also infrequent among young birds. They usually do not sing, so that territorial adults seldom detect them unless they come to the songs of the adults. When detected, the young bird usually evades the challenges and supplantings of an aggressive adult rather than showing challenging and cringing behavior. At times one loud-peeps or faint-peeps when supplanted. Immatures over six months old perform cringing more often, and a few younger females begged with fluttering wings as if to a parent. More commonly, nomadic immatures perform displacement behavior, flitting the wings or flicking the tail, toe-looking, bill-wiping, etc. There is seldom any aggressive display. Usually an older immature supplants a younger one with little display.

At times young males show that they can perform clumsy challenging displays. Once the dependent five- and six-week old young males of two families, wandering around the same swarm of ants, spread into low-challenging poses at each other. They mixed the postures with flitting the wings, flicking the tail, and chipping as if highly excited or panicking, and did not snarl. Soon they followed their parents away.

Another young male showed adult sequences of agonistic behavior when only 90 days out of the nest, or about 116 days after egg laying. He had barely been driven away from his parents at 58 days out of the nest and been driven away by the male of the adjacent territory at 64 days, when he entered the next-to-adjacent territory at about the time a hawk killed the resident male. (Following the trail of an antswarm, I found on the leaf litter a spot of blood and a few of his feathers, plus a white feather of a *Semiplumbeus* Hawk or, less probably, a White Hawk). The resident female fed both their young birds, about 30 days out of the nest. Four days later the wandering young male helped her in a ferocious dispute with a neighboring pair. He used high- and low-challenging as noisily and persistently as any mated territorial male, but was somewhat clumsy in his displays and gave

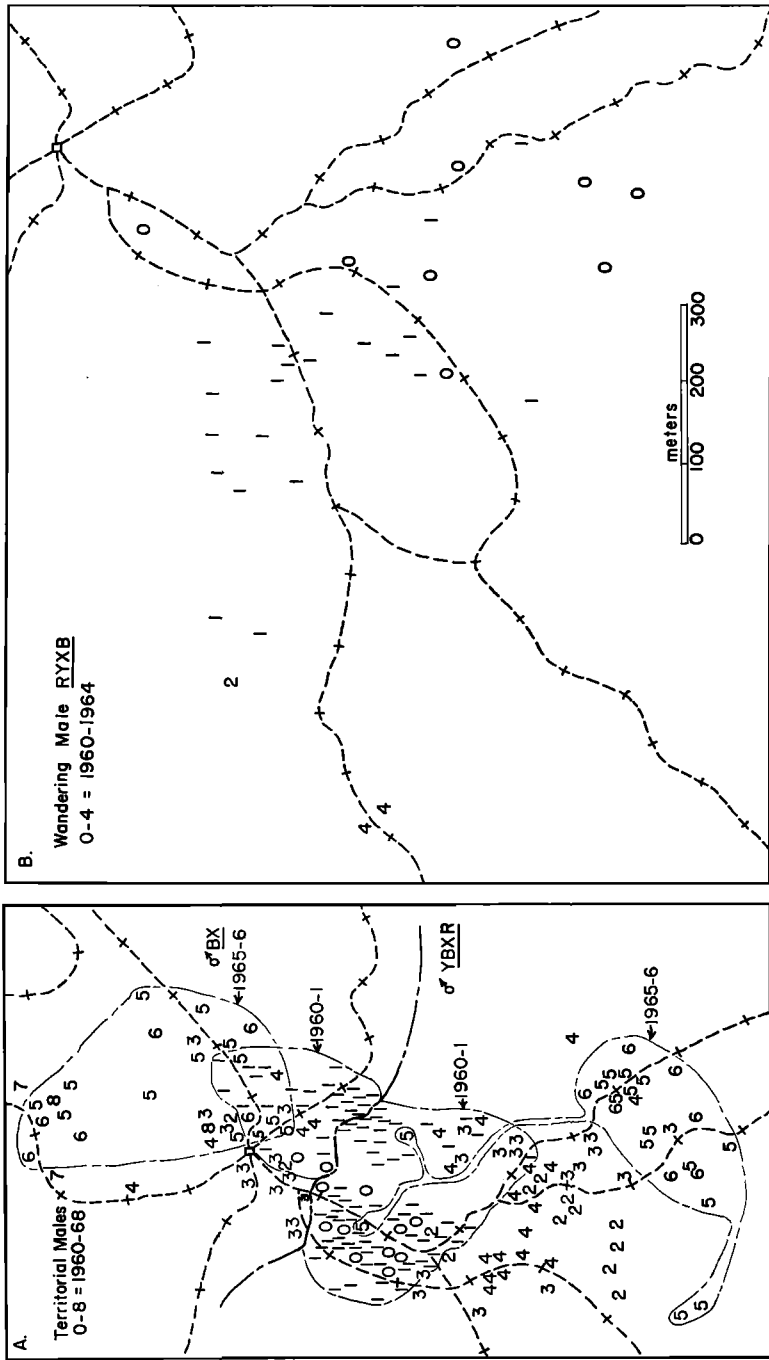


Figure 19. Wanderings of male Spotted Antbirds. A, Territorial males BX (above dot-dash line) and YBXR (below the line) shifted away from each other over the years; other males moved into the gap after 1962. Each number represents a sighting during the year specified (0 equals 1960, and so on). B, Wandering male RYXB moved widely until he settled down in a territory and gained mates north of Zetek Trail in 1962 to 1964.

rather falsetto snarls. He was still paired with the same female and on the same territory one year later. No other young male showed such agonistic displays. Presumably this was because no other male studied gained a mate and territory in the breeding season when he was hatched.

Normally, a young male wanders for a few months and then settles in a broad area overlapping the corners of several adult territories (Figure 19). He may shift to a completely new area or shift his home range gradually, but he does not wander nomadically. Ordinarily he starts singing and stops evading local territorial males in the rainy or breeding season after he hatched. At times he starts in the dry season, only a few months after hatching. The area is sometimes one he has occupied the preceding several months, sometimes a new area. He sings frequently if he does not have a mate. He disputes with neighboring mated males but tends to be pushed toward the center of his area by them, sometimes to the extent that he deserts the area and commences singing in a less crowded one. In his area the young male is fairly noisy at chipping and chirring as well as at singing and snarling. Displaced males, like wandering immatures, are not noisy until they find new areas. Usually the young male finds a mate by or during the first breeding season after he hatched, and older males are unmated only when they have lost mates to a neighbor or when their mates disappear.

Once a male is mated and starts nesting on an area, he may shift it gradually over the years, but he seldom deserts the area for a new one. So far only one male out of over 100 has shifted his territory across an intervening territory when his mate disappeared. Figure 19 shows more normal patterns of shifting with the years. Male YBXR, following the disappearance of one mate, stole the mate of his neighbor to the southwest and gradually shifted into the area she had occupied (1963-64). When he lost this mate, he wandered into his former areas occasionally (1965 records), but resettled with a new mate to the south. Male BX shifted northeast with a new mate 1964 to 1971. In many other cases, new mates or new neighbors caused minor shifts in territories.

Females shift gradually when under six months old, but either settle or shift drastically when old. Young females are very evasive and low on the peck order the first few months they are independent. They are even less likely than young males to show conspicuous alarm behavior or agonistic displays. However, one young female sang a few times when about 75 days out of the nest. The female does not pair the first few months she is independent, even if a territorial unmated male flirts with and feeds her assiduously. She may consort with a male for several days, accepting his food, but she does not nest or sing or attack intruding females. Once such an intruding female became the mate of the male, and the young female wandered away. Some females nest as early as six months of age, as in Bicolored Antbirds, but I have no record

of a young female Spotted Antbird breeding in the breeding season in which she was hatched. Nearly all are mated and breeding in the next breeding season after their hatching.

After a female gains a mate, she sings readily to him or in confrontations with neighboring pairs, challenges and chases trespassing females, and is quite noisy and adult in alarm and other behavior. She stays with her mate in one area as long as he survives. When he is on the nest incubating, she sometimes wanders to feed at ant swarms in nearby areas; she is much less limited to the territory than he is. If the male disappears, the female either gets a new mate and stays in more or less the same area or deserts it completely, settling with an unmated male on his more or less distant area.

Thus the general area used by a pair is determined by the bird that was there first. A new female or persistent lack of a female commonly causes minor shifts but rarely a major one, a new male causes no shift, persistent lack of a male causes a complete shift, and a settled pair stay together and shift the area used relatively little over the years.

DOMINANCE AND TERRITORIALITY

On his area the male is completely dominant; he challenges and chases trespassing males, especially ones that sing at or challenge him. He challenges and drives away trespassing females unless they chirp at him. Trespassers that return persistently and are quiet or use the cringing display may be ignored if the male is foraging or otherwise occupied, or if the trespassers stay out of his way, but direct confrontations start new attacks or challenging.

As in Bicolored Antbirds, there is a reversal of dominance as soon as the male leaves his area and enters the contiguous areas of other males. The male is now subordinate, even if he is older than the neighbor. The "age rule" of dominance, that older birds dominate younger ones, has been replaced by the "territorial rule," that birds in their own areas dominate others. The dominance reversals with space suggest that the home areas of Spotted Antbirds are territories, by the definition that a territory is "a space in which an animal or group dominates others that dominate it elsewhere."

The territorial boundaries, or zones of reversal of dominance between territories, are rather sharp and stable in Spotted Antbirds. At times males chase each other back and forth across such boundaries; more commonly, males sing back and forth across the boundaries. A male comes to playback of tape-recorded songs within his area and toward the boundary of his area, but sings to playbacks near the boundary.

Females challenge and chase trespassing females, and the latter chase them back when the combatants have crossed the territorial boundaries. However, females are not as combative as males, and they tend to be subordinate to trespassing males. Of 1,194 recorded supplantings and displacings where

the sex of both Spotted Antbirds was recorded, 805 records were between males, 213 between females, 150 were records of males dominating females, and 26 were records of females dominating males. In the last cases, the female was almost always an adult female on territory supplanting or displacing her own son or a trespassing juvenile or first-year male, and in most cases her own mate was also present and chasing the trespassing male about. On one occasion the resident female snarled at an intruding male three times, then retreated as he quietly foraged her way. A resident female being crowded out by an intruding male sometimes snarls faintly now and then, but is ignored much of the time. One young male snaked his neck out toward the snarling resident female, and she stopped challenging. On several occasions when the resident male was not present, a wandering male supplanted the resident female or chirped to her as both occupied the swarm without disputing. In some cases, a returning young male supplanted his own mother. Resident females sometimes wander into neighboring territories, especially when following army ants, because a neighboring male is likely to ignore them if they flirt with him and because the neighboring females are not very persistent at chasing them.

TERRITORY SIZE, DENSITIES, AND BIOMASSES

The pairs of Spotted Antbirds on the study area in August of 1964 are shown in Figure 20. In 1964 and other years there has been about one pair of Spotted Antbirds every 4.7 hectares (12 acres), or 21.3 pairs per square kilometer. In May, just before the first young of the year leave the nest, there is one wandering bird per 50 hectares or so, or two per square kilometer. In May each year there are about 45 resident and wandering birds per square kilometer, or some 700 birds on the island of Barro Colorado. Since each bird weighs 15.4 to 19.0 g (excepting two egg-laying females at 21.7 and 19.9 g), and the average weights for 16 adult males, 10 other adult females, 2 juvenile males, and 10 juvenile females were 17.5 g, there are some eight g per hectare as compared to three or less g per hectare for the Bicolored Antbird (Willis, 1967).

HABITAT SELECTION

On Barro Colorado, Spotted Antbirds are relatively common everywhere. However, they are most abundant in the young forest and in certain regions

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Figure 20. Pairs of Spotted Antbirds on territories on Barro Colorado Island in August, 1964. Names of pairs are placed approximately at the center of recorded observations (see Figure 19). Trails are marked off in 100-m sections, which are numbered on the map every 500 m. The laboratory of the Smithsonian Institution is at the upper right.

of old forest. The wide areas of old forest with open undergrowth near the end of Wheeler Trail, from Armour 8 to 20, and the canyons in old forest between Balboa and Wheeler Trails do not seem to attract either wandering immatures or territorial adults. Adults in such areas have huge territories. Areas of old forest with dense patches of *Ananas magdalenae*, such as Zetek 9 to 17, have large populations of Spotted Antbirds. So do vinecrowded young woodlands with occasional treefalls in the vicinity of Wheeler 5 to 15 and along Barbour Trail.

The impression I have is that if one stands in the undergrowth and sees mostly large trunks and leaves of scattered saplings, he is likely to be in a place where few Spotted Antbirds wander or reside. If he can scarcely see the bases of trunks for the leaves of low bushes or *Ananas* or for treefalls or vines or lianas, Spotted Antbirds are likely to be numerous. However, some areas of young woodland have rather open undergrowth and still have many Spotted Antbirds. In these areas, I look for bird flocks and for treefall areas when I am looking for Spotted Antbirds.

DISCUSSION

The lack of adult behavior patterns, including alarm patterns, in wandering immature Spotted Antbirds probably has both morphological and environmental bases. Exceptions to the general lack of alarm and agonistic reactions, such as the young male (p. 84) that got a territory and mated early, suggest that immediate environmental pressures are more important than inability to perform actions because of lack of structures or practice.

Whether because of environment or heredity, the lack of conspicuous alarm patterns in young is probably enforced by natural selection. Young birds do not associate with mates or young that could be warned by alarm behavior, so their offspring or potential offspring will not be helped by calling or displaying. Moreover, young birds that gave alarm calls or displays might be unable to escape an alert predator or might bring up territorial adults to compete with them or drive them away. Any advantages the young might gain by distracting or warning the predator are presumably overbalanced by the above and other disadvantages.

Probably the young bird has little to gain and much to lose by singing or "challenging" at adults. If it keeps quiet, adults may overlook it. There is no reason for it to sing, for it has no mate or young. It probably would lose challenging duels with adults, which show very aggressive behavior if challenged on their established territories.

The fact that young males tend to settle in a region even before they start singing and aggressive displays suggests that they gain by settling, perhaps because they familiarize themselves with places to hide from predators and

because they can estimate local competition. Probably the occasional shifts to a new areas occur when local competition reaches too high a level to start singing or challenging to set up territories; however, more detailed studies are needed.

Adult males tend to shift gradually, mainly when there is a change of mates. Their status is already established in a given region, and to start out in completely new regions would probably reduce them almost to the low status of wandering young birds as well as expose them to predation because of unfamiliarity with the new areas. They are not much more likely to find a new mate more easily by moving, since the settled females around them are generally already paired. The silent and mobile unmated females probably would come to a male that stayed put and sang much more rapidly than he could find them by wandering quietly off his territory. Unmated males sing and wander more in their home areas than do mated males, thus increasing chances of females finding them or their finding females.

It is more difficult to understand why females starting to form pair bonds at under six months of age do not nest and sing and drive away trespassing females. A female that finds a male and territory immediately can stay unless, of course, a more mature unmated female comes along and displaces her. Perhaps the young female is not ready to fight or nest; her learning foraging, antipredator, and other abilities might be slowed if she became occupied prematurely with agonistic or reproductive activities. Since the female is rather unimportant in territorial activities, only intruding females need be chased. Apparently the danger of intruding older females must be slight, or the disadvantages of being displaced and having to seek another mate are relatively unimportant, since the young female does not react very vigorously to trespassing females. It is not evident why the young female does not attack, unless fighting would tend to interfere with other activities or directly eliminate aggressive young females from the population. Perhaps movement (sampling territories and available males?) is an advantage to the young female, however.

At times adult males shift according to the preferences of the new mate, as in the case of male YBXR (Figure 19), and as in the Song Sparrow (*Melospiza melodia*) pair in which the male enlarged his territory to include a nest his mate built outside of it (Nice, 1943: 191). Probably the male sets the general area but the female can modify it, adapting it for the special requirements of a mated and nesting pair within limits set by neighboring pairs.

Adult females, unlike adult males, leave the territory after losing the mate if no new mate appears within a short time. The female is subordinate to neighboring males if she has no mate to protect their territorial dominance, hence will be subordinate whether she stays or moves. By moving, she

probably exposes herself to predation but definitely increases her chances of finding an unmated male with a territory.

That the presence of a territorial male gives the female confidence in displacing a trespassing male, and that flirting sometimes stops male aggression, reminds one of social patterns in some monkeys, where the offspring of a dominant female tend to be bolder when she is near, and "presenting" (as in baboons) is often a gesture of a subordinate. Such patterns are probably likely to arise in animals that are strongly dimorphic sexually or by age. The plainer or smaller morph is not equipped to outface the brighter or larger morph in competitive agonistic displays, hence develops behavior patterns that evade the disadvantage.

There is currently much discussion of the reasons for sexual dimorphism and associated diethism (such as subservience and flirting by female Spotted Antbirds) in animals and humans. Verner and Willson (1966) noted the extreme development of sexual dimorphism and the "double standard," in which males are polygamous but females stay with one mate, in birds of habitats that have local places of high productivity. Orians (1969*b*: 602) further suggested that, in animals in which the male cannot (mammals) or need not (locally food-rich environments) take care of young, that males are likely to become polygamous, to fight with other males for access to females or to localized environments, and consequently develop hypermasculine colors, size and behavior. Selander (1966: 141) suggested that on islands, with reduced interspecific competition and many available niches, woodpeckers tend to develop high sexual dimorphism to allow males and females to spread into different niches. Jehl (1970) suggested that for the Arctic, with its short breeding seasons, sandpipers have developed sexual differences in bill size to permit quick recognition of sexes and rapid pairing.

It is interesting that a common factor emphasized by these and other biologists (Crook, 1964; Lack, 1968; etc.) has been that irregular environments, with locally or temporarily superabundant foods, lead to sexual dimorphism and diethism. Several students of humans have also suggested that environments with irregular distributions of resources lead away from egalitarianism both in economics and in the roles of men and women. Lewis (e.g., 1968) suggested that in humans the uncertain and changeable slum subculture favors care of offspring by females and hyperfemininity and hypermasculinity. Apparently the uncertainty of jobs, except service ones to dominant members of society, the fact that some males have more money than others and that some others can pretend importance, favors sequential polygamy, male strutting, and a complex of related factors much like the ones Verner has suggested for Long-billed Marsh Wrens. Glubb (e.g., 1963: 145) has suggested that the warlike but chivalrous, hypermasculine and hyperfeminine culture of the Bedouins of Arabia may be adaptive for their periodic, varying

sources of pasturage, as was the similar culture of chivalry in feudal European societies cut off from trade by the Arab control of the Mediterranean. Where life is uncertain, the masculine but chivalrous fighter can win pasturage or his neighbor's animals or women. By this view, the present tendency to sexual equality and away from heroics and warfare is more adaptive in evenly poor or evenly rich countries than in "developing" countries, because the last have rich areas next to poor ones.

Perhaps female or young animals and humans in irregular or uncertain habitats would be highly disadvantaged at getting food if they did not have different appearances or behavior than the males. Certainly, the tendencies to sexual differences in care of the offspring, in plumage, and in courtship seem greatest among birds of variable or peripheral habitats and least among birds of mature or even habitats. The latter have sparse but even food supplies split up by competing species, and are perhaps most efficiently used by mated pairs working for food the same way rather than by sexually dimorphic birds working in different ways.

Spot-backed Antbirds, so closely related to Spotted Antbirds that some ornithologists might place them in the same species, are less sexually dimorphic than are Spotted Antbirds. The female Spot-backed Antbird has a white throat, but otherwise both sexes look like slightly dull (somewhat female-like) but spot-backed versions of male Spotted Antbirds.

The presence of strong sexual dimorphism in only one of a pair of closely related species suggests that dimorphism is not generically fixed, but related to differences in specific niches. Reproductive differences between Spot-backed and Spotted antbirds are little known, but are unlikely to be striking. Skutch (1969: 292) recorded mutual grooming in Spot-backed Antbirds, and I have noted several calls and behavior patterns similar to those of Spotted Antbirds. The main differences I have noted are ecological ones, primarily that Spot-backed Antbirds seldom follow army ants. It may be that irregular ant-following by Spotted Antbirds is the aspect of their environment that favors sexual dimorphism and diethism.

If ant-following rather than generic relationship is important in the question of sexual divergence, one should compare the moderately closely related Bicolored Antbirds and Spotted antbirds. Bicolored Antbird females behave and look much like males. Indeed, male-male pairs sometimes form and persist for years, so the birds themselves clearly do not distinguish the sexes well. Bicolored Antbirds are moderately large (30 g), and are thus dominant enough that few species can drive them away from swarms of army ants. They depend on ant swarming to provide a steady source of food. Spotted Antbirds are small (17.5 g) and are regularly chased away from the good central regions of swarms by Bicolored Antbirds and many other species. They cannot depend on ant swarming to provide a steady source of food.

Instead, they forage at local or irregularly "available" sites (i.e., not pre-empted by larger birds) over the ants or forage away from ants (see below).

How could sexual dimorphism and diethism be favored by catching concentrated but irregularly available food over ants part of the time? The most obvious result of dimorphism and diethism is that Spotted Antbirds do not drive trespassing birds of the opposite sex away from swarms, or split up the swarm with them, as strongly as do Bicolored Antbirds. Instead unmated male and female Spotted Antbirds can congregate at small but rich sites, or move quickly to irregularly available sites, if they happen to be present together. A territorial species is thus transformed into a semi-territorial species. When the local territorial male is on the nest, his female permits wandering young males or even an occasional neighboring male to trespass. Her loss in being subordinate to the trespasser is overcome in part by his susceptibility to flirting and his tendency to let her stay. The wandering young female, the wandering mated female whose male is on the nest, and the female that has lost a mate are all tolerated by territorial males to some extent. If the mates of these territorial males are present, there is little place for wandering females; but even territorial females are rather "femininely" nonaggressive in Spotted Antbirds. Even when the trespasser is of the same sex as the resident bird, movement to a different corner of the swarm, off to forage not far from ants, or waiting for habituation to intruders is sufficient to permit foraging in a species not obligately tied to ants.

The habituation of aggression in local males and females can be rapid if a different-looking bird is involved, especially if that bird chirps and flirts and thus arouses incompatible sexual tendencies. Spotted Antbirds need rapid habituation, for they have such small territories and move out of them so little that a wandering bird following a colony of ants is likely to encounter a new pair of Spotted Antbirds each two or three days. Bicolored Antbirds, all of which have large territories and foraging ranges, encounter new pairs much less often.

The sexual dimorphism of Spotted Antbirds perhaps is a compromise, one that permits facultatively tolerant ant-following while still maintaining the rather rigid territoriality needed for use of evenly distributed food away from ants. Such facultative toleration of trespassers is probably dependent on the food supply being very irregular for Spotted Antbirds at swarms. If food is likely to change from one moment or site to another, it may be more efficient for individual Spotted Antbirds to allow others in close to rich feeding sites, drive them away from intermediate sites, and avoid them at poor sites. Mobility and flexibility of response may be more important than unvarying defense. The lowering of the general level of agonism by one half, by simply putting males and females into "different species" in behavioral and morphological characters, may also attract less attention from dominant birds like

Bicolored Antbirds when the Spotted Antbirds do find a rich site. However, the level of agonistic behavior is still high among male Spotted Antbirds, and fairly high among females. Probably any "altruism" toward trespassers occasioned by the sexual dimorphism is permitted genetically because in many cases the trespassers will be relatives, and permitted ecologically because the trespassers generally will be helping exploit locally superabundant foods.

Male Spotted Antbirds have developed somewhat brighter colors and stronger songs than Spot-backed Antbirds, suggesting that there has been an increase in male "assertiveness" in Spotted Antbirds as well as a decrease in female assertiveness. Possibly male Spotted Antbirds are better able to chase competitive males away from their mates or good feeding sites at ant swarms if they have bright colors. There must be many disadvantages to loud songs and bright colors, such as increased conspicuousness to predators, so that the assertiveness of males must be favored by their greater ability to drive away trespassers if competition does become serious.

To summarize, evolution of sexual dimorphism and diethism probably is favored in irregular environments, such as alternating between ant-following and ordinary foraging, for many reasons. Reasons for one sex becoming less brightly colored, less assertive, include the following: antagonism is likely to be unusually high because of concentration at rich local food supplies, and lowered assertiveness in one sex is a quick way of lowering antagonism and permitting temporary use of the rich supply; lowering antagonism means that fewer competitors of the same or other species will detect combatants and home on the rich food site; wandering individuals (often genetic relatives of the territorial ones) are less likely to be driven off, thus permitting their survival under fluctuating conditions that force them to wander, and allowing use of rich food sources like ant swarms day after day; small size of "territories" compared with the movement of or geographical changes in resources compels a wanderer to encounter many others, and different or nonaggressive behavior or plumage facilitates quick habituation; females can sneak in quickly at rich food sites; and females can be protectively colored for incubation or other purposes.

Reasons for the other sex becoming more assertive have mostly been discussed by Orians (1969*a*) and others, and include: males (or females) can grab good sites if they are brightly colored (etc.) and win in local fights with others; in an ephemeral or local environment, females can be stimulated more quickly and recognize males of the right species more easily and quickly; and the larger sex can sometimes protect against the suddenly appearing predators characteristic of an irregular environment.

Factors acting both ways, to decrease the assertiveness of one sex and increase it for the other, include some of the above plus the low interspecific competition of irregular environments, which favors spread of niche by sexual

specialization or use of irregularly superabundant food in the way Spotted Antbirds use ant swarms.

One must emphasize, however, that an ant swarm that is irregular to a Spotted Antbird is not at all irregular to a Bicolored Antbird; one often has to study a species closely to know whether it faces irregular conditions or not. Of course, the irregular conditions that favor strong sexual dimorphism and diethism are often much more apparent than they are for Spotted Antbirds, which are not very dimorphic or diethic.

Spotted Antbirds are strongly territorial and drive trespassers off rapidly. They thus actually show aggressive and submissive behavior less often than do Bicolored Antbirds, which permit trespassers nearby but show much agonistic behavior. Spotted Antbirds can forage away from swarms of army ants reasonably well, hence do not have such strong reasons for staying near a domineering resident pair at a swarm as do trespassing Bicolored Antbirds. The trespassers' lack of persistence makes it possible for the resident to chase them off with little waste of time or energy. When a Spotted Antbird returns persistently, it is eventually tolerated to some extent.

Presumably aggression or submission are selected for only when they gain for an animal more than they lose for it. They can be selected for mainly in a moderately localized (irregular) environment, since in a widespread environment or an extremely localized one efficiency at getting food is better than efficiency at defending, or staying, and territorial or other systems evolve that minimize the necessity of agonistic behavior. I suspect territoriality limits aggression rather than being basically aggressive itself. The fact that among territorial birds submission in neighboring areas lowers the expression of aggression there certainly lowers the general level of aggression in the population. If there is going to be aggression, it may be better to have territoriality as a brake on it rather than to have it expressed in fights for dominance every time two animals meet. If an animal that cannot gain by aggression is able to develop nonaggressive interactions, of course the territorial system and its associated locally submissive behavior can be dropped.

FORAGING BEHAVIOR

The first reactions of a Spotted Antbird when one approaches and tries to study its foraging behavior are likely to be chirring and mobbing, flight to cover, or chipping and panicking; less striking reactions include singing as the bird moves over to the mate. Ordinarily the bird begins to forage more and more regularly, and soon almost ignores the observer. Birds watched over the years have become fairly tame, so that they scarcely chirr even when I first appear. Data in this section, unless otherwise specified, represent observations of birds that were neither showing alarm patterns nor other non-foraging activities, such as feuding or bathing or preening.

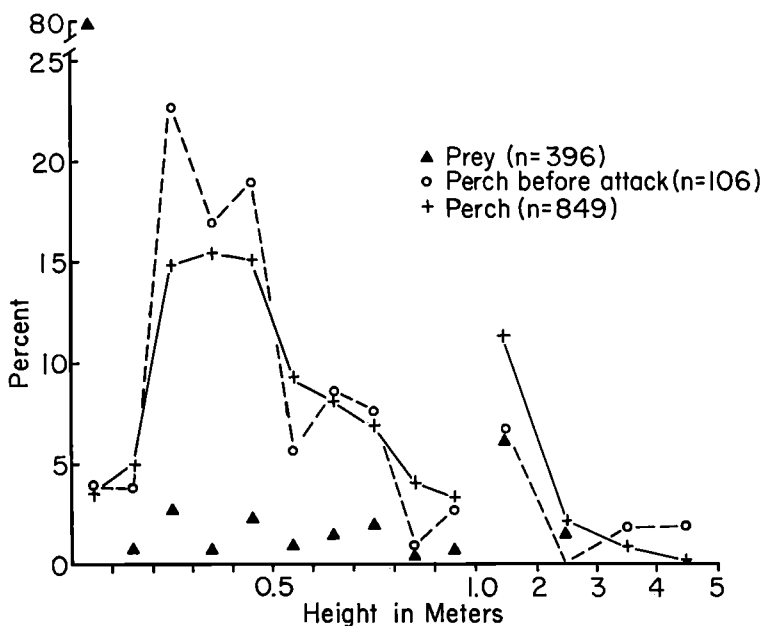


Figure 21. Heights of foraging away from swarms of ants: heights of perching, of perches taken before trying for prey, and of prey items tried for.

PERCH SELECTION

Foraging Spotted Antbirds generally wait on perches low in the forest undergrowth (Figure 21). They frequently take perches near the vertical and horizontal (Table 2). Perches over 4 cm in diameter are seldom taken, whether the perches are under 45 degrees from the horizontal or not (Table 3). However, the birds sometimes hop along such perches or on the ground for short distances.

The small Spotted Antbird, with feet about 3 cm long, uses perches of about the same diameters as does the larger Bicolored Antbird, which has feet about 4 cm long. Apparently neither clings very effectively if the claws cannot grasp half the circumference of the perch, but Spotted Antbirds cling to relatively large perches more often than do Bicolored Antbirds. The latter occasionally cling to large perches by repeated grasping or sliding with the feet or by fluttering the wings, especially when capturing an insect. Spotted Antbirds seldom do so, perhaps partly because they are lighter and often can hover to get such prey or need not support such great body weights.

A relative of the Spotted Antbird, the Scale-backed Antbird of Amazonia, is a small bird that specializes in clinging to perches of small to large diameter for long periods. It has feet about 3.5 cm long. The Spotted Antbird seems

TABLE 3
ESTIMATED DIAMETERS OF PERCHES OF SPOTTED ANTBLRDS

Diameter, Cm	Foraging Away from Ants		Foraging with Ants		Preening	
	Records ¹	Percent	Records ¹	Percent	Records	Per- cent
1	16- 25	15.8-18.1	72-127	30.5-35.6	24	31.6
2	38- 61	37.6-44.2	93-159	39.4-44.5	30	39.5
3	31- 42	30.7-30.4	36- 54	15.3-15.1	16	21.1
4	11- 9	10.9- 6.6	15- 9	6.4- 2.5	3	3.9
5	1- 0	1.0- 0	15- 6	6.4- 1.7	2	2.6
6	2- 0	2.0- 0				
7	0- 1	0- 0.7				
8	2- 0	2.0- 0	2- 0	0.8- 0		
10			1- 0	0.4- 0		
10 +			2- 2	0.8- 0.6	1	1.3
Total	101-138		236-357		76	

¹ Perches under 45° angle, followed by perches over 45° angle.

to be more of a generalist, intermediate to the Scale-backed Antbird and the Bicolored Antbird, in the diameter of perch relative to body size.

The feet of these three birds are very similar (specimens examined at the American Museum of Natural History). The toes and claws of Bicolored Antbirds are less slender than those of Spotted and Scale-backed antbirds, a relation one might expect from the greater body size of the Bicolored Antbird. The soles of the feet all have roughened or "cobblestone" surfaces, which perhaps grip the perches when the birds clamp the feet but slide easily when they swing around perches. Tarsal lengths are about the same in all three species, varying from about 22 mm in Spotted Antbirds to 24 mm in Scale-backed and 27 mm in Bicolored Antbirds. The differences in clinging between Spotted and Scale-backed antbirds and the similarities between Spotted and Bicolored antbirds do not correlate well with the morphological series of Spotted to Scale-backed to Bicolored antbird. The long and slender toes and short hind claw in the Scale-backed Antbird, relative to the size of these parts in the slightly smaller Spotted Antbird, may show morphological adaptations for clinging with the body nearly level on vertical perches.

Spotted Antbirds usually forage in moderately open undergrowth, near a vine tangle or fallen tree into which they flee if the observer or passing hawks disturb them. In very open undergrowth they move rapidly and are difficult to watch; they do not forage much. Dense growth, such as thickets of wild pineapple and the interior of treefalls, serve mainly as preening or hiding places; the birds seldom forage unless ants are flushing insects.

TABLE 4
ATTEMPTS AT PREY BY SPOTTED ANTBIRDS AWAY FROM ANTS¹

Prey Location		Attempts at Given Height (Meters)												Total	
		0.1	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9	1.0	2	3		?
Air	S ²	1											1	2	4
	L ³						1	1							2
Leaf, twig	S		1	4	2	3	2		4	1	1	11	4	4	37
	L	1		2	1	1						2		5	12
Stem, liana, limb	S	4	1	3		2	2	3		1	1	3		14	34
	L			2		2		2	3		1	5	1	3	19
Trunk, log	S					1						4			5
	L											1			1
Ground	S	290													290
	L	9													9
	T ⁴	10													10
Unspecified	S		1											3	4
	L	1													1
	?											1			1
Total		316	3	11	3	9	4	6	8	2	3	27	6	31	429

¹ 1 October 1960 to 30 September 1961. ² Sallying (n = 374). ³ Lunging (n = 44). ⁴ Leaf tossing (n = 10).

FORAGING AWAY FROM ANTS

To forage away from ants, a Spotted Antbird waits several seconds to several minutes on each perch, looking around and down at the ground. For 28 intervals between foraging attempts of birds foraging uninterruptedly, the average was 111.8 seconds and the extremes 8 and 283 seconds. The foraging bird sits, half-sits, or stands. At times it reverses on the perch or flies a few meters to a new perch. Passive waiting is the rule, active hopping or clambering or fluttering the exception. Now and then the bird lunges at prey, with or without a flight to a nearby location, or sallies like a flycatcher to snap up the prey on the wing (Table 4).

The most common method, sallying to the ground, involves a quick jump or jumping flight at prey on or near the ground, a brief fluttering capture on or near the ground, and a quick bounce or bounce-flight back to a perch above the ground. The V-shaped attack and return takes less than a second unless the antbird hops or spins and flutters to capture the prey.

If prey hides under the leaf litter, the bird sometimes stands on the ground with legs splayed and tail raised slightly and tosses one fallen leaf after another. As is the case for Bicolored Antbirds, each leaf is grasped in the bill and tossed

one way or the other with a quick lateral motion of the head and neck or head and body.

In sallies to vegetation, the Spotted Antbird is lighter and more agile than is the larger Bicolored Antbird. The former hovers readily, if briefly, to snap prey off leaves, lianas, logs, trunks, and other vegetation or out of the air.

Generally a Spotted Antbird is perched near the ground before a try at prey, and most prey comes from the ground (Table 4). Only rarely, away from swarms, is prey taken as much as two or three m above the ground. Once, however, a pair went to five m up to snap up winged *Azteca* ants emerging in large numbers from a nest. Birds away from swarms are not subject to competition near the ground, or can easily move to other equally good sites if competitors supplant them. Interspecific competition away from swarms of ants is discussed later, under the heading of "association with interspecific flocks."

SEARCHING FOR ARMY ANTS

Often one sees or hears singing or chipping Spotted Antbirds traveling through the forest undergrowth. At times the bird moves in one direction, perhaps commuting to a nest or going to an antswarm it already knows about. In the evening, after about 17:00, many of these traveling birds may have been going to bathe or traveling toward their roosting areas. At midday I less often noted travel. In the early morning, many birds were singing or traveling, or both, rather rapidly in irregular patterns. They looked about and foraged a little as they went, but they did not forage as efficiently as did settled birds later in the day. I suspect that a similarly high rate of traveling among Red-throated Ant-Tanagers in the early morning (Willis, 1960a: 164–165) represents searching for swarms of ants, and I suspect that Spotted Antbirds also search for swarms in the first few hours after dawn. If one bird of a wandering pair finds ants, it stops singing, then gives occasional songs that lead its singing mate to the ants. Birds that have not found ants settle down to foraging away from ants.

On nine occasions when I played the recorded loud-songs of Bicolored Antbirds, Spotted Antbirds appeared. Probably Spotted Antbirds, which often associate with Bicolored Antbirds at swarms of ants, use the calls of Bicolored Antbirds as clues to the location of swarms. In other playings of recorded songs, other ant-following species came to the songs of Bicolored Antbirds and some came to the songs of Spotted Antbirds (Willis, 1967: 25). In contrast to the loosely territorial Bicolored Antbird, the strongly territorial Spotted Antbird seldom comes to the songs or recorded songs of its own species unless the sound comes from its own territory. Once a loud song-dispute between two pairs of Spotted Antbirds brought up a wandering first-year male,

but one resident male quickly chased him away. More often song duels between a pair at a swarm and a distant pair end in the departure of the distant pair, which then forages away from any swarm.

As well as coming to the calls or songs of other ant-following species, the Spotted Antbird reacts like any habitual ant-follower to a "trail" (the ant highway between bivouac or nest and the swarm raid) of *Eciton burchelli*. It follows low over the trail, perhaps giving sharp chips as it goes, until it reaches the swarm of ants. When the bird chooses an ant trail that leads it to an inactive raid, it reverses and follows another branch trail to the main ant raid. Spotted Antbirds daily investigate a stately ant bivouac in their territory, and return periodically throughout the day if no ants are swarming. If bickering flocks of Bicolored Antbirds are waiting near an inactive bivouac, Spotted Antbirds wander about nearby and investigate the ants periodically. However, they stay out of the way of pugnacious larger birds, and they are not as prone to stay near the bivouac and rest as are birds more dependent on the ants. Spotted Antbirds are likely to wander off and start foraging elsewhere. When the ants do start raiding, these birds are likely to be an hour or two later at finding it than are more strongly dependent ant-followers. However, the Spotted Antbird returns to a given stately bivouac in its territory so persistently that it is likely to be the first or only bird present if the ants delay swarming until late in the day.

FOLLOWING THE ARMY ANTS

The Spotted Antbird commonly follows army ants if any are available and there are not too many dominant larger species of birds about. Figure 22 indicates that there is little change in the percentage of birds at swarms during the year. A slight decrease in the frequency of attending swarms at midyear probably results in part from my flushing birds away from undiscovered nests or young (and consequently away from ants). Moreover, the wandering immatures common in other months often follow ant colonies more persistently than do territorial adults. In periods when I have searched for Spotted Antbirds away from swarms, such as during census work from 1963 to 1971 (excluding January-March 1965, when I was taking movies at swarms), I nearly always found a higher percentage of Spotted Antbirds away from swarms than during the first year of study. Censuses by someone working with Spotted Antbirds are needed, rather than by a person committed to studies of birds at swarms. Probably more than 50 percent of their food comes from swarms, and I doubt that more than 60 percent of foraging Spotted Antbirds are away from swarms over the course of the year.

The Spotted Antbird is the only bird I know that takes about 50 percent of its food at swarms. Below it the next species is the Red-throated Ant-

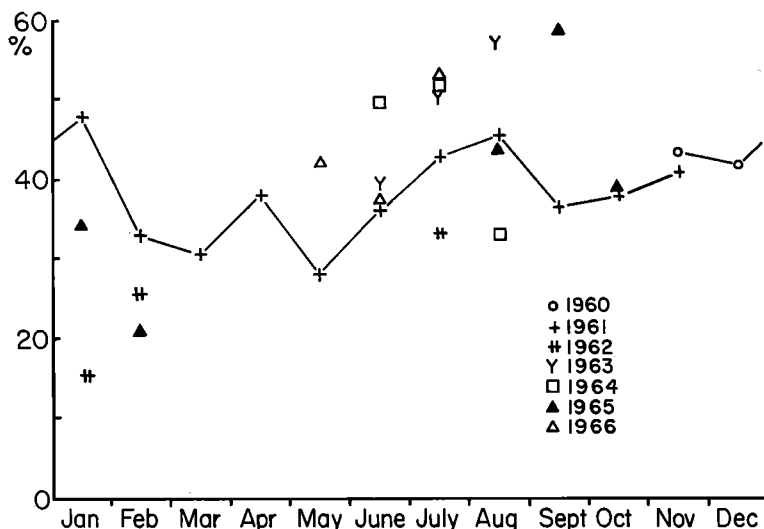


Figure 22. Percentage of foraging Spotted Antbirds recorded away from swarms of army ants and nests.

Tanager at about 20–30 percent (Willis, 1960a: 160). Above it the Barred Woodcreeper is at about 70 percent. I know very few birds in the middle range of the scale, between 10 and 80 percent, in contrast to the fair number of species above 80 percent and the huge number of casual visitors below 10 percent.

In the absence of competitors, a Spotted Antbird forages over ants much the same way that it forages away from ants. However, it often clings, pitches, and reverses actively rather than waiting patiently as it does away from swarms. It moves from one vertical sapling or fallen liana or twig to another, to and fro along the swarm front. As a swarm moves ahead, the attending bird periodically flutters ahead, so that it keeps over the central section of the front much of the time. It is much like a Bicolored Antbird in its foraging behavior over the ants.

Of 1,692 records of foraging height away from competitors, 1,547 or 91.4 percent were under one m and 1,091 or 64.5 percent were under 0.4 m (Figure 23). As is the case away from swarms, most birds are on perches near the vertical or horizontal, rarely on perches overhanging as much as 30 degrees (Table 2). Whether or not the perches are below or above 45 degrees, most perches selected are under three cm in diameter. Perches of under one cm in diameter are used more frequently than they are away from swarms. Generally the perch is a bare one, with a clear view of the ground.

Spotted Antbirds foraging actively at good sites and away from competing

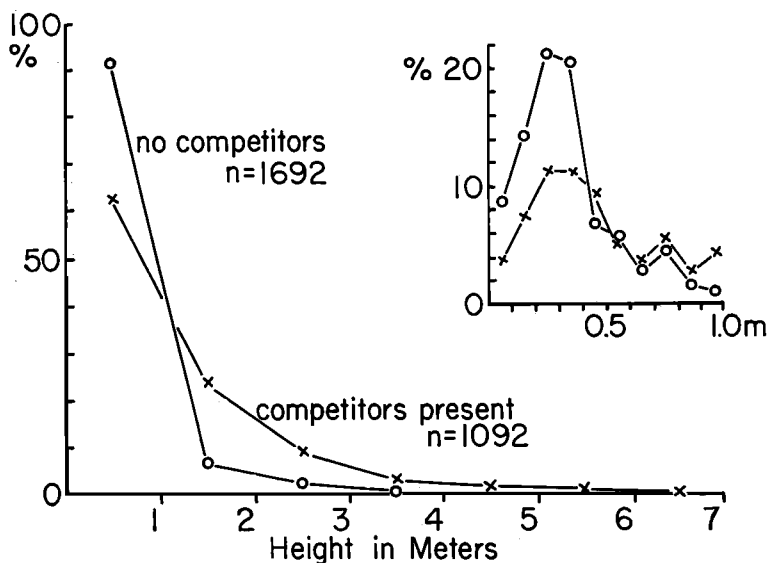


Figure 23. Heights of foraging Spotted Antbirds at swarms of army ants when competing larger species of antbirds were present and when they were absent.

larger birds tried for prey at average intervals of 22.9 seconds ($N = 41$) over swarms of *Labidus praedator* and 43.2 seconds ($N = 35$) over swarms of *Eciton burchelli*, for a combined average of 32.3 seconds. The interval for birds away from swarms averaged 111.8 seconds ($N = 28$). The almost fourfold advantage of working over ants is less when competing larger antbirds are present, however.

As is the case away from swarms, most prey is captured by sallying to the ground (Tables 5, 6). At times the bird pecks at the leaf litter and quickly swings back up, or stands on the ground tossing dead leaves until prey is uncovered and pecked. Only once did one dig deeply into the leaf litter, using its beak. Once one peered under a bark strip on the ground. Rather more frequently than away from swarms, and more often than does the larger Bicolored Antbird, the light and agile Spotted Antbird sallies into the air or to foliage above the ground to snap up a flying or fleeing arthropod. At other times the Spotted Antbird pecks prey out of the air or off foliage, either with or without a preliminary flight to a point near the prey. However, unless competitors are present, it seldom hops about peering and pecking like an antwren or warbler.

PREY AND PREY TREATMENT

At and away from swarms, most prey items are the length of the exposed beak (14.0 mm, or 1.0 B = 1 bill length) or less. Small items are swallowed

TABLE 5
ATTEMPTS AT PREY BY SPOTTED ANTBIRDS AT SWARMS OF *LABIDUS PRAEDATOR*¹

Prey Location	?	Attempts at Given Height (Meters)											Totals			
		0.1	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9	1.0	2		3	4	
Air	S ³ L ⁴		1 1(1)	(1) 1	1 2	1 1	1							1(1) 1	9(3) 6(1)	
Leaf, twig, trash	S L	6(5) 2	2 6(2)	(1) 1	1(2) 4	1(1) 2	(1) 3	(3) 1	1					4(2) 2(1)	3 23(3)	
Stem, liana, limb	S L	5 1(5)	6 4	5(2) 2	(1) 3(2)	5(1) 1(1)	1 1	1 1	2(1) 1(2)	2 1	4			7(2) 7(2)	3 2 35(6) 30(15)	
Trunk, log, buttress	S L	9(2) 3(2)	1 2	4 2	2 (1)	1 1	1 1	1 1	1 1	1 1				1 (1)	21(2) 7(4)	
Ground, rock	S L T ⁵ ?	202(70) 1(9) 3(5) 0(3)													202(70) 1(9) 3(5) 0(3)	
Unspecified	S L	10(1) 2(0)													10(1) 2(0)	
Totals		43(16)	222(89)	18(3)	10(4)	13(6)	9(2)	6(2)	4(3)	4(3)	4(0)	4	23(9)	8	1	369(137)

¹ 30 September 1960 to 30 September 1961. ² No competitors present, no parentheses; competitors present, in parentheses. ³ Sallying, n = 297 (97). ⁴ Lunging, n = 69 (32). ⁵ Leaf tossing, n = 3 (5).

TABLE 6
ATTEMPTS AT PREY BY SPOTTED ANTBLDS AT SWARMS OF *ECITON BURCHELLI*¹

Prey Location	Attempts at Given Height (Meters)													Totals			
	?	0.1	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9	1.0	2	3		4	5	6
Air	S ² L ³	2(2)	3		1(1) 2	1(3)		1(1)	1(1)		1(1)	1(1)	1(1)			23(15) 2(1)	
Leaf, twig, trash	S L	1(3) 3(2)	2(2)	3(1) 2	3(4) 2	4(3)	3(1) 1	5(1) 2	3(7) 2	3(1) 1	1(1)	22(21) (4)	5(16) 2(1)	2(6)	1(3)	78(84) 18(9)	
Stem, liana, limb	S L	23(12) 7(3)	1(1) 3(2)	3(1) 3	1(2) 3	1(4) 3(1)	2(2) 2	2(1) 2	1(1) 6(2)	1(2) 3(1)	1(1) 1	6(15) 4(6)	2(10) (3)	1(3) (1)		45(58) 42(21)	
Trunk, log, buttress	S L	10(11) 4(3)	1 1	2(1) 4(1)	1(1) 3	2 (2)	2 1	1(1) 1	1 (1)	1 (1)		10(3) 1(1)	2(8)	4(4)	5(5)	28(34) 15(9)	
Ground, rock	S L T ⁴ D ⁵	762(255) 28(27) 14(13) 1(0)	1													763(255) 28(27) 14(13) 1(0)	
Unspecified	S L	7(3)	1			1						1(1)		1(2)	3(3)	10(6) 0(3)	
Totals		88(52)	814(303)	14(6)	15(5)	20(10)	9(13)	10(3)	12(3)	14(12)	8(5)	3(3)	44(52)	11(40)	4(16)	1(11)	1067(535)

¹30. September 1960 to 30. September 1961. No competitors present, no parentheses; competitors present, parentheses. ² Sallying, n = 947 (452). ³ Lunging, n = 105 (70). ⁴ Leaf tossing, n = 14 (13). ⁵ Digging, n = 1 (0).

TABLE 7
PREY OF SPOTTED ANT BIRDS AWAY FROM ANTS¹

Kind	Estimated Size (mm)											
	?	0-5	10	15	20	25	30	35	40	45	50	60
Unspecified		14	12	11		1						1
Sowbug			3									
Spider	4		1	4		1						
Arachnid					1							
Centipede							1					
Roach				1		1						
Orthopteran			1	5		2						
Moths	3		1	2	1							
Caterpillar				2	1		3	1		2	1	
Ant	2		1									
Total	9	14	19	25	3	5	4	1	0	2	1	1

¹ Barro Colorado Island, 30 September 1960 to 27 August 1969.

so rapidly I was seldom able to identify them or even to tell whether the bird had captured the prey. Some were sowbugs, moths, beetles, and spiders. Items juggled or chewed long enough that I could estimate their lengths as fractions of beak length or identify them are listed in Tables 7 and 8. These items probably bracket the upper size limit of prey taken by Spotted Antbirds. Roaches, spiders, crickets, katydids, moths, caterpillars, centipedes, and others were frequent prey. One bird carried a lizard (*Anolis limifrons*) twice the length of its head, then dropped it.

Prey over 1.5 B is seldom taken, unless long and narrow like a caterpillar or centipede. Items over 1.0 B and some smaller items usually required special processing. A Spotted Antbird never holds prey in the feet while pecking with the bill. Commonly it chews medium-sized prey or shakes it vigorously before gulping it more or less energetically. At times prey from 0.7 B to 3.0 B, especially caterpillars, are pounded or flailed on perches as well as chewed back and forth. Moderate to large prey (0.5 B up) is sometimes taken to the ground, where the bird dissects it in much the same way as does a Bicolored Antbird. I rarely noted Spotted Antbirds dissecting prey away from swarms. At swarms dissection was more common, but not so common as in the large Bicolored and Ocellated Antbirds.

NUMBERS AT SWARMS

The number of individuals at swarms of ants changes rather little during the year (Figure 24). Young Spotted Antbirds enter the population from

TABLE 8
PREY OF SPOTTED ANTBIRDS AT ANT SWARMS

Kind	Estimated Size (mm)										
	?	0-5	10	15	20	25	30	35	40	45	50
Unspecified	108(214) ¹	61(26)	53(18)	34(42)	1(3)	3(2)	1(2)				1
Sowbug	5(2)	1									
Spider	3(8)		6(2)	8(10)	1(3)	(2)					
Spider egg sac	(1)										
Scorpion						1					
Centipede					(1)		1			(1)	
Bristletail				(1)							
Roach	3(1)		4(2)	12(21)	2(8)	2	2				
Orthopteran	(2)		3(2)	18(15)	4(3)	1(3)	(1)			1	
Beetle			(1)		(1)	(1)					
Caterpillar				1	(1)		2(1)			1	
Moth	5		1	4							
Ant	1(1)										
Lizard (<i>Anolis</i>)				(1)							
Total	125(229)	62(27)	67(24)	77(90)	8(19)	7(8)	6(4)			2(1)	1

¹ Numbers outside parentheses, 1 October 1960 to 30 September 1961; numbers within, 1 October 1961 to 27 August 1969; Barro Colorado Island.

June to November. The numbers of swarms of *Labidus praedator* peak in the wettest months, October and November, and dip in the driest months, January to April. Colonies of *Eciton burchelli* swarm all year. However, in March and April some split into new colonies. It is not known when colonies of *Labidus praedator* reproduce. Figure 25 indicates the number of swarms per Spotted Antbird territory in 1960-1961; the estimates assume that 40 percent of the swarms of *Labidus praedator* were missed during strip censuses (Willis, 1967; figure 2, p. 9) and that there were 21.3 territories per square kilometer. The activity cycles of ants and birds should lead to an increase in numbers of Spotted Antbirds at swarms from June to March, than a decrease until the first young antbirds leave the nest the next June.

There is seldom more than one pair of Spotted Antbirds at a given swarm (Table 9). The resident pair normally drives trespassing pairs away, or the latter take separate branches of the swarm, so that there is either temporal or spatial exclusion. Wandering birds are sometimes tolerated at the same branch of the swarm, but generally forage well away from resident birds and have to take the poorer foraging positions noted in the next section. Spotted Antbirds supplant each other from long distances, up to 20 m at a time, so that trespassing birds of the same sex as residents seldom forage near them. Intraspecific supplantings are rather uncommon in Spotted Antbirds com-

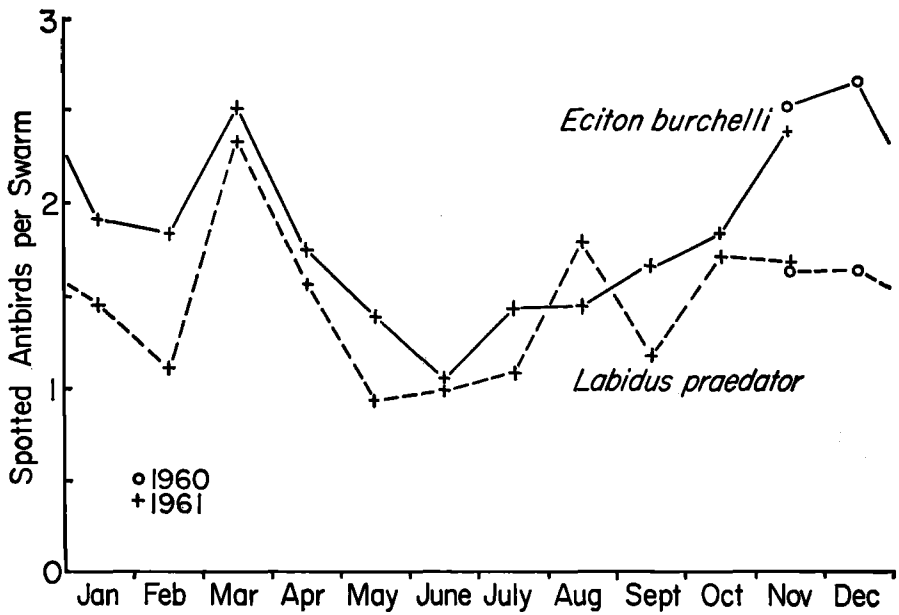


Figure 24. Spotted Antbirds at swarms of *Eciton burchelli* and *Labidus praedator* in 1960-1961.

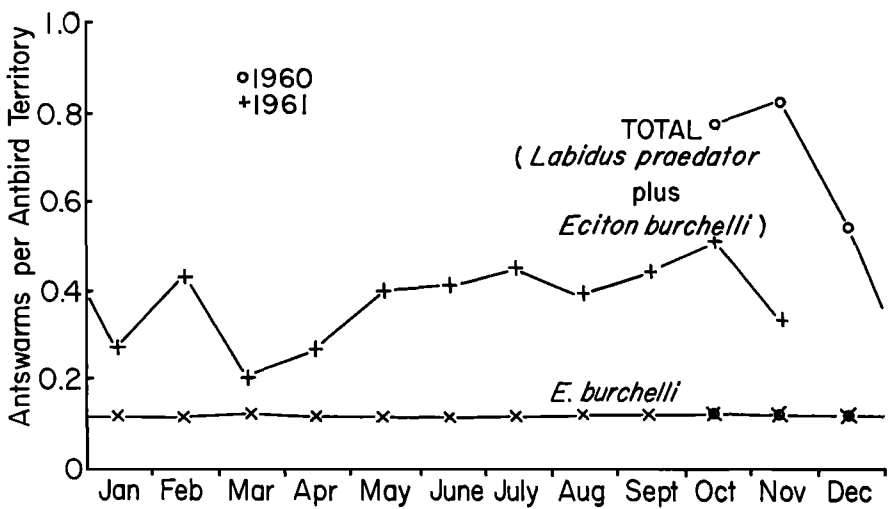


Figure 25. Number of ant swarms per Spotted Antbird territory in 1960-1961, assuming 21.3 pairs of Spotted Antbirds per square kilometer and using data on ant swarms from Willis (1967:7-9).

TABLE 9
PAIRS OF SPOTTED ANTBIRDS AT SWARMS OF ARMY ANTS

Ant Species: Pairs:	<i>Eciton burchelli</i>					<i>Labidus praedator</i>			
	0 +	1	2	3	4	0 +	1	2	3
1960									
November	3	7	1	1		9	20		2
December	5	9	3	2	1	6	7	2	
1961									
January	8	12				2	6		
February	12	14				7	4	1	
March	8	9	1	2		2	3		
April	14	17	6			3	3	1	
May	22	20	4	1		7	2	1	
June	22	13				4	4		
July	28	28	2			5	5		
August	18	28	2			2	6	1	
September	20	25	5			5	4		
October	21	28	6			6	10	1	
Totals	181	210	30	6	1	58	74	7	2

pared with Bicolored Antbirds (Willis, 1967: 43), because Spotted Antbirds drive trespassers away so quickly that one sees few attacks.

COMPETITION AT SWARMS

Many species of birds follow swarms of ants, which are often narrow and crowded with individual birds. At such times interspecific and intraspecific attacks may be frequent. Table 10 lists overt supplantings, casual displacings (when a bird obviously retreats from another), and returns (when a bird waits until a larger bird leaves, then moves in to the area where it was feeding) of and by Spotted Antbirds on Barro Colorado. As in many tables and figures in this report, the basic data come from the first full year of relevant and relatively unbiased observations (here 30 September 1960 to 30 September 1961); later observations are perhaps biased by being concentrated in certain months of the year and in other ways, but are added here in separate columns for comparison. The table includes all of the recorded supplantings, but only clear and obvious displacings and returns are listed.

Bicolored Antbirds, twice the size of Spotted Antbirds, readily supplant or displace them. A hiss and a snap, and a supplanting Bicolored Antbird takes the perch of a Spotted Antbird if the latter sallies for food or waits

TABLE 10
ATTACKS ON AND BY SPOTTED ANTBIRDS AT SWARMS OF ANTS

Species	Supplantings	Displacings	Returns
1. Spotted Antbird	422(746) ¹	80(103)	1(0)
2. Bicolored Antbird	223(205)	183(80)	41(43)
3. Ocellated Antbird	30(37)	55(30)	13(11)
4. 2 and 3	3(4)	5(1)	26(20)
5. Gray-headed Tanager	7(3)	24(3)	3(2)
6. Plain-brown Woodcreeper	5(2)	5(4)	
7. Chestnut-backed Antbird	0(40)	1(5)	0(1)
8. Slaty Antshrike	2(2)	1(2)	
9. White-whiskered Puffbird		5	
10. Squirrel Cuckoo	1	0(3)	
11. Great Rufous Motmot		1(1)	
12. Scaly-throated Leafscaper	1		
13. Buff-throated Woodcreeper		1	
14. Barred Woodcreeper		1	
15. Swainson's Thrush	1	1/1 ²	
16. Gray-cheeked Thrush	1	1/1	
17. Veery		0/2	
18. Thrush (species)	0/1	1	
19. Kentucky Warbler	0/2(4)	0/1	
20. Canada Warbler	0/0(2)	0/0(3)	
21. Acadian Flycatcher	0/1		
22. Ruddy-tailed Flycatcher	0/0(1)		
23. Checker-throated Antwren	0/1(1)		
24. Red-capped Manakin	0/1		
25. White-flanked Antwren	0/0(1)		

¹ 30 September 1960 to 30 September 1961, no parentheses; 1 October 1961 to 27 August 1969, in parentheses. ² Records below slash lines indicate species subordinate.

nearby. The two forage in much the same way, and a Bicolored Antbird rarely permits a Spotted Antbird within two meters of its perch. However, Table 11 lists a few records of Bicolored Antbirds permitting Spotted Antbirds to forage close to them ("ignores") and of Spotted Antbirds foraging past Bicolored Antbirds ("infiltrates"). Generally the Bicolored Antbird was preening or feuding with another of its own species at such times. At times, however, the Bicolored Antbird was foraging actively but still permitted the Spotted Antbird to work nearby. Normally the larger species grunts frequently, a call note often directed at any nearby supplantable competitor, and supplants the Spotted Antbird after a few seconds. If the Spotted Antbird tries

TABLE 11
RECORDS OF FORAGING POSITIONS OF SPOTTED ANTIBIRDS AT ANT SWARMS WHEN COMPETITORS PRESENT

Competitor	Position										
	Ignored	Infil- trates	Hides	High	Ahead	Behind	Near Me	End	Wander	Separate Fork	Deserts
1. Spotted Antbird ¹	4(15) ²	0(1)		12(2)		5(3)	12(12)	0(5)	1(4)		2(3)
2. Bicolored Antbird	87(46)	5(9)	2(1)	85(42)	77(63)	62(68)	72(69)	56(74)	41(59)	18(32)	1(9)
3. Ocellated Antbird	35(40)	3(4)	3(0)	25(11)	18(38)	19(28)	21(17)	15(41)	11(23)	3(5)	7(2)
4. Gray-headed Tanager	10(0)		2(0)	3(3)		1(0)	1(2)	2(0)	1(2)		
5. Plain-brown Woodcreeper	1(0)				0(4)	0(1)	2(0)				
6. 2 and 3	14(11)	7(4)	5(0)	70(51)	149(92)	119(127)	115(53)	112(128)	77(83)	48(49)	12(17)
7. 2 and 4		1(0)	2(0)	2(4)	4(6)	6(5)	4(1)	11(8)	11(8)		0(1)
8. 2 and 5					0(5)	0(2)			0(1)		
9. 2 and 3 and 4	0(1)		1(0)	1(1)	7(4)	6(15)	6(5)	11(18)	5(13)	8(2)	2(2)
10. 3 and 4				2(2)	2(2)	1(2)	0(6)	0(4)	1(6)	1(0)	0(2)
11. Chestnut-backed Antbird				0(1)		0(1)	0(5)	0(1)	0(2)		
12. White-whiskered Puffbird								1(0)			
13. Squirrel Cuckoo	1(0)										
14. Swainson's Thrush	1(0)			2(0)					1(0)		
15. Gray-cheeked Thrush	2(0)										
16. Thrushes (species)	4(0)							1(0)	2(0)		1(0)
17. Canada Warbler	0(1)										

¹ Most intraspecific records omitted. ² Outside parentheses, records 30 September 1960 to 30 September 1961; inside parentheses, records 1 October 1961 to 27 August 1969.

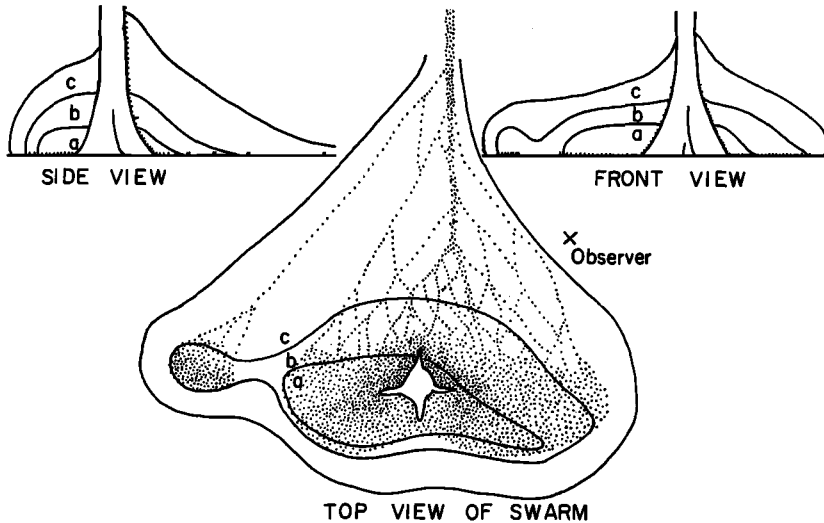


Figure 26. Foraging zones around a swarm of ants, as seen from the top and front and side. "Zone a" is taken by dominant birds, "Zone b" by subdominants, and "Zone c" by subordinates.

for prey when the Bicolored Antbird is not busy, the supplanting comes more rapidly—even as the Spotted Antbird reaches the ground on a split-second sally.

The even larger Ocellated Antbirds do not often supplant or displace Spotted Antbirds, because the smaller birds stay well away from the former much of the time. Normally the dominant Ocellated Antbirds take the center of a swarm, the subdominant Bicolored Antbirds take a concentric but shifting ring around them, and the subordinate Spotted Antbirds take a peripheral and shifting ring next to the Bicolored Antbirds rather than move near Ocellated Antbirds (Figure 26 "Zones a, b, and c").

Many other large or moderately large ant-following species, such as the Gray-headed Tanager, also supplant the Spotted Antbird. In general, the effect of multiple supplantings by Chestnut-backed Antbirds on the infrequent occasions when the latter follow ants is about the same as the effect of Bicolored Antbirds—the Spotted Antbird has to forage peripherally or at the other end of the swarm. Slaty Antshrikes four times supplanted and three times displaced Spotted Antbirds, but the former normally forage well above the latter at swarms. The Plain-brown Woodcreeper and the Barred Woodcreeper seldom supplant the Spotted Antbird, for woodcreepers generally forage high in the undergrowth or on pole-sized or smaller tree trunks in relatively open undergrowth and seldom work the swarm at the same places

or times as does the Spotted Antbird. Often the woodcreepers and antbirds ignore each other even when foraging close together.

Occasionally large White-whiskered Puffbirds, Great Rufous Motmots, or Squirrel Cuckoos at swarms flush a Spotted Antbird more or less accidentally by flying down past it in a chase of some large prey. In cases not listed in Table 10, passing coatimundis three times displaced Spotted Antbirds, and a foraging Scaly-throated Leafscraper ignored the ants but supplanted a Spotted Antbird that was waiting over them.

The Spotted Antbird occasionally supplants passing smaller birds, such as the Ruddy-tailed Flycatcher and the Checker-throated Antwren. These and other birds of the "antwren alliances," wandering interspecific flocks, often drift near a bird flock at a swarm of ants, peer and flutter about in their usual fashion, or stare at the ants as if curious and drift on. They are normally present so briefly that they scarcely are exposed to supplantings by the larger ant-following birds. It may be that the antwrens avoid close contact with large antbirds because of occasional supplantings, but usually birds of the antwren alliances seem to ignore the ants and ant-following birds rather than avoid them. Ordinarily most of the antwrens forage higher in the undergrowth, 2 to 10 meters up, than do the ant-following birds.

The Canada Warbler is one small bird that readily shifts back and forth between ant-following and antwren aggregations. The Spotted Antbird readily supplanted or displaced the Canada Warbler on the few occasions when a warbler foraged low enough in the foliage to come near one at an antswarm. Migrant thrushes, which rarely stay with antwren flocks but readily join ant-following flocks (Willis, 1966a: 198), occasionally supplant or displace the smaller Spotted Antbird. However, Spotted Antbirds occasionally displaced or supplanted thrushes nearly twice their size.

When large competitors exclude it from the best foraging zones over the ants, a Spotted Antbird moves peripherally. Table 11 lists instances of Spotted Antbirds foraging in these places: above, ahead of, and behind swarms or near the observer; behind logs or in dense vegetation; infiltrating the ranks of larger antbirds briefly, or foraging peacefully near them; waiting at the ends of swarms or at separate (and usually smaller and rather poor) forks of swarms; and deserting the swarms completely as direct results of the activities of larger birds. These data are taken from comments in field notes and do not represent organized studies. Only a small fraction of the observed cases were recorded; the records are useful mainly as indications that Spotted Antbirds react to larger competitors in several ways and to show the bases for Figure 26. One problem is that the dense forest undergrowth makes it difficult to see birds ahead of the swarm and birds at the ends of the swarm as compared with birds behind the swarm or near the observer. However, birds

behind the swarm or near the observer generally must be tame individuals. Birds at a separate fork or birds deserting a swarm are unlikely to be noticed more than once during a period of observation, while birds foraging near the observer can be recorded repeatedly.

For Table 11, I recorded an individual as doing a given activity when that activity was separated in my notes from the previous record of the same individual at the same activity by a record of that individual at some other activity or by observations of some other bird. A bird that foraged near me for 20 minutes is counted once if I did not note that it moved off for a time or if there was not a series of observations on other birds followed by a note that the given individual was still near me. As categories, "wandering" and "deserting" refer to birds changing their locations so much that they did not stay long in any one of the "location" categories; however, in some cases a bird wandering before or after stopping to forage, such as behind the swarm, was counted as a record for wandering and a record for behind the swarm.

In view of the fair difficulty of seeing birds ahead of the swarm, the total for Spotted Antbirds ahead of the ants and competing antbirds by one or more m is still rather high. Spotted Antbirds commonly range back and forth ahead of the ants when interspecific competitors are present. The larger competitors generally face the rear of the swarm rather than ahead, so that the occasional small prey leaping ahead of the ants is available for Spotted Antbirds without great risk of supplantings. However, the area of good foraging is rather narrow ahead and to the sides of the ants (Figure 26), because most prey items quickly hide under cover unless they are reflushed by the ants.

"Foraging at the ends of the antswarm" generally means birds taking positions directly over the ants, in cases where there were not enough large antbirds fully to occupy the whole length of the swarm. In such cases the large antbirds sometimes concentrate at the end of the swarm away from the observer (Figure 26) and leave a large but very good foraging zone at the end near the observer. At other times the large antbirds move back and forth or stay at the center, while the small Spotted Antbird takes whichever end is momentarily unoccupied.

There is a very wide foraging area behind the swarm, where the coalescing trails of ants form a wide "fan" with many foci of moderate activity. However, much of this region is rather poor for prey, since the ants and the birds ahead have already captured much of the prey that has not reached a safe hiding place. However, Spotted Antbirds do rather well searching for the last small prey on the under sides of leaves, or work foci of activity near the observer unless larger birds are tame enough to forage there instead.

Four times Spotted Antbirds foraging behind the ants turned to "thievery,"

or to stealing pieces of arthropods from the homeward-bound army ants. In Bicolored Antbirds, thievery is restricted to subordinate individuals, ones that are getting little prey because dominant birds exclude them from good foraging areas (Willis, 1967: 30). In the four cases of thievery I observed among Spotted Antbirds, several Bicolored and other antbirds were occupying the main swarm. In each case, the Spotted Antbird flew down to the ant trail, picked up an ant and booty, shook the ant off, and ate the booty. None of the birds tried thievery more than once, although three watched the ant trail for a minute before leaving.

Foraging high above the ants requires hopping and peering, as the Spotted Antbird investigates tangles or suspended fallen limbs and other protected places. The Ocellated and Bicolored Antbirds sometimes grunt at the small bird above them, and supplant it at times even when it is two or three m above their heads, so foraging above other species is not always safe. When two or more species of competing birds are present, Spotted Antbirds forage high above the ants less frequently than when only one species is present (Table 11). When only one competitor is present, it usually takes "Zone a" (Figure 26) and leaves the other zones free, unless there are many individuals of its own species.

If several competing species were present, Spotted Antbirds were slightly less likely to forage near me; often tame subordinate Bicolored Antbirds (generally the second species present) took this position (Willis, 1967: 62) at such times. A species like the Bicolored Antbird, which tolerates trespassing individuals until as many as 15 attended one swarm, often spreads out to occupy both "Zone b" and "Zone c" or takes much of all three zones, forcing Spotted Antbirds to go to minor foci of activity at the outskirts or to separate branches or to desert the swarm.

Although the Spotted Antbird can still find some food by foraging about the periphery or over a swarm of ants if many larger antbirds are present, it often deserts swarms of ants if there are many large competitors. One often finds Spotted Antbirds wandering around the bivouac or along the trail of ants rather than at the main swarm, or sees Spotted Antbirds only a few minutes during several hours of watching at a swarm. Since the large antbirds concentrate around the large and consistent swarms of *Eciton burchelli*, the Spotted Antbird is often relegated to small branch swarms, to rather inactive raids, to the temporally unpredictable starchy raids of *Eciton burchelli*, or to raids of *Labidus praedator*.

If undergrowth is very open, the wary Spotted Antbirds often stay on the periphery of a swarm or in dense cover nearby, moving in over the ants only occasionally. Their behavior is effectively almost the same as when competitors exclude them.

DISCUSSION

Perhaps Spotted Antbirds forage relatively seldom from perches of low curvature (i.e., large radius), such as fallen logs or the ground, because large perches block visibility, especially when these birds get most of their food from the leaf litter. Limited visibility might also block their view of approaching predators. Certainly, Spotted Antbirds usually forage in moderately open undergrowth rather than in tangles that could block their view of both predators and prey. However, they avoid very open undergrowth, and often stay near tangles. The dangers of predation probably rise as habitats become very open or very dense. Perhaps perch sites and prey are less common in very open sites, while prey hide too easily in very dense sites. Also, Chestnut-backed Antbirds occupy dense sites and chase out Spotted Antbirds (Willis and Oniki, MS).

There are many species of antbirds that forage by hopping or walking on logs or lianas or the ground, including in the Panamanian lowlands such birds as Streak-chested Antpittas, Black-faced Anthrushes, and White-bellied Antbirds. The morphology of the foot in such clinging birds as Spotted and Bicolored antbirds may hinder use of such horizontal perches of low curvature. Neither the Spotted Antbird nor any of its relatives is very good at hopping or walking progressively, but their large feet and legs permit them to cling to vertical perches that hopping and walking antbirds scarcely use. Probably the long legs of the other antbirds permit them to hop effectively or to stand up above the ground so they can see prey or predators. The morphological adaptations for clinging and the behavioral avoidance of dense or very open sites probably restrict foraging opportunities for Spotted Antbirds; but predators and competitors probably would cause losses that would offset gains if Spotted Antbirds were less specialized.

Swarms are sometimes unattended even when there are no competitors and nearby Spotted Antbirds are foraging away from ants. Since birds foraging at swarms find prey four times as often as birds away from swarms, I suspect such antbirds fail to find the ants rather than find them and leave them. It is possible, however, that some Spotted Antbirds desert the ants after getting sufficient food or because there are no other birds about to help keep the lookout for predators. Spotted Antbirds search for ants mainly in the early morning. Probably they restrict their searches partly because of danger from predators and partly because they cannot forage well while searching, since they forage best with relatively long waits at perches. Searching persistently until a swarm is located might be less efficient than foraging away from ants if it takes too long to find the ants; losses would outweigh gains. Bicolored and Ocellated antbirds, which are dominant at the easily located and regular nomadic swarms of *Eciton burchelli*, search until they locate the

ants; they find little of their food away from ants. Spotted Antbirds, low on the interspecific peck order, cannot depend on such swarms. Where the ants are easily located and competition is low, as at "statory" (Schneirla, 1957: 262) colonies of *Eciton burchelli*, Spotted Antbirds do revisit repeatedly during the day. Possibly food availability is more important than danger from predators.

The standard argument against predators' restricting foraging ranges of prey has been the one that a prey species will evolve behavioral or other mechanisms that enable it to use the food in the presence of the predator. However, in evolution a species develops the ability to exploit certain foods and accordingly becomes abundant; then a predator begins to exploit it and reduces its numbers in peripheral or unsafe zones. Then the species is replaced or evolves further, and a new predator comes in or the old one evolves, and so on *ad infinitum*. Alternation and lag effects are thus characteristic of predator-prey interactions, not evolution to the point where a species uses all possible food unaffected by predators. This is probably especially true of complex systems with numerous predators, and less true of simple systems. In a complex system, the prey is restricted in foraging because it must waste time watching for a variety of predators or keep to safe sites, unless it is able to beat the system by developing a high reproductive rate outside the system (an outlet available to migratory birds, which can be tame and exploit dangerous niches; Willis, 1966a: 222). The predators thus limit the food supply open to any one species of prey, opening niches for other prey species and encouraging species diversity indirectly as well as removing prey individuals from the population directly (Paine, 1966: 65).

Predators thus may limit the places safe for a species and the kinds of food available to it, much as do competitors, prey protective devices, environmental productivity, environmental complexity, different or varying weather, and other factors. Species diversity should increase at first as any of these factors increase, but too much of each will then decrease diversity because species will be lost faster than they can be evolved or moved in. It may be that greater environmental stability, structural heterogeneity, or productivity does not give greater species diversity *ad infinitum* but only up to a point. In a very productive or perfectly constant environment, as well as in poor or variable environments, species will be eliminated. With high and constant productivity, for instance, specialized species can eliminate generalists; with many predators, some prey species will be eliminated. Margalef (1968: 41) notes that eutrophication and high productivity usually leads to lowered species diversity; of course, very low productivity has the same effect. The biological interactions of predators and competitors become more important than the physical factors when the latter are optimal; however, it may be that for maximum species diversity there are optimal levels of food supply and of predators as well as of temperature or rainfall, and that decrease or increase

in the first two away from optima can lower species diversity just as can decrease or increase in the last two. Aristotle's "golden mean" may apply to communities and species as well as to individuals.

Perhaps the Spotted Antbird's greater movement at antswarms, as compared with its activity away from ants, is caused by the fluctuating activity of the ants themselves; the locations where prey is likely to appear change rapidly as the ants move, whereas one place may be about as likely as another away from ants. However, this may not be quite true away from ants, as a Spotted Antbird moves periodically; perhaps its activity eliminates or inhibits the likely prey at any one place after a few minutes, or it deserts a place that does not produce prey. It does not need to move otherwise, except to keep up with the wandering antwren flocks it often joins away from ants.

The relative lack of prey dissection in Spotted Antbirds as compared with their larger relatives suggests that the small arthropods taken by the former are relatively easy to break apart. In all these antbirds the average maximum length of prey correlates well with the average beak length, so that there must be an allometric rather than a direct increase in toughness of prey with length of prey. The great increase in size of bill among birds eating large insects (puffbirds, motmots) and very large seeds (Galapagos finches, Bowman, 1961) probably compensates for an allometric increase in hardness that exceeds the increase in prey length; but ant-following antbirds seem to compensate more by behavioral means, namely an increase in dissection time. Such increases would clearly be a disadvantage under conditions of strong competition, and should lead to the development of large beaks. This suggests that, even though these antbirds compete for space at swarms of ants, there is either not enough competition to cause evolution of very different beak sizes or that the large antbirds can gain more food with small beak sizes even though they have to spend time dissecting. Since large organisms are much rarer than small ones in the leaf litter (Williams, 1941), there should be strong selection against large birds or large beaks. Dominance, however, goes to the largest and (with increase in food per capture if prey are large) should provide counterselection. Superior competitive abilities of the smaller birds may force the larger birds to take larger prey to some extent. However, it is likely that the large birds take prey as small as they can efficiently use, considering that small items add to capture time more than to pursuit time (see MacArthur and Pianka, 1966: 603). The exclusion of smaller species by larger ones can be an advantage to the larger ones even when they take different size ranges of food, as long as the larger ones gain more than they lose by chasing, and the dominance "zones" of Figure 26 are an extension of morphological and behavioral differences between the species over swarms of ants.

When no competitors are present, Spotted Antbirds forage low over the

ants in much the same ways as do Bicolored and Ocellated antbirds. This suggests that this is the best foraging zone for Spotted Antbirds as well as for larger birds. When larger antbirds exclude Spotted Antbirds, they forage very actively around the periphery of swarms. Although the great and temporally extended activity of excluded Spotted Antbirds shows that they are "adaptable" and relatively unspecialized, with refugia to which they can turn, compared with nonexcluded birds, their activity wastes energy and time and exposes them to predators. Moreover, each individual bird forages over a wider zone, so that driving away trespassers becomes more necessary and populations must be lower. In extreme cases, all the Spotted Antbirds forage away from ants.

Such subordinate species probably must be relatively unspecialized in any competitive situations, or be locally excluded as what Hutchinson (1951: 575) has termed "fugitive" species. At swarms of ants, Spotted Antbirds are in a sense fugitive species, but they are rather successful at finding nearby refugia and have high population levels. The success of a species need not be related to its degree of specialization or to its dominance status, even if a constant environment should lead to elimination of fugitive and unspecialized species. There are plenty of irregular or locally rich environments that permit fugitive species and generalists to be successful, even in the tropics.

Competitive exclusion by dominance at swarms of ants suggests that the various species behave as competitors whether or not they take the same foods. The large Ocellated and Bicolored antbirds probably use little of the small prey that the Spotted Antbird would take, but they exclude Spotted Antbirds from their foraging areas as completely as if the latter were another member of their own species. Intraspecific disputes and supplantings are much more frequent and vigorous in all three species, but simple avoidance of large species by small ones (Table 11) probably accounts for much of the decrease interspecifically. Often the two larger antbirds start grunting, their notes for a supplantable competitor, and the Spotted Antbird flees or moves away. There is no need to fight or supplant unless there is resistance. Intraspecifically, mates and young are tolerated as close as are members of another species. Moreover in Ocellated Antbirds independent young and their mates are also tolerated; and in both Bicolored and Ocellated antbirds pairs eventually tolerate other pairs within a few meters, or almost as close as they tolerate young or mates, as long as the subordinate birds are submissive.

It must be that all this fighting for space at swarms is possible because there are actually local food surpluses, and hence subordinate species and subordinate individuals of dominant species can stay and survive. If there were a shortage of food, the best-fitted birds should eliminate the others or push them into other niches, and actual fighting or other evidence of competition would be rare or anecdotal in nature (competitive exclusion principle;

Grinnell, according to Miller, 1964: 236). Without watching the evolutionary or experimental course of a competitive interaction, one is uncertain that the disputing leads to separation of niches and the statistics are going to be anecdotal and can always be criticized. However, the fighting does seem to lead to a spatial pattern of separation of niches, even if fighting may actually hinder evolution of differences in beak size (see below) or morphologically based niche differences.

It is possible that disputing, even though it forces subordinate species to evolve or be excluded, actually inhibits morphological evolution of a dominant species. If it can chase away the others, interspecific competition is eliminated as a selective pressure for evolution. As other species rapidly become more efficient, the dominant one only turns to more and more aggressive behavior. It becomes progressively less efficient, and is gradually replaced by species that need not waste foraging or other (Ripley, 1959: 132 "aggressive neglect" of nests) time on aggression. More likely, judging from the birds at ant swarms, the other species move in and the dominant ones can no longer gain by attempting to displace them. The dominants then have to undergo rapid evolution to become more efficient, which may be an evolutionary crisis and lead to local extinction.

In either case, evolution in optimal environments is probably toward elimination of crude aggression and toward institution of morphological and other differences not related to aggression. This may also apply toward predators as well as to competition. Thorny and poisonous plants are less common in mature forest than in successional or difficult habitats; human use of pesticides seems self-defeating. In other words, the meek inherit the evolved earth because the strong can efficiently defend only in an irregular world, such as over army ants at the present time, and then only before evolution produces meeker but quicker species. In an evolutionary sense, aggression is eventually good for the downtrodden but bad for the aggressor unless the downtrodden are quickly and completely exterminated.

Since the competitive exclusion principle states that monopolies tend to develop, one wonders why there are actually few monopolies in nature. One can hardly think of a type of food that is eaten by one and only one organism, for instance. If one accepts the principle *a priori*, he must look for opposing principles that frustrate its complete fulfillment. One obvious counterprinciple is the "specialization principle," that morphology or behavior restricts the range of things an organism can use; it would be difficult for an antbird to monopolize both insects and diatoms. The failure of Bicolored and Ocellated antbirds completely to exclude Spotted Antbirds from swarms of ants is partly explained by this principle, but as important is what I have called (Willis, 1966b: 671) the "irregularity principle," that irregularities in time and space leave surpluses that can be exploited by quickly-moving species

that have alternate food sources. When times are bad, or rather irregularly bad, they prosper. Spotted Antbirds should prosper in moderately good years for food and in moderately irregular climates, more than in very good years for food or in constant climates. In very good years or in constant climates better-adapted competing species should exclude them. Spotted Antbirds are uncommon in the constantly wet parts of the Chocó of Colombia. They reach high abundances in regions with moderately strong dry seasons. However, they disappear in regions with extremely strong dry seasons.

The Plain-brown Woodcreeper seems to occupy the same sort of peripheral and subordinate stations at the swarms, but has different refugia—high in the trees, areas of large-trunked trees and little ground cover, etc. (Willis, 1966*b*: 668). By the irregularity principle, it should be less common in areas of constant climate than in areas of greater irregularity, such as Barro Colorado. In constant climates, specialists should outcompete it. The species is uncommon in the Chocó and in the constantly wet upper reaches of Amazonia compared with regions with moderate dry seasons.

There are, however, alternative explanations for these distributional patterns. Possibly the Spotted Antbird and the Plain-brown Woodcreeper cannot nest or get enough food in such regions for reasons of high rainfall, or for various reasons based on specializations rather than on irregularity. The question of whether the difficulties come from the biological or the physical environment are not yet answered. It is perhaps desirable to see what ranges of conditions a species occupies and what changes take place when specified conditions are changed rather than to speculate on the relative importance of competition versus other factors.

I have elsewhere proposed (Willis, 1966*a*: 217) that migrant birds are unassertive and rarely compete directly with resident birds, even small ones like Spotted Antbirds, at swarms of ants. A few attacks by Spotted Antbirds on thrushes of somewhat under twice the weight are about the only exceptions to the general rule that larger birds supplant smaller ones in interactions at swarms. However, the recently analyzed records of Spotted Antbirds foraging at the periphery of a swarm rather than over it when many thrushes were present (Table 11) indicate that there may be more effect of migrants on Spotted Antbirds than I thought in the earlier paper, where I tabulated only obvious supplantings and displacings. Moreover, it is possible that there were few young Spotted Antbirds leaving the nest in late 1960, a year of high numbers of thrushes, than in 1961. I saw only one young male Spotted Antbird in the fall of 1960, and many the next fall. However, in 1960 I was neither looking for young birds nor experienced at detecting them. There were many first-year Spotted Antbirds about from January to June, 1961.

Still, it is possible that the unusually large number of swarms of *Labidus praedator* in the wet year of 1960 were so completely overoccupied by

thrushes and other birds that fewer young Spotted Antbirds survived that year than in the dry year of 1961, which was a poor fall for antswarms but an even poorer fall for thrushes. There is thus the possibility that Spotted Antbirds have less success in nesting in years of abundant swarms, because of overcrowding by migrants, than in poorer years for ants.

However, the number of such habitual ant-followers as Ocellated and Bicolored antbirds and of various resident occasional ant-followers may also have been high in 1960 and contributed to any lower success for Spotted Antbirds. The available data (Willis, 1966*a*, figure 2) do not support this hypothesis; but in 1960 I was inexperienced and probably scared away many resident birds, especially in October.

More detailed analyses of the relative success of nesting in Spotted Antbirds and abundances of migrants and residents in different periods of fall migration may help determine whether this species is actually affected by the migrants more than I thought in 1966, when I asserted that migrants use surplus foods and generally do not crowd resident species or affect their breeding unless they displace them by nonaggressive infiltration. The Spotted Antbird is the ant-following species that is most likely to be influenced by migrants, as almost all other ant-following resident species are larger or more aggressive than are ant-following migrants.

Johnson (1954: 50) emphasized an attraction between birds of the antwren flocks and those of the ant-following aggregation. There seems to be a social attraction, as the moving antwren alliance often joins or wheels about the more stationary ant-following alliance. However, I have noted little foraging use of swarms by antwrens even in Amazonia, where there are more species of birds in antwren alliances than on Barro Colorado. Johnson stated that the antwren or "social" aggregation "usually joins the feasting activities" of the ant-following birds, but he refers mainly to Slaty Antshrikes and to Plain-brown Woodcreepers to support this contention. The latter are primarily ant-followers, and secondarily members of antwren alliances, rather than the reverse as he thought. The antshrikes occasionally move down to the ants as the antwrens move past, but usually drift off after a few minutes with the ants. Some other medium to large species, such as Buff-throated Woodcreepers, also shift from one type of alliance to the other at times. Normally antwrens and most small members of the antwren alliance except migrants do not capture any prey flushed by the ants. If there are no ant-following birds about, birds of an antwren alliance generally ignore an active ant swarm. Johnson (1954: 45) was the first ornithologist I know clearly to distinguish between antwren and ant-following alliances, but he did not present data to support his conclusion that the whole antwren alliance normally or actively forages with ant-following birds as the alliance passes them.

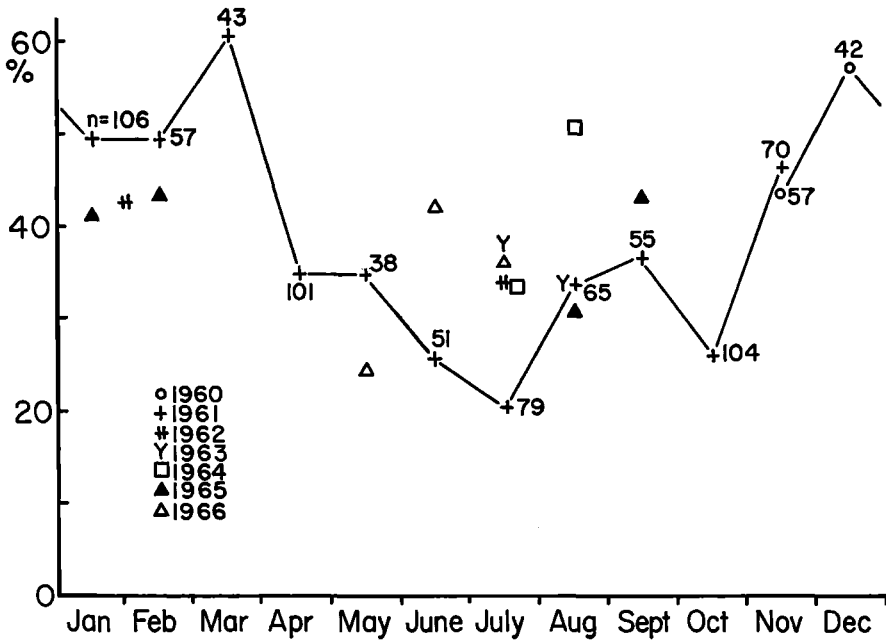


Figure 27. Percentage of Spotted Antbirds with the wandering antwren flocks when away from swarms of ants and nests.

ASSOCIATION WITH INTERSPECIFIC FLOCKS

Out of 798 Spotted Antbirds watched away from nests and away from swarms of ants from 1 November 1960 to 31 October 1961, some 299 or 37.5 percent were with interspecific wandering flocks or joined interspecific flocks as I watched them. When I could not determine whether the bird was with a flock, I did not count it in the 798. A Spotted Antbird was counted as being with a wandering flock if one or more other species associated with it for one minute or more.

There is only a slight decrease in the percentages of Spotted Antbirds with flocks during the nesting season, April to November (Figure 27). In some nesting months, such as August in 1964, September in 1965, and June in 1966, the percentages of Spotted Antbirds with flocks were over 40 percent. Perhaps some of the lowering of percentages during nesting months results from flushing Spotted Antbirds near undiscovered nests or young and from including birds leading young about: birds limited in their movements by nests or young are less likely to be with interspecific flocks, since these flocks move about rather rapidly at times.

Spotted Antbirds readily join and follow wandering flocks for varying

periods of time, but they always seem to be peripheral species. Their foraging methods tie them to watching the ground for long periods of time, so they follow the motions of the more actively foraging members of flocks very imprecisely. Commonly a Spotted Antbird is left behind or drifts off from the flock for brief periods. However, when it does change its foraging perch it often flies toward the flock rather than in other directions.

Spotted Antbirds are especially likely to join flocks when one watches them. Typically the antbird moves rather rapidly when one approaches, then settles down near a dense treefall or near a flock of birds. Many Spotted Antbirds watched for five minutes or more ended up with bird flocks, even ones that first went to treefalls. Those that have seen the observer many times before are less prone to move rapidly to treefalls or to flocks, however.

Table 12 indicates that Spotted Antbirds with flocks tended to preen or forage quietly somewhat more often than did birds away from flocks, which tended to mob, to panic, or to flee so I could not tell what they were doing. Of 749 observation periods of Spotted Antbirds away from flocks from 1960 to 1966, 330 or 44.1 percent were in the fleeing-mobbing-panicking categories and 419 or 55.9 percent were in the preening-foraging categories. Of 608 records of Spotted Antbirds with flocks, 204 or 33.6 percent were in the former categories. Chi-square for these data is 15.52, highly significant ($p < 0.00008$ according to Hartley and Pearson, 1950). Some birds in the "alarmed" categories may have been near an undiscovered nest or young; since such birds tend to be away from flocks, the totals for alarmed birds away from flocks may be too high. However, in the mainly nonbreeding period from 1 January to 30 April 1961, 34 of 144 Spotted Antbirds with flocks, or 23.6 percent, and 58 out of 132 away from flocks, or 43.9 percent, were alarmed (Chi-square is 12.81, $p < 0.00035$).

The first nine full months I worked on Barro Colorado, the percentage of alarmed birds away from flocks exceeded the percentage of such birds with flocks by 12 to 47 percent. From 1 November 1960 to 30 June 1961, 62 of 215 with flocks, or 28.8 percent, mobbed or panicked or disappeared; 110 of 220 away from flocks, or 50 percent, were alarmed (Chi-square is 25.09, $p < 0.00001$). From then until 1966, however, there have been 10 of 23 months when the percentage of alarmed birds was higher by 4 to 29 percent among birds with flocks (for all records from then to 1966 Chi-square is 2.814, $p < 0.1$ and not significant). Probably this happened because, not realizing the significance of alarm behavior, I tended after the first few months not to record every chip or chirr. Also, my later work was censusing, with irregular coverage of tame birds some weeks and birds unaccustomed to the observer other weeks; and I persistently followed certain birds to see their bands whether they were alarmed or not, and thus got alarmed birds habituated to me, rather than watched any bird that was not alarmed as I did the first

TABLE 12
ACTIVITIES OF SPOTTED ANTBLRDS AWAY FROM SWARMS AND NESTS

Main Activity	First Year ¹		1961-1966 ²	
	Number ³	Minutes ⁴	Number	Minutes
A. No young nor flock				
1. Activity uncertain	38	131	42	235
2. Flees or chirrs	103	339	138	548
3. Wanders	76	440	92	497
4. Forages	181	2018	222	2173
5. Preens	5	32	10	49
6. Bathes	4	16	4	24
7. Feuds	84	734	81	735
B. No young; with flock				
1. Activity uncertain	12	38	37	146
2. Flees or chirrs	76	259	75	342
3. Wanders	10	36	14	87
4. Forages	187	2087	192	2486
5. Preens	7	52	8	54
7. Feuds	23	113	31	316
C. Young; no flock				
1. Activity uncertain			2	42
2. Flees or chirrs	27	601	42	820
3. Wanders			6	21
4. Forages	14	272	28	745
5. Preens			1	14
7. Feuds			12	79
D. Both young and flock				
2. Flees or chirrs			24	285
4. Forages	3	60	33	564

¹ 1 November 1960 to 31 October 1961. ² 1 November 1961 to 30 July 1966. ³ Number of sessions when the activity occurred times number of birds performing it. ⁴ Two birds watched during one minute, "2 minutes" are recorded, etc.

year. Tame birds, whether at or away from flocks, tend to forage and preen and ignore the observer; to a certain extent birds in treefalls and near dense cover also are tame.

Until I analyzed the data and wrote the above account in early 1967, I had completely overlooked the tendency of Spotted Antbirds to be more alarmed away from flocks. The above data thus came from a naive observer. In 1967 I watched more closely, and found that 43 of 71 birds away from flocks showed more alarm behavior than foraging or preening (2 others showed equal time) while 10 of 75 birds with flocks showed more alarm behavior (1 more showed equal time); Chi-square for these data is 35.3 ($p < 0.00001$).

In many cases flitting, flicking, darting to cover, and similar reactions would not have been recorded unless I was watching carefully. In some cases a bird chased away from a flock began to chip or chirr and then stopped alarm calls on reentering the flock. Less systematic observations in 1968–1971 indicate that greater alarm outside of flocks is normal behavior.

Some birds may join flocks because mates can be located more easily in flocks. Both sexes of Spotted Antbirds without mates sing at or away from flocks, and court mainly at swarms of ants where there is a good supply of food for courtship feeding. They join flocks about as readily when mated as when mateless. When a bird comes off the nest, its mate answers its songs as readily whether it is with a flock or not, so it is not likely that the arriving bird normally homes on the flock.

Foraging Spotted Antbirds with flocks generally watch the ground rather than their companions above, so that their companions do not flush food for them. As is detailed below, they have different foraging sites from all other species in the flocks; they do not go to food supplies uncovered by other species or avoid places where other species have foraged any more than away from flocks. They forage much the same way away from flocks as in flocks. On a few occasions, Spotted Antbirds watched Scaly-throated Leafscrapers tossing dead leaves; once a leafscraper supplanted such a watching antbird. However, leafscrapers are rarely flock members.

OTHER MEMBERS OF FLOCKS

Appendix 1 lists frequent members of wandering interspecific flocks of the forest interior on Barro Colorado, with notes on their foraging behavior and social structure and roles in flocks. There are several kinds of interspecific flocks not considered in this appendix, notably the bird flocks that follow army ants (see Johnson, 1954: 41, and earlier parts of this paper) and the forest-edge tanager and honeycreeper flocks (Moynihan, 1962a: 2). Flocks of parrots and other birds in fruiting trees, overhead flocks of swifts, and wandering flocks of toucans are also outside the bounds of this section of the present paper. The two types of flocks considered are the groups that gather around White-flanked Antwrens in the forest undergrowth and the groups that gather around Gray-headed Greenlets in the upper levels of the forest. Using Moynihan's term "alliance" as shorthand for a "wandering interspecific flock" or its separated members, these may be called the "antwren alliance" and the "greenlet alliance," respectively.

Spotted Antbirds attend only the antwren alliances, since members of the greenlet alliances forage high above them. However, the two alliances sometimes fuse as a large alliance, especially in places where birds foraging at intermediate levels link the two. The antwren alliances on Barro Colorado are depauperate in species, especially in the open middle levels (15–20 m up),

and split apart from the greenlet alliances more readily than do the species-rich and better-linked alliances in the Amazon basin and even those in other localities in the Canal Zone.

Appendix 1 shows the four main types of birds in these alliances: clan-forming residents (probably mostly family groups); pair-forming residents; solitary residents; and solitary migrants. Two clan-forming (young stay with adults) residents, the White-flanked Antwrens and the Grey-headed Greenlets, are the "nuclear" species (in the sense of Winterbottom, 1943: 439, and not in the confusing [see below] senses of later authors, including Winterbottom, 1949: 259). The antwren and the greenlet are very similar in their foraging and social behavior, being ecological counterparts for each other in the undergrowth and the forest canopy. With Slaty Antshrikes, they are the commonest forest birds on Barro Colorado. Both look about rather actively as they hop in the terminal sprays of green foliage, and both glean small arthropods from the foliage or sally out to snap them from the air nearby. Both are in territorial groups of two to five birds most of the year, suggesting that young stay with their parents up to a year as is likely for ant-tanagers (Willis, 1960a: 165) rather than being driven away as is the case for Spotted Antbirds. Members of such groups keep in contact by frequent short chirping notes as they travel. A human approaching White-flanked Antwrens elicits loud "cheep doo" alarm calls and flight, but they soon become tame. The high-foraging greenlets react with buzzing scolds when a human is nearby; normally they ignore the observer or arboreal mammals after a few calls. Other forest-living species of greenlets in the Amazon are mostly paired residents rather than clan-forming residents, and follow rather than lead antwren alliances; the alliances seldom split into low and high-foraging groups in that region.

The Dot-winged Antwren, a regular member of forest flocks in British Honduras (Willis, 1960b), tends to center on dense tangles of vines at low to middle levels in second-growth woodland; it is becoming uncommon on Barro Colorado as the forest matures, and its habitats are local, so that it tends to form centers for flocks in these areas but to drop out of flocks as the other birds move into less cluttered forest. In the vine tangles and dense nearby foliage they flutter about actively in green leaves for tiny insects and are often seen in family-size groups that follow each other with chirping notes and dispute noisily with other such groups. R. H. Wiley (MS) has recently confirmed statistically that Dot-winged Antwrens use dense foliage. The Dot-winged Antwren has a chirr almost identical to that of a Spotted Antbird when a human first appears, but it very rapidly (compared with a Spotted Antbird) starts loud *peup* notes or chirps and resumes foraging.

In the upper levels, the White-shouldered Tanagers are to some extent ecological counterparts of Dot-winged Antwrens. They forage actively on

green foliage in vine-covered trees, they travel in small territorial groups, and they are becoming uncommon on Barro Colorado as the forest matures. They scold loudly for a few moments when one approaches them closely at a forest overlook but quickly resume foraging and chirping. I am not sure whether they are more often leaders or followers of interspecific flocks, but on Barro Colorado their high mobility between patches of habitat and their being uncommon insure that they are usually attendants of the greenlet alliances if they are with flocks at all.

Sulphur-rumped Tanagers form constantly chirping family groups or clans in the canopy. They forage both in foliage and at fruiting trees, and move so rapidly that they often leave greenlet flocks. At times they seem to be major species in greenlet alliances, but at other times they join or form centers for the forest-edge "tanager and honeycreeper" alliances. At times they link the two kinds of alliances, but at other times they wander separately.

There are other such species in flocks elsewhere in the Canal Zone. In humid forests of the Caribbean slope of Panamá, but not on Barro Colorado, Tawny-crowned Tanagers form noisy groups in some alliances. Song Wrens, which have disappeared on Barro Colorado as the forest matured but form clannish groups and sometimes join antwren alliances in other wooded parts of the Canal Zone, are noisy when disturbed but quickly habituate to the observer or else flee. They differ from the other clan-forming birds mentioned in poking under leaves on the forest floor and in similarly enclosed sites rather than foraging in open foliage. They commonly associate with Red-throated Ant-Tanagers. I am not sure whether Song Wrens follow or lead such flocks, but they move so slowly it is surprising they often associate with the motile White-flanked Antwrens and the even faster ant-tanagers.

Red-throated Ant-Tanagers, once common on Barro Colorado but now becoming rare as the forest matures, and the Red-crowned Ant-Tanagers of drier woodlands of the Pacific slope of the Canal Zone, sometimes form nuclear intraspecific groups for interspecific flocks, but tend to move too rapidly to be permanent centers. As a result, they tend to move from one flock to another, except at midday when their rate of travel is slow (Willis, 1960*b*).

Many species of antwren and greenlet alliances form pair bonds but drive away their grown young and trespassers, so that one sees only one or two birds of a species in each alliance. Such "pair-forming" birds tend to follow the nuclear or "clan-forming" species rather than lead them. On Barro Colorado, besides Spotted Antbirds, Checker-throated (Fulvous-bellied) Antwrens, Wedge-billed Woodcreepers, and Slaty Antshrikes are the commonest pair-forming members of alliances.

Territorial pairs of Checker-throated Antwrens chirp to each other; a human elicits loud *peesk* calls and flipping (pivoting from a position facing

right of the observer to a position facing left of him, or vice versa) back and forth, then flight; they become tame somewhat more slowly than do White-flanked Antwrens, but more rapidly than do Spotted Antbirds. Slud (1960: 100) suggested that Checker-throated Antwrens forage in the same way as do White-flanked Antwrens, but I find that the former and their Amazonian relatives (the Brown-bellied, White-eyed, Rufous-tailed, and Stipple-throated antwrens) all forage in the same way as North American Worm-eating Warblers; that is, all clamber like furnariids in green foliage and poke or rummage for arthropods in scattered, dead rolled-up leaves that have not yet fallen from twigs in the forest undergrowth. They and their relatives follow White-flanked or similar gleaning antwrens assiduously, and are regular members of the forest flocks everywhere.

The Wedge-billed Woodcreeper also occurs singly or in pairs, unless dependent young are present, and follows antwren alliances rather than leading them. It hitches rather silently up tree trunks from near the ground to the forest midlevels, gleaning or prying small arthropods from the bark and crevices. When antwrens call loudly at a human or a potential predator, the woodcreeper adds a sneezing *chiff* to the din. Like the antwrens, it fairly soon becomes tame or ignores the observer.

Slaty Antshrikes are so common on Barro Colorado that they are bound to be in flocks occasionally; in addition, they often follow flocks or are joined. According to studies by Yoshika Oniki (pers. comm.), pairs of Slaty Antshrikes occupy small territories, drive away grown young or trespassers, forage by looking about carefully for large to medium-sized arthropods on twigs and in foliage from near the ground to 18 or 20 m up, and call faintly to each other as they move rather slowly about. Frequent dissection of large prey and slowness of movement often means that the antshrikes drop behind a flock or follow its movements imprecisely. In addition, they have such small territories that a local antwren alliance is often with a neighboring pair. Slaty Antshrikes are usually rather tame and phlegmatic in response to humans, but can be incited to call *ah*, *grrrrrrt*, a caw followed by a growl, when additional factors (such as a nest or extremely noisy antwrens) excite them.

Dot-crowned Antvireos, relatively local and uncommon in areas of very open undergrowth on Barro Colorado, are intermediate between White-flanked Antwrens and Slaty Antshrikes in size and foraging behavior but are like the latter in pair territoriality. They are usually found in antwren alliances, but I am not familiar with their reactions to humans or predators or their roles as followers or leaders.

The Plain Xenops, singly or in pairs, follows antwren flocks very persistently and quietly. It gives its *wreep* alarm call infrequently, mainly at hawks. It generally ignores humans or flees silently. It creeps or hangs on rotten twigs in the middle and lower levels of secondary woodland, prying intently into the

twigs or under the bark for tiny arthropods. Perhaps it is uncommon and local on my study area on Barro Colorado and in mature forests generally because the twigs on which it feeds seldom lodge above the ground in the open and vertically-oriented lower levels of tall forests. Like the Dot-winged Antwren, it is a regular member of forest flocks in secondary or woodland habitats, such as in British Honduras (Willis, 1960*b*) and in the Panamá Canal Zone outside of Barro Colorado.

Other intently rummaging furnariids are important members of forest flocks, in most cases, either singly or in pairs, in the highlands of Panamá and in Amazonian forests. One lowland species, the Buff-throated Foliage-Gleaner, is a regular and persistent follower in antwren alliances in the Canal Zone but has disappeared from Barro Colorado as the forest matured. It ignores the observer after initial loud *snare!* calls, or flees silently. It rummages in epiphytes or in piles of dead leaves caught in the undergrowth to midlevels of the forest; such piles of leaves and epiphytes disappear from the lower midlevels as horizontal limbs are shaded out and fall with forest growth.

Two intently foraging large woodcreepers of the genus *Xiphorhynchus* are regular members of alliances on Barro Colorado, as are other members of the genus elsewhere. Both occur singly or in territorial pairs, chase off trespassers other than dependent young, and follow alliances desultorily and imprecisely rather than leading them. Both hitch up tree trunks; they peer closely and peck in crevices or under crossing lianas, probe into epiphytes, and pry off loose pieces of bark with their long bills, but do not hammer wood or rummage deeply into enclosed places. Black-striped Woodcreepers tend to work the lower sides of limbs in the canopy and midlevels of tall forests; they follow greenlet alliances occasionally and antwren alliances rarely. Buff-throated Woodcreepers tend to work the upper sides of limbs in the middle and lower levels of woodlands and second growth. They follow antwren alliances strongly and greenlet alliances occasionally. The Black-striped Woodcreeper is common on my study area on Barro Colorado while the Buff-throated Woodcreeper is uncommon; it is common and a regular flock-follower in woodlands elsewhere on Barro Colorado and in the Panamanian lowlands generally. Both species give loud alarm calls and flee readily on first sighting a human or a potential predator; they are quiet and ignore a human later (i.e., they habituate gradually).

There are many other pair-forming members of flocks on Barro Colorado, such as the Chestnut-backed Antbird of antwren alliances, the Long-billed Gnatwren of antwren alliances near dense thickets or in second growth, the Tropical Gnatcatcher and Fulvous-vented Euphonia of greenlet alliances, and so on. All except the Gnatcatcher tend to forage intently or in dense places, all follow rather than lead alliances, and all react strongly to potential predators and become tame gradually.

There are other flock members that are solitary, avoiding or chasing away or ignoring members of their own species. These include one woodcreeper, several flycatchers, and some manakins. All forage openly, by flycatching or sallying into the air or to open foliage. All flee readily, even to the extent of deserting flocks, even though many seem relatively tame in response to a human at first.

The Plain-brown Woodcreeper, a solitary and silent follower of flocks unless a hawk or human causes it to give loud *stiek* calls, is uncommon in flocks mainly because it usually follows army ants. It is not tame, even after one follows a flock for some minutes, and it deserts readily. It waits on tree and sapling trunks in the upper undergrowth to the upper midlevels of the forest, then flies out to foliage or to trunks for the medium to large insects it dissects. It follows flocks rather imprecisely but sometimes does so for long periods.

Manakins, an important family in second growth and woodland in tropical America, are poorly represented in forest flocks on Barro Colorado. All the species tend to gather at fruiting bushes and follow antwren flocks rather irregularly—mainly when feeding on insects. Manakins are solitary to flocking birds without pair or family organization or evident territorial behavior, except at leks and when young are following females. They tend to ignore the observer, then flee quietly, and they desert flocks readily. Ochre-bellied Flycatchers, which have become uncommon on Barro Colorado as the forest matured, behave as manakins do in most of these respects—as does the Plain-brown Woodcreeper, except that the woodcreeper goes to swarms of ants rather than to fruiting trees. The Golden-collared Manakin, which sallies to the foliage of the low undergrowth in woodland and second growth, has almost disappeared on Barro Colorado as the forest grew tall and shaded out the dense lower levels. The Red-capped Manakin, which sallies to foliage in the upper undergrowth, is now the only common manakin on Barro Colorado. The Red-capped Manakin flees silently from the observer of flocks, although it becomes tame at fruiting bushes or at leks. It probably takes some insects in competition with Spotted Antbirds when it forages low, but generally the two species forage at different levels. The Blue-crowned Manakin does well in Panamanian forests that do not have such a long dry season; it seems to be unrecorded on Barro Colorado, but sometimes joins alliances elsewhere in the Canal Zone.

Tyrant flycatchers, members of the largest family of tropical American birds, are also poorly represented in alliances on Barro Colorado. The solitary, silent Black-tailed and Sulphur-rumped flycatchers, which still follow antwren flocks and flit into the air in the upper understory of woodlands elsewhere in Panamá, have disappeared in the last 20 years as the forest matured. The minute Ruddy-tailed Flycatchers, solitary and silent birds that follow flocks

readily, are the only resident species still widely distributed through the forest undergrowth. They generally ignore the observer, but flee silently if he stays nearby. They sally short distances to green foliage or into the air in the upper undergrowth of the forest, hunting very small insects. Bentbill Flycatchers, solitary and silent unless displaying noisily at their dispersed leks, are small flycatchers of the low to intermediate levels of the dense vine tangles favored by Dot-winged Antwrens. Bentbill Flycatchers follow flocks imprecisely and are often seen away from them, because they stay in their patches of habitat rather than with flocks that move beyond the patches. Olivaceous Flatbills, solitary and silent flycatchers of the undergrowth to midlevels of irregular liana-crowded forest in areas of treefalls, follow flocks readily whenever the flock is near such patches of habitat but stay alone in their habitat at other times. The very small, generally solitary Golden-crowned Spadebills sally to foliage in the upper to lower undergrowth in areas where Dot-crowned Antwrens live; they ignore humans, are relatively silent, and follow flocks rather rarely.

Yellow-margined Flycatchers sally to foliage in the midlevels to lower canopy and follow greenlet alliances, as do Olivaceous, or Dusky-capped, Flycatchers. Both species seem to travel in pairs, and to forage in rather vireolike ways, but more observations are needed. It may be that these flycatchers are the counterparts of the antvireos and antshrikes of the forest undergrowth.

Large frugivorous cotingas rarely join antwren or greenlet alliances, although in the Amazon and many other forests away from Barro Colorado small insectivorous becards (*Pachyramphus*, *Platypsaris*) are pair-forming members of greenlet-antwren alliances. Large woodpeckers, trogons (except insectivorous species of the forest undergrowth, such as Black-throated Trogons on Barro Colorado), parrots, toucans (except small species), and other forest birds seldom join alliances for very long, although some congregate at fruiting trees or go around together (toucans). Small insectivorous birds are the main members of forest alliances; even manakins leave flocks when eating fruit.

The replacement of oscines (songbirds) and members of the superfamily Tyrannoidea (tyrant flycatchers, manakins) by the Furnarioidea (ovenbirds, woodcreepers, antbirds) in forest flocks is a general trend in the Neotropics as one goes from the forest canopy or edge to the forest undergrowth (Appendix 1), from second growth into deep forest, from savanna or dry areas into wet regions, from the highlands to the lowlands, and from the periphery of the tropics into the heart of upper Amazonia. Antbirds tend to replace ovenbirds and woodcreepers, also. On Barro Colorado, the growth of the forest in the 48 years since the island was set aside has resulted in the loss of more songbirds than suboscines, in the virtual restriction of resident songbirds to the canopy and forest edge, and in the disappearance of many oscine

and tyrannid and dendrocolaptid and furnariid birds from the antwren alliances, as compared with such alliances in less mature forests a few hundred yards across the Panamá Canal. Antbirds are about the same on the two sides of the canal in number of species, and are slightly more abundant on the Barro Colorado side in number of individuals. They thus form a far higher proportion of the depauperate flocks on the Barro Colorado side.

Several migrant and wintering birds, principally warblers, readily join and follow antwren flocks on Barro Colorado and elsewhere in the Canal Zone. The three commonest species forage by flitting about in the foliage like antwrens, but are solitary and quiet birds. Canada Warblers move about actively in the foliage of the undergrowth from 1 to 15 m up. Chestnut-sided Warblers are active in foliage of the middle levels of the forest. Bay-breasted Warblers move and peer more sluggishly at nearly all levels, especially in the midlevels. Black-and-white Warblers creep over the trunks and large limbs of trees, picking off small prey. Acadian Flycatchers snap up prey from the air and foliage of the lower levels from 1 to 15 m up.

All the migrants tend to be tame in response to humans, to chip loudly or call excitedly when resident flock members do so, and to resume foraging quickly after any interruption. None are very intent or extensive foragers, although the Acadian Flycatcher approaches the latter condition and the Black-and-White Warbler the former; they tend to be generalized foragers at many levels.

Thrushes and warblers that forage intently (such as the Wood Thrush and the waterthrushes, *Seiurus* spp.,) tend to be such slow foragers that they do not often follow flocks; they tend to be extremely timid and to have protective colors. Flycatchers that forage extensively (such as wood pewees, *Contopus* spp.) tend to do so at local clearings rather than move through the forest; they are seldom flock members. They ignore humans at first, but then disappear if one remains. One variably foraging winter resident, the Great Crested Flycatcher, sometimes joins greenlet flocks in the canopy when foraging like a vireo; when it forages extensively it is usually at clearing edges and hence does not follow well. I am uncertain how it interacts with the congeneric Dusky-capped Flycatcher.

COMPETITION AMONG FLOCKING BIRDS

In contrast to the frequent supplanting among flocks of birds over swarms of army ants, there is little overlap in foraging and little supplanting among the birds that join wandering flocks. The Spotted Antbird is especially isolated ecologically from other birds of the flocks, except for the Chestnut-backed Antbird and the wintering Kentucky Warbler, because only these three species work the ground rather than the foliage or air as do most members of the flocks. Occasionally a Spotted Antbird supplants the small White-flanked

or Dot-winged or Checker-throated antwrens when they forage near the ground, or the larger Slaty Antshrike supplants a Spotted Antbird when it moves up into the foliage or comes near an antshrike dissecting prey on the ground, but most of these other species work well above the ground even when the Spotted Antbird is not present. Canada Warblers occasionally take prey like that taken by Spotted Antbirds, but the antbirds and warblers generally forage in different ways and places.

Chestnut-backed Antbirds, which are about the same size as Bicolored Antbirds, sometimes ignore the smaller Spotted Antbirds but at other times supplant them with loud rasping *charngh!* notes from distances of as much as 20 m. I noted above some other cases of supplantings on the infrequent occasions when Chestnut-backed Antbirds followed army ants, and an instance when one supplanted a Spotted Antbird at the nest. Spotted Antbirds normally avoid Chestnut-backed Antbirds as they move around the tangled treefalls or the dense patches of wild pineapples that the latter favors. In such tangles the Chestnut-backed Antbirds forage mainly by hopping near or on the ground and pecking or jumping upward at moderately large arthropods on overhanging lianas or leaves or trash; they should compete with the open-foraging, downward-leaping Spotted Antbirds rather little. They often capture and dissect large prey, while Spotted Antbirds seldom do so. However, there is a considerable overlap in the places and ways of foraging and sizes and kinds of food taken.

All recorded attacks have come since 1965, perhaps because Chestnut-backed Antbirds became very common in dense new growth around tangled treefalls after a windstorm on 1 October 1961. Since Chestnut-backed Antbirds tend to stay in dense tangles or move mainly between such tangles, they do not follow wandering flocks persistently. Thus, they are only a minor and perhaps temporary exception to the rule that birds of the wandering flock do not attack each other.

Of the wintering birds that join flocks, only Kentucky Warblers forage much like Spotted Antbirds. These warblers hop along the forest floor and over low lianas and debris, pecking here and there or hop-fluttering upward to peck their minute prey off low overhanging leaves (Willis, 1966a: 208). They thus tend to forage upward for very small prey, where there are sprouts, while the Spotted Antbirds forage downward in more open situations for larger prey, but there is some overlap. Away from swarms I never saw antbirds supplant warblers, because the latter generally keep out of the way of the similarly sized but heavier antbirds. However, Kentucky Warblers often hop after or around Spotted Antbirds, keeping at a distance of 10 to 20 m. I suspect that the Kentucky Warblers, which often forage at ant swarms, associate with the Spotted Antbirds because the latter often lead them to ants. Once a Kentucky Warbler came to the tape recorder when I played the song

of a Bicolored Antbird, another swarm-following species. The Kentucky Warbler does not follow antwren alliances closely or frequently, perhaps because it is somewhat slow-moving.

One seldom sees supplantings of or by Spotted Antbirds away from swarms. In the years 1960–1966, I recorded only 85 supplantings and displacings of Spotted Antbirds by others of their own species. In addition to the supplantings noted above, I saw one Bicolored Antbird come up to a male Spotted Antbird singing away from a swarm and supplant him three times, looking down from each successive perch as if for ants. One other Bicolored Antbird supplanted a Spotted Antbird in another such incident. Three times on one occasion a Spotted Antbird supplanted a Bentbill Flycatcher when it chirred nearby like a Bicolored Antbird (see Willis, 1967, Plate 1, for sonograms of the very similar calls of Bentbill Flycatchers and Bicolored Antbirds.)

DISCUSSION

The wandering interspecific flocks of tropical forests resemble the chickadee-titmouse-warbler flocks of northern woodlands in being composed of small insectivorous birds that travel moderately rapidly through the forest. Northern flocks break up during the nesting season to a greater extent than do tropical flocks, which are evident most of the year. Probably one reason Spotted Antbirds and other members of tropical flocks can stay with flocks during the nesting season is that tropical birds have small broods and need not visit the nest as frequently as do northern birds. Conversely, the possible necessity of staying with flocks may add to the reasons for having small broods. The large number of species available in tropical forests probably increases the possibilities of joining and following other species. Large territory sizes because of low numbers of individuals for most species (James Karr, pers. comm.) may also facilitate following for longer distances.

Many interspecific flocks are mainly assemblages at concentrated sources of food or some other environmental resource. Birds at swarms of army ants and in fruiting trees, nesting assemblages of seabirds on islands, and roosting blackbirds in marshes are examples of this type of interspecific flock. However, even these groups nearly always congregate more densely than seems necessary for efficient utilization of the environmental resource. At the other extreme, judging by the distributional patterns of feeding, environmental resources seem to be scattered for the antwren alliances. Even though such birds sometimes forage irregularly, carefully working one area and moving rapidly through others, the alliances sometimes circle about and work the latter areas carefully only a few minutes later. Although detailed analyses are needed, the flocks seem to work wide areas rather evenly over the course of a few hours or days.

Local areas sometimes vary greatly in food or other resources even in

continuous forests. Some flocks in eastern Asia (Stanford, 1947: 508; McClure, 1967: 149) apparently follow set routes and even appear at set times of day. However, there seem to have been no long-term studies by observers actually tracking habituated or undisturbed flocks instead of simply encountering a flock at the same place or time repeatedly. It is thus difficult to know if temporal or spatial localization of food or another resource is forcing these birds to associate. If there is spatial localization but no temporal localization, the birds should still scatter over the route of the flock unless flocking has some advantage.

Dot-winged Antwrens and Bentbill Flycatchers and other birds that prefer vine tangles do tend to restrict their activities to such areas on Barro Colorado. However, the general rule seems to be that the more restricted a bird is to certain areas, the less likely it is to be a consistent member of antwren or greenlet alliances. The Dot-winged Antwren is a much more consistent flock member in British Honduras (Willis, 1960*b*) where its habitat is fairly widespread, than on Barro Colorado or in the Amazon where its habitat is restricted. The most consistent members of flocks are those birds, such as White-flanked Antwrens, that use the habitat moderately evenly.

The species with scattered habitats are restricted in many cases because they cannot follow moving flocks. Dot-winged Antwrens follow antwren alliances persistently when these alliances are in vine-crowded areas but drop out as the alliances move into more open forest. Spotted Antbirds also follow antwren alliances fairly persistently when cover is nearby, but tend to drop out when the antwrens move into very open undergrowth.

Following and leadership is clear in most of these flocks, and is another line of evidence that indicates the birds stay together rather than being forced together because of localized resources. So far only Moynihan (1962*a*: 18) has studied following and leading quantitatively, and he has worked with forest-edge flocks rather than with flocks of the forest interior. However, preliminary indications are that Spotted Antbirds and perhaps other members of the antwren alliances are not forced together by localized environmental resources, and that they do actively associate with each other. The Spotted Antbird seems to use a bird flock as it uses a treefall, as a safe place to stop when one chases it.

Active association in an area of scattered resources, rather than even or random scattering, would seem disadvantageous to birds because (1) prey of one bird might be eaten or frightened by other birds of the flock (Goss-Custard, 1970: 18–19) (2) predators of one bird might be attracted by the noise, etc., of the flock (3) one species might physically or competitively interfere with the activities of another, since (4) slowing down or speeding up so flocks can stay together is always a disadvantage (Nichols, 1931: 181), and, since (5) staying with flocks can interfere with feeding young and with

other reproductive activities, (6) reactivity to other species may use DNA or brain cells and energy that could be used for feeding or reproduction. If any of these occurs, or even if they do not, there should also be some advantages in associating with other species.

Those who have reported on flocks have suggested many possible advantages. The following list is probably incomplete, and the categories overlap, but it will do for a start. The earliest authors or major authors I have found for a suggestion are listed; "perhaps" means that the author states the suggestion indirectly or only hints at it.

A. Food-giving advantages

- (1) Animals flush food for each other (perhaps Belt, 1874: 123; Neave, 1910: 80).
- (2) Animals may pilfer from others or get food from their leavings (Rand, 1954: 31).
- (3) Animals lead each other to good food sources (Nichols, 1912: 45).
- (4) Animals can avoid sites just used by others (Miller, 1922: 125), or niches usually used by others (Morse, 1967: 101).

B. Predation-avoiding advantages

- (5) Intently foraging animals forage best if aerially alert foragers give the warning (perhaps Moynihan, 1962a: 120; Willis, this report).
- (6) The more animals, the more likely they are to see predators; scare one, scare all (Bates, 1863: 347).
- (7) More animals allow individuals to hide behind each other, using each others' bodies as cover (Williams, 1964; W. D. Hamilton, *vide* Goss-Custard, 1970: 35).
- (8) More animals confuse a predator (Miller, 1922: 123; Lorenz, 1963: 142).
- (9) More animals can mob, attack, collide with, or intimidate predators; aggressive animals attract weaker ones (Swynnerton, 1915: 348); loud-voiced species protect faint-voiced ones (R. H. Wiley, MS).
- (10) Clumping increases the irregularity of the environment for predators, making them move further for each try at prey, given that (5)-(9) above occur; reduced predator success lowers predator numbers (Trivers, 1971: 44).

C. Mate-gaining advantages

- (11) Animals get mates more easily by associating.
- (12) Birds locate or stay with mates or young more easily (Willis, this report).

D. Stimulation advantages

- (13) Species facing occasional times of lowered stimulation, such as drab winter forests, may need "social facilitation" to bring them to normal or necessary levels of food-searching (L. Kilham, pers. comm.) or predator avoidance (Moynihan, 1962a: 120).

E. Learning advantages

- (14) Young, migrant, vagrant, or otherwise inexperienced birds can learn local predators or sites where predators occur or seldom occur.
- (15) Inexperienced birds can learn where there are locally superabundant foods.
- (16) Inexperienced birds can learn how others forage and avoid competition.
- (17) Inexperienced birds can learn where to go for various resources, such as a lake or wintering ground or roost site.

F. Navigation advantages

- (18) Averaging variable headings of individuals gives correct resultant to home (Hamilton, 1967: 58).

G. Population-control advantages

- (19) Animals can estimate interspecific competition and restrict reproductive rates (Wynne-Edwards, 1962: 418).

What few data there are suggest that the Spotted Antbird and most other species of Neotropical forest-interior flocks gain few food advantages by associating. I rarely saw one species flush food for another or locate a good food source that another species then used. It was never evident that Spotted Antbirds or other species avoided foraging in the same sites more than would be the case by chance alone. Miller (1922) suggested the latter from watching bushtits (*Psaltriparus minimus*), but Richard B. Root (pers. comm.) has seen bushtits foraging one after the other in the same foliage. Statistically valid studies are needed for bushtits and other flocking species.

Several lines of evidence suggest that food advantages are usually not primary in the Neotropical alliances. First, flycatching birds are not common in such alliances, whereas they should be the main members if birds flush prey for each other. Tyrant flycatchers, although the largest family of Neotropical birds, are mostly uncommon in flocks. The yellow-rumped flycatchers of the genus *Myiobius*, the Dusky-capped Flycatcher, and the flycatching Canada Warbler are exceptions, and may well exploit food flushed by other species even if most species of the alliances do not. Swynnerton (1915) mentions savanna flocks that definitely gathered around drongos flushing food; I have noted brief association of Spotted Antbirds with Scaly-throated

Leafscrapers. These cases grade into flocking associations such as those around army ants, and may play varying roles in many flocks.

A second line of evidence that food advantages are not primary in the antwren alliances is that most such birds take different foods in different ways (R. H. Wiley, MS, has recently confirmed this quantitatively for three species of antwrens in flocks on Barro Colorado Island), and fight with each other or go for the same prey items relatively infrequently. These behavior patterns contrast strongly with those among groups where food is the primary reason for social aggregation, as it is for birds over swarms of army ants. Separation of niches is the rule among birds of antwren alliances, overlap of niches the rule among birds with ant-following flocks. The relations of Spotted Antbirds with competitors at swarms of ants and in antwren alliances illustrate the difference between the types of flocks very well, since the same species is involved. More data are needed to judge if some species overlap, since Morse (1967, 1970) suggests that some flocking birds separate their foraging niches better than do lone birds, presumably by avoiding niches of other species or because of aggression.

Third, northern birds seldom join interspecific flocks when they are feeding young, at the time their food needs should be highest. Fourth, Spotted Antbirds and manakins and other birds that gather at concentrated food sources commonly leave alliances to do so. Fifth, birds that find abundant foods in localized habitats (including most of the ant-following birds that do not forage away from ants) generally stay in such habitats or move directly from one to the other rather than wandering with alliances.

There is also little direct data for or against the theory that predation is less on birds that join flocks. Rudebeck (1950: 87) found that European Sparrow-hawks (*Accipiter nisus*) catch more prey outside flocks and succeed on more attempts outside flocks, but Morse's (1970: 163) analysis indicates the difference Rudebeck found in Sparrow-hawk success is not significant. Of course, the figures should be in terms of successful attempts per 100 birds in and outside flocks, for it may be that a predator only makes attempts on flocks when it is as certain of getting prey as when it attacks an individual bird. That is, if the Sparrow-hawk avoids attempts on birds in flocks there may be an advantage for prey to flock even though the few attacks on unprepared flocks (such as noted by Tinbergen, 1946: 96-97, for the cross-hedgerow style of hunting) are relatively successful. Even the easily observed raptors of open country often turn out to have unexpected foraging methods (see Willis, 1963, for one example); and data are almost lacking for raptors in tropical forests. However, radio transmitters may soon make it possible to get more data, so that students of raptors may be able to get quantitative observations

on kills per 100 birds on attempts inside or outside of flocks, as well as information on how hawks react to flocks.

Unfortunately for quantitative studies, bird-eating forest-falcons of the genus *Micrastur*, hawks of the genus *Accipiter*, and owls of the genus *Glauucidium* are typically birds of second growth and forest edges, not of the extensive tracts of forest that are best for interspecific flocks. Bird-eating hawks seem to do best at interfaces between habitats, or in irregular habitats; the Sparrow-hawks that pounce on birds by crossing a dense hedge (Tinbergen, 1946: 96–97) are an example. There are many species of hawks in tropical forests, and most terrify small birds or catch a few, but the majority of Neotropical raptors specialize on snakes and other animals that do not form interspecific or intraspecific flocks.

One possible specialist on birds of forest flocks is the Tiny Hawk, *Accipiter superciliosus*, a bird so small (20–28 cm long) that it apparently can approach interspecific flocks without being detected—at least, two of the four times I have seen it it darted through flocks unsuccessfully so fast that the birds scarcely had time to react. (Perhaps toucans and large insectivorous cotingas and trogons cannot join antwren alliances because the small birds flee from them?) Even the Tiny Hawk works the canopy and forest edge, not the forest interior. Barred Forest-Falcons also work ant-following flocks and antwren alliances to some extent, but do so by scattering the flock and then waiting for regrouping birds or (at ant swarms) feeding on insects. They stay in second-growth woodland.

The negative correlation between bird-eating hawks and antwren alliances could be considered one point in favor of the theory that birds join flocks to escape predation, but the correlation could be caused by concurrently varying factors: less light in the forest interior, for instance.

A second point is that some birds are less nervous in flocks than outside of flocks. Murton (1967) reports this for Wood Pigeons (*Columba palumbus*) in England. Lack (1968: 135) suggests, apparently from his own casual observations, that birds in flocks can feed more efficiently because they waste less time looking around nervously. The data for Spotted Antbirds point this way.

Moynihan (1962a: 120) reports that Plain-colored Tanagers are less shy towards man away from flocks than in flocks. His comment that “tame and unsuspecting” birds may be warned by other more alert or suspicious species almost states the hypothesis that intently foraging birds join alert species that call the alarm (see following paragraphs) but fails to suggest an evolutionary advantage for being unwary away from flocks. It seems that the level of shyness should be directly proportional to the danger, so that a species which is not shy away from flocks and is shy within them is either in more danger

when it joins flocks or is wasting foraging time looking for predators and being alarmed when the danger is to other species and not to it. Under either condition, I would expect the species to come to avoid flocks.

In some cases, it may be adaptive for birds to associate with others to increase their own vigilance. If a bird normally lives a predator-free life and only occasionally goes into predator-rich zones, it may then be best for it to join others so it can follow the old dictum "When in Rome, do as the Romans do." Presumably its level of vigilance will be adaptive for the old zone and not for the new or infrequent zones in such cases. The bird may also learn local predators in such cases. Moynihan (pers. comm.) has found that non-flocking birds isolated from their normal habitats often join flocks. The tendency of migratory birds to join flocks is probably due to learning advantages of this and other types. However, I doubt that the resident Plain-colored Tanagers were shyer in flocks than outside flocks for these reasons.

Moynihan's tanagers probably had little to fear from him. Treetop birds like these generally lack special "chirring" or rasping calls for ground predators, and small birds usually have little to fear from large, slow-moving animals like humans. Moreover, the tanagers around the Barro Colorado clearing where Moynihan worked have long lives (Cebbs, 1964) and have become especially habituated to the numerous scientists. Their greater nervousness in flocks is probably a maladaptive response to alarm notes or movements of other species that have less experience with man, not an adaptive response. In other words, if Moynihan had been a significant predator he could have pounced on tame tanagers away from flocks and eliminated them from the evolutionary picture, but it is doubtful that doing so would make tanagers tame and unsuspecting away from flocks.

Possibly Moynihan meant that Plain-colored Tanagers were "alarmed" rather than "shy," as the former usually implies displaying and calling at danger rather than fleeing from it. Alarm behavior is highest at intermediate levels of danger rather than directly proportional to danger; shyness or flight replaces alarm behavior at high levels, and other activities suggesting lack of concern at low levels. Birds inexperienced with man in antwren alliances certainly act as if man were a significant predator when he first appears, and call the alarm loudly. After the initial calls and displays, however, birds are generally less shy or alarmed than if they are alone. Solitary birds in flocks, like lone ones away from flocks, tend to ignore a human or call, then vanish. Nuclear species of flocks, ones that forage moderately intensively and form clans of their own species, tend to call loudly and then forage without showing alarm behavior. Pair-forming members of flocks tend to call loudly and become tame rather slowly, but do not desert flocks the way solitary members often do (Appendix 1).

A third point that tends to support the hypothesis that birds join flocks to escape predation is that Spotted Antbirds and many other species that follow alliances are birds that forage intently (i.e., examine nearby and enclosing surfaces carefully), while birds that form intraspecific or nuclear groups for alliances tend to be ones that forage by looking more extensively (i.e., checking foliage and air at moderate distances). Birds that look very extensively (i.e., checking for prey at considerable distances and looking about slowly) such as flycatchers, tend to be solitary and either ignore flocks or desert them readily (Appendix 1). Migrant warblers, which forage moderately extensively and join flocks, perhaps do so rather than form family groups because they scatter during migration. Also, as noted above, they can learn local predators or other local conditions from local birds. Perhaps rummagers and birds working in enclosed sites or looking at the ground or tree trunks would have to waste much foraging time watching for predators if they did not join species that can be alert for aerial predators at the same time as they forage.*

There may thus be a definite value in associating with other species rather than with other members of the same species, especially where there are many specialized species that forage intently but need to move rapidly. Six Checker-throated Antwrens, all sticking their heads in rolled-up leaves, would probably be less safe than two Checker-throated Antwrens associating with four White-flanked Antwrens flitting in the open foliage. The hypothesis suggests one possible reason why the White-flanked Antwren keeps its grown young with it while the Checker-throated Antwren does not, even though both are in the same genus. It also explains why the Spotted Antbird and other intent foragers generally drive grown young away while many medium-intent foragers keep their young with them: competing young are valuable if they can help look about for predators but not so valuable if they cannot. Fly-catching birds would gain little by keeping their young or even mates, both because they need to work large spaces and would compete with each other and because each individual can keep its own lookout rather well.

Leafscrapers and waterthrushes are intent foragers but are exceptions to the rule that such foragers tend to follow flocks. Leafscrapers probably forage too slowly to be able to follow flocks. Hence they are solitary and have developed very cryptic plumages and inconspicuous behavior patterns as an alternate way to avoid predation. Both they and waterthrushes flee if flushed, giving loud notes. Waterthrushes are sometimes limited to stream banks,

* William Dilger (letter) suggests that species like Hermit Thrushes, which forage in enclosing vegetation, tend to look about more rapidly than species like Eastern Bluebirds, which watch for prey and predators in the open. Perhaps the rapid looking about of many species of enclosed vegetation puts them in greater danger from predators than does slow and inconspicuous scanning of many birds that look very extensively.

but other reasons for their not following flocks are not evident. They are protectively colored.

Some birds, such as Red-throated Ant-tanagers, move too fast (Willis, 1960*b*) to be good alliance members; such birds tend to develop flocks of their own species. Such birds can scarcely be intent foragers unless predators are few. Probably the development of a foraging niche is limited by the development of behavior patterns and morphology such that the niche will not cause too high a death rate for the possible reproductive rate. Following an interspecific flock is one way of exploiting a niche that requires considerable activity without incurring excessive predation. Following is possible only within a certain range of speeds and environments where the nuclear or followed or "host" species have the right behavior patterns. If the various species adjust their speeds to each other, as has been noted for ducks and shorebirds (Nichols, 1931: 181) in flying groups, they may have to forage less efficiently or feed their young less well but can survive better.

Swynnerton (1915: 354) found that some birds associate with noisy, aggressive drongos. Similarly, R. H. Wiley (MS) suggests that on Barro Colorado an intent forager, the Checker-throated Antwren, has a call that is more effective in mobbing than those of the two medium-intent species of antwrens that forage with it. The conspicuous call, possible because the Checker-throated Antwren is protectively colored (a necessity for an intent forager on hanging dead leaves) and perhaps important in its own protection, may help and thus attract other species that do not have such calls. In this case, intent species gain by having less intent species keep the lookout while less intent species gain by having a bird about that is able to mob predators more effectively; this would be a symbiotic association.

The Spotted Antbird and many other intent foragers have similarly loud calls, which may warn other species of a flock or help them mob predators as well as being of value to the individual bird itself. However, the Spotted Antbird and Checker-throated Antwren and other species with such sharp calls seem to join flocks rather than lead them. Since the main advantage in flocking should be to the followers, the sharpness of the mobbing call is unlikely to be as important as the advantage to an intent forager of having nearby birds that can look for predators all the time while foraging. More data on who follows whom are needed to evaluate the relative contribution of the loud calls and of the protection of intent foragers to flock organization.

Conspicuous mobbing calls also characterize certain important members of Amazonian flocks, especially the Cinereous and Dusky-throated antshrikes. Birds may join them because they are both good at keeping the lookout (being "flycatchers") and at mobbing.

The mate-finding function of joining interspecific flocks is uncertain. Spotted Antbirds generally sing for mates, and do so whether they are with

other species or not. It may be that singing is somewhat inhibited when the bird is not with a flock, but comparative data are lacking; this would be another antipredation advantage. Much of courtship feeding occurs when birds are at swarms of ants rather than in flocks, but the fact that less time is used in fear behavior because of joining a flock could make more time available for foraging or courting. Possibly some birds find the mate more easily when leaving the nest if the mate is with a flock, but Spotted Antbirds seem to sing to each other rather than home on antwren alliances. Since only one bird out of five would be with an alliance rather than with ants or away from both, going to alliances would be somewhat inefficient. However, I found it useful to check all antwren alliances when doing a census search for particular individual Spotted Antbirds, so Spotted Antbirds may use the same technique at times.

The possible advantages of learning by joining antwren or other alliances have not been demonstrated. If predators are not specialists, learning which ones to avoid would certainly be possible in alliances at less cost to a species than in intraspecific flocks or clans. It is possible that Spotted Antbirds learn that certain parts of the forest are safe by staying with antwren alliances; but the safe places for the low-dwelling Spotted Antbird are unlikely to correspond to safe sites for the higher-dwelling majority of the flock. A bird may also learn what kinds of places are exploited by other species and avoid wasting time investigating such places; but for the Spotted Antbird there are more competitors that do not join antwren alliances than there are ones that do.

Spotted Antbirds live in a rather homogeneous habitat, hence probably do not need to join a flock to navigate to a food site or safe "home" or stay within it; in fact, joining an interspecific flock is more likely to lead a bird away from home. The possibility that Spotted Antbirds may assess interspecific competition and then adjust reproductive rates by joining antwren alliances is also remote, because they compete little with other members of alliances.

The peripheral and irregular attendance of Spotted Antbirds with antwren alliances probably results partly from their slow foraging and partly from their hesitation at moving into the more open sites that alliance members go through. Moreover, when food is available near treefalls or other sources of cover the Spotted Antbird can use these as substitutes for the protective flocks. Spotted Antbirds are probably mainly followers because they forage intently and inconspicuously. They gain little by forming clans, and thus are quiet much of the time they are in flocks (notes to the mate or young are infrequent); other species could not follow them easily even if there were a reason to follow.

Few large birds occur in antwren alliances; the largest moderately frequent

member is the Black-throated Trogon (20–25 cm long). Perhaps large size frightens other birds. Some large birds move too slowly (woodpeckers) or too rapidly (toucans), and many others are fruit eaters and hence limited by fruiting trees. Fruit-eating species sometimes form other types of alliances, some of which wander in somewhat the same way as do the antwren alliances (see Moynihan, 1962*a*: 2); at other times the alliances at fruiting trees may be competitive or internally antisocial aggregations like those over army ants but still have some predator-avoiding functions.

The antwren alliances and the ant-swarm flocks, both important to Spotted Antbirds, are at opposite extremes of the spectrum of tropical flocks. On Barro Colorado the “blue and green tanager and honeycreeper” flocks (Moynihan, 1962*a*: 2) are almost intermediate in characters—there is a moderate amount of interspecific competition and fighting and a moderate amount of social wandering and stopping to feed.

Moynihan classifies the birds in flocks he studied as “active” versus “passive” species, the former following and the latter being followed. However, by this terminology the relatively inactive Spotted Antbird is an “active” species and the constantly moving White-flanked Antwren a “passive” species. Since intent foragers will generally be “active” followers and flitting species often will be “passive” leaders, this is generally true. I suggest that the words “following” and “followed” or “attending” versus “attended” are self-explanatory and less confusing.

The terms “nuclear” and “circumference” species have had a confusing history since Winterbottom (1943: 439) proposed them for what I call the clan-forming and solitary to pair-forming birds. Although his terms suggest central versus peripheral location in flocks, he was trying to indicate that intraspecific groups form nuclei for attendant birds. Davis (1946: 169) divided the species of flocks in Brazil into “regular” or usually flocking and “accidental” or rarely flocking. Winterbottom (1949: 259) then buried the idea of intraspecific flocks as nuclei by combining his and Davis’s categories into a confusing system: nucleus, other regular, regular accidental, and accidental species.

Moynihan (1962*a*: 67), reviewing the confusion, decided to call “nucleus” species those that contribute to flock formation whether they are followers or leaders, while “attendant” species were those that “do much less to stimulate the formation and/or maintain the cohesion of mixed flocks.” Like Winterbottom, he suggested that intraspecific flocks evolutionarily are often suitable centers of interspecific flocks; but he suggested that many other species later become integral parts of flocks.

Moynihan also used the terms “regular” and “occasional” (he considered “accidental” misleading) for the percentages joining or associating with flocks: he specifically states that a rare species that regularly follows flocks may

statistically be less frequent in them than a common species that is occasional in flocks. McClure (1967: 146) attributed other meanings to Moynihan's terms, those of relative abundance in flocks: "species usually present were regular, less often seen ones occasional."

Confusion abounds, and some may feel it best to drop terms that arbitrarily split intergrading phenomena until we have more data on the phenomena themselves. Perhaps we should either drop the confusing terms "nucleus" and "attendant" and "regular" and "occasional" or replace them with descriptive, self-explanatory adjectives. "Nucleus" species and "attendant" species are deeply imbedded in the literature, to be sure. But, where these mean "clan-forming" and "followers," respectively, in Winterbottom's (1943: 439) terminology, they refer to dozens of characters in Moynihan's terminology. There they may refer to noisy versus quiet species, to drab versus bright species, to aggressive versus retiring species, etc. It seems more direct to use the appropriate adjectives or to decide on one meaning for "nuclear." For McClure's (1967: 146) definitions of "regular" versus "occasional," we can speak of "frequent" and "infrequent" species, if we must break a series into two parts; for Moynihan's definitions of "regular" versus "occasional," similarly, we can speak of "persistent" and "nonpersistent" species.

It is possible that clan-forming birds are less important as followed species in some flocks in some regions, especially in forests in the Amazon Basin. Most flock members there seem to be pair-forming birds rather than clan-forming birds, even the antwrens (Gray Antwren, Long-winged Antwren) that divide up the foraging niche of White-flanked Antwrens or occur with them over much of the region. Evolution should be toward greater specialization and toward greater intensity of foraging in species-rich faunas. "Jacks-of-all-trades" ordinarily become less common in such faunas, as parts of their niches are successively expropriated by competition from evolving specialists. The greater intensity of foraging and greater specialization in rich avifaunas should result in pair-forming birds replacing clan-forming ones. Not only is there too little food in a given area to allow young to be tolerated near their parents, but the young cannot help parents much in predator detection if young are foraging very intently. In rich faunas like those of the Amazon, species that form pairs may group directly and follow each other alternately, or follow noisy and conspicuous species, rather than follow clans as do birds in Panamá.

The family or clan as a unit of organization seems to be most frequent among birds of second growth or woodland, especially in areas of moderate species diversity; pair-forming species take over in tall forests, with higher diversity, as well as in open areas with low diversity. Red-crowned Ant-tanagers, mostly pair-forming birds of forests, and Red-throated Ant-tanagers, mostly clan-forming birds of second growth, illustrate the shift within a single genus (Willis, 1960a: 165). Selander (1964: 206) notes that clan

formation in cactus wrens is characteristic of mesic environments, as is clan formation in the genus *Thryothorus*. In wrens generally, forest and desert species are paired or solitary while species of intermediate habitats form clans. Factors favoring clans in successional intermediate types of habitats are perhaps high reproductive success (Snow and Snow, 1963: 40); moderately low species diversity, with the consequent necessity of flocking with one's own species if there is any value to flocking; irregular or uncertain food supplies that may be superabundant, if they occur at all, and hence can be exploited by all of a family; etc. The hypothesis that there is a decrease in clan-forming species as one enters either forest or "wasteland" from such intermediate habitats as canopy, forest edge, second growth, or savanna should be checked statistically, of course. Such trends are known for monkeys, ungulates, cats, and other animals; I do not know if they occur in humans, unless the city can be considered a forest for humans. Moderate irregularity of the environment with respect to predators and food supplies, rather than absolute levels of these factors, is probably the basic factor leading to the prevalence of clan formation over the formation of interspecific or occupational groupings. This is because clans are less common in deserts and other "wasteland" areas where conditions are extremely and uniformly harsh as well as in situations where physical conditions are extremely and uniformly favorable.

SUMMARY

The small, sexually dimorphic Spotted Antbird (*Hylophylax naevioides*, Formicariidae) joins other birds at swarms of army ants and in interspecific flocks in lowland forests between Honduras and Ecuador. A detailed ethological analysis, mainly accomplished by observation of color-banded birds on Barro Colorado Island in the Panamá Canal Zone, suggests how its behavior is related to its habitat, to competition for food, and to avoiding predators.

Preening and other maintenance activities take little time, but avoiding such small environmental hazards as sunlight, rain, and external parasites account for some behavior patterns, perhaps even mutual grooming in mated pairs.

Freezing as a reaction to potential predators and other large environmental hazards is rare; there is no specialized call ("keening") with the posture as there is in some related antbirds (Willis, 1967: 13). Perhaps Spotted Antbirds forage so actively that freezing would seldom be useful in avoiding predators. Far more common is hyperactive panicking and chipping, which may serve four functions: warning or teaching relatives, warning or startling predators, confusing predators, and scaring dominant competitors. Spotted Antbirds mob and chirr at passing humans or other mammals, as do related antbirds; the noise and display perhaps causes predatory mammals to move away because any prey would be alerted. Spotted Antbirds are relatively incurious and slow to become tame, perhaps because they are slow fliers and forage in moderately open undergrowth and would not be safe if they were tame or came to squeaking noises.

Perhaps submissive displays, "whimpering" calls and "cringing," are rare because birds usually flee rather than stay to face a dominant bird. Two aggressive displays are more common: "high-challenging" is a brief and introductory upright posture associated with a "bugling" call; long "snarling" calls go with "low-challenging," a similar but horizontal posture that displays the pale back-patch and breast conspicuously. Agonistic displays are strongest at the centers of territories and weakest at the boundaries; the theory that these displays arise from conflicts of attack and escape "drives" seems less universally applicable than the theory that aggressive display arises from interference with attack and submissive display from interference with flight in situations where the opponent is about the same size. (When the "opponent" is small, maintenance behavior is used; when the "opponent" is large, reactions to danger are used.)

Courtship behavior involves five main activities: mateless males sing loudly; mateless females wander to them; chirping and "flirting" occur when a bird of the opposite sex appears; courtship feeding by the male cements

the pair bond and precedes all copulations and nestings; mutual grooming occurs among mated birds and between parents and young. Agonistic behavior is not prominent in courtship; perhaps it is useful mainly for species of ephemeral and otherwise irregular habitats, where there are short pair bonds and many sibling species.

Young males settle on territories in their first year. Pairing occurs when the male is on territory. A female usually first nests in the breeding season after her hatching. Females, perhaps because they are subordinate to trespassing males, usually wander nomadically to new mates if the old ones disappear. Widowed males, which are still wholly dominant on their own territories, generally stay on them.

The nest cup is usually pendent from slender twigs on a small sapling, 0.3 to 1.4 m above the ground. Building, by both male and female, takes several mornings. Material is gathered near the nest. Two eggs are laid, two days apart. Incubation, performed by both sexes, required 15 days in two cases and 16 days in one; the two young at one nest hatched a few hours apart, but the two young at the last nest nearly a day apart. Male and female feed young, which stay in the nest almost 12 days. The complete nesting cycle takes 35 to 40 days.

Young can barely hop when they leave the nest. Parents lead the young to low perches in dense vegetation and perform striking distraction displays if one tries to capture the young. The male of a pair feeds one fledgling, the female feeds the other. As the young acquire adult plumage, complete by about six weeks after leaving the nest, the parents stop feeding them and finally drive them off. Parents renest soon after or before the previous brood becomes independent. Predators rob over 90 percent of nests, but pairs renest up to 10 times during each rainy season, April to November.

The help by the male at all stages of nesting is probably related to habitat, because animals of regular habitats are generally sexually egalitarian while animals of irregular habitats tend to have division of labor and sexual dimorphism and diethism.

Independent young show little alarm behavior and little agonistic behavior when they wander nomadically, perhaps because any noise would attract dominant adults. The change from the "age rule" of dominance to the "territorial rule," after the young bird gets a territory, marks the point where simple aggression stops and aggression braked by limits begins; territoriality is not simple aggression but a limit on aggression.

A Spotted Antbird follows swarms of army ants about half the time. It moves to the periphery of swarms or to a position high above the ants when larger antbirds attack it. When excluded from the large and regular nomadic raids of *Eciton burchelli*, it finds the irregular swarms of *Labidus praedator*, irregular statary raids of *Eciton burchelli*, or forages away from ants al-

together. Although a subordinate species, it has many foraging alternatives. At one pair per 4.7 hectares (12 acres), this generalized species is much commoner than the larger and dominant competitors that are more restricted to feeding with army ants.

A Spotted Antbird forages mainly by waiting near the ground and darting down to snap up small prey, of one beak length or less. It prefers perches of small diameter but often uses vertical perches unless it is preening. At swarms of ants it moves more actively and attempts to capture prey about four times as rapidly as it does away from swarms. If competitors are present, it indulges in warblerlike activity, wandering and snapping up prey.

Away from ants it sometimes joins the wandering interspecific flocks of antwrens and other birds ("antwren alliances") of the forest interior. It is somewhat more timid with respect to humans when away from the alliances, and flees either to such flocks or to dense cover when chased. Perhaps such intently foraging species as the Spotted Antbird join interspecific flocks because they would otherwise have to use more foraging time showing alarm or looking for predators. This hypothesis and observations suggest that birds that tend to forage actively in such a way that they cannot be alert are followers, unless they hide in dense cover or are very cryptic; that species that forage by looking about moderately alertly form intraspecific groups and are leaders; and that birds (like flycatchers) that look about very alertly to forage tend to be solitary and to desert flocks readily. For birds on Barro Colorado, there is little evidence for and several points against the alternative hypotheses that birds of a wandering alliance flush food for each other, lead each other to food, exclude each other from their own niches, locate mates, or practice population control by evaluating interspecific competition (Wynne-Edwards, 1962: 418). Species that join such flocks are ones that rarely dispute or take the same foods or niches, for instance.

Many of the behavioral and morphological characteristics of Spotted Antbirds can be correlated with the low degree of irregularity of their environment in regard to food and predation. A moderately high degree of aggression at army ant swarms is probably an adaptation to the variable niche of a subordinate species; the definite but poorly enforced territorial system is an aggression-limiting adaptation to a more predictable environment away from swarms. Aggression is perhaps most useful when food supplies or cover can be defended and are worth defending, which is most likely to be true in irregular environments. Sexual dimorphism and female flirting or submission are probably also adaptations to moderately irregular lives when Spotted Antbirds are excluded by dominant large birds at ant swarms; otherwise Spotted Antbirds are sexually egalitarian, as is usually true of animals of regular habitats. Much evidence for birds indicates that moderately irregular environments are an influence in the other direction: that is, toward strong

courtship displays, aggressiveness, strong male dominance, short pair bonds, polygamy or promiscuity, one sex only caring for offspring, and alert or cryptic solitary foraging. Intraspecific clan formation also occurs in moderately irregular environments, however. Similar trends have been noted in human societies of economically irregular environments—the slum societies studied by Oscar Lewis (1968) and the Bedouins studied by John Glubb (1963), for instance.

GAZETTEER OF LOCALITIES

Localities where I have observed Spotted Antbirds are listed here. Coordinates refer to approximate sites of observations, which may be several kilometers from the town or geographical feature used as a name. Coordinates are to the nearest minute of north latitude and west longitude, respectively. Coordinates are followed by elevations, in meters, estimated from available maps or from altimeter readings, and by the average yearly rainfall, in millimeters, estimated from the vegetation and from averages at nearby stations.

PANAMÁ

Cerro Campana.—8° 40', 80° 04'; 900 m; 2,700 mm. Mountaintop, partly forested and partly cleared, overlooking Punta Chame west of the Canal Zone. Antbirds seen 29 August 1961 and 25 to 28 June 1968.

Cerro Azul.—9° 15', 79° 20'; 700 m; 2,500 mm. Ridge, partly forested, northeast of Tocumen Airport and east of the Canal Zone; observations 23 June 1964, 31 May 1966.

PANAMÁ CANAL ZONE

Agua Salud.—9° 12', 79° 48'; 25–100 m; 3,000 mm. Creek into Gatun Lake north of Frijoles, in wet forest about 40 to 60 years old.

Barro Colorado.—9° 10', 79° 51'; 25–165 m; 2,730 mm. Forested island in Gatun Lake (see text).

Bohio Peninsula.—9° 12', 79° 51'; 25–100 m; 3,000 mm. Peninsula into Gatun Lake north of Barro Colorado, with secondary forest 40–60 years old.

Buenavista Point.—9° 11', 79° 50'; 25–50 m; 2,800 mm. Peninsula into Gatun Lake northeast of Barro Colorado; secondary forest 20 to 40 years old.

Escobal Road.—9° 14', 79° 58'; 110 m; 3,500 mm. Rolling hills, wet forest 40–60 years old, on side road by Rio Medio north of Gatun Lake.

Madden Reserve.—9° 06', 79° 37'; 50–200 m; 2,500 mm. Secondary forest 10 to 60 years old on rolling hills along continental divide.

COLOMBIA

Apartadó.—7° 56', 76° 40'; 100 m; 3,000 mm. Patches of wet lowland forest on flats northeast of town; visited 8 to 9 March 1965.

Chigorodó.—7° 45', 76° 40'; 130 m; 3,500 mm. Patches of wet forest on flats northeast of town and river; visited 10 March 1965.

Puerto Belgica.—7° 43', 75° 17'. 130 m; 2,500 mm. Isolated patches of tall forest in pastures northwest of town on Cauca River; visited 9–10 June 1962.

Remedios.—7° 02', 74° 41'; 770 m; 2,500 mm. Extensive forests north of town, on rolling hills; Spotted Antbird seen 5 May 1962.

Rio Verde.—A branch of the Rio Sinú, in partly cutover hill forests east of the Serranía de Abibe. Rainfall from 2,500 mm. at mouth of Verde (7° 50', 76° 17') at 150 m elevation to over 4,000 mm. on west slope of Filo de Abibe (7° 45', 76° 31') at

635 m. Except on the east slope of the Filo on 26 March, Spotted Antbirds seen every day on hike up and back, 20 to 28 March 1965.

San Pedro.—8° 27', 76° 18'; 150 m; 2,500 mm. Patches of dry forests on rolling hills west of Rio San Juan and north for five kilometers, 12 and 15 March 1965.

Tanandó.—5° 37', 76° 39'; 60 m; 9,000 mm. Very wet, nearly flooded low forests just west of Rio Atrato a few miles upstream from Quibdó; 23 February 1962.

Tucurá.—7° 56', 76° 10'; 150 m; 2,800 mm. Wet forests on rolling hills east of Rio Sinú, 16–17 June 1962; forests cut down by 1965.

Yuto.—5° 30', 76° 32'; 100 m; 9,000 mm. Very wet hill forest by road south to Rio San Juan, a few kilometers from the Rio Atrato; 24 February 1962.

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APPENDIX 1

CHARACTERISTICS OF MEMBERS OF FOREST FLOCKS ON BARRO COLORADO ISLAND

Species	Characteristic															
	a	b	c	d	e	f	g	h	i	j	k	l	m	n	o	
Antwren, White-flanked	1	1	1	1	1	1	1	1	c	c	c	a	a	1	1	
Greenlet, Gray-headed	1	1	1	1	1	1	1	1	c	c	c	g	g	5	g1	
Tanager, Sulphur-rumped	1	1	1	1	-	-	-	2	u	u	c	g	g	5	g8	
Tanager, White-shouldered	1	1	1	-	-	-	2	u	u	u	g	g	g	5	g6	
Antwren, Dot-winged	1	1	1	1	1	1	1+	2	u	u	a	a	a	1	9	
Gnatcatcher, Tropical	1+	1	2	2	-	-	2	1	u	u	r	g	g	5	g4	
Euphonia, Fulvous-vented	1+	1	2	2	-	-	2	2	u	c	c	g	g	5	g7	
Antvireo, Dot-crowned	1+	1	2	2	2	2	2	1	u	u	c-	a+	a	1	11	
Antshrike, Slaty	2-	1+	2	2	2	1+	2-	2	c	c	c	a+	a	1	3	
Gnatwren, Long-billed	2-	1	2	2	2	2-	2	1	r	r	r	a	a	5	19	

APPENDIX 1 (continued)

Species	Characteristic															
	a	b	c	d	e	f	g	h	i	j	k	l	m	n	o	
Antwren, Checker-throated	2	2	2	2	2	2	2	1	c	c	c	a	a	1	2	
Antbird, Spotted	2	2	2	2	2	2	2	2	u	u	c	a-	a	1	8	
Antbird, Chestnut-backed	2	2-	2	2	2	2	2	2	r	u	u	a-	a	1	18	
Flycatcher, Dusky-capped	2+	1-	2	2	-	-	2	2	u	c	c	g	g	4	g3	
Flycatcher, Yellow-margined	2+	1	2-	2	-	-	2	2	c	c	c	g	g	4	g2	
Xenops, Plain	2	2	2	2	2	2	2	1	u	u	r	a	a	2	10	
Woodcreeper, Wedge-billed	2	2	2	2	2	2	2	1	c	c	c	a	a	2	4	
Woodcreeper, Buff-throated	2	2	2	2	2	2	2	1	c	u	r	a	a	2	7	
Woodcreeper, Black-striped	2	2	2	2	2	2	2	2	u	c	c	g	g	2	g5	
Puffbird, White-whiskered	3-	2+	2	3	3	3-	2	2	u	u	c+	a	a	-	12	
Flycatcher, Ruddy-tailed	3-	1-	3	3	3	3-	2	1	c	c	c	a+	a	4	5	
Flycatcher, Bentbill	3-	3+	3	3	3	3-	2	2	u	u	u	a	a	4	13	
Flycatcher, Ochre-bellied	3-	3+	3	3	3	3-	2	2	u	u	r	a	a	4	16	
Spadebill, Golden-crowned	3-	3+	3	3	3	3-	2	2	u	u	c	a	a	4	17	
Flatbill, Olivaceous	3	3	3	3	3-	3-	2	1	u	u	u	a	a	4	14	
Manakin, Red-capped	3	3	3	3	3	3	2	2	c	c	c	a	a	3	6	
Manakin, Golden-collared	3	3	3	3	3-	3-	2	2	r	r	r	a	a	3	20	
Woodcreeper, Plain-brown	3	3	3	3	3	3	2	2	u	r	c	a+	a	2	15	
Redstart, American	1-	1-	3	3	3	3	2	1	u	u	c+	g	g	5	m9	
Warbler, Canada	1-	1-	3	3	3	3	2	1	c	c	c	a	a	5	m1	
Warbler, Chestnut-sided	1-	1	3	3	3	3	2	1	c	c	c	a	a	5	m3	
Warbler, Bay-breasted	1+	1	3	3	3	3	2	1	c	c	c	a+	a	5	m2	
Vireo, Red-eyed	2-	1	3	3	3	-	2	1	u	u	r	g	g	5	m8	
Warbler, Kentucky	2-	1+	3	3	2	3	2	2	u	u	c	a	a	5	m7	
Warbler, Black-and-white	2	2	3	3	3	3	2	1	u	u	c	g-	a	5	m6	
Flycatcher, Great Crested	2+	1-	3	3	3	-	2	2	u	u	c	g	g	4	m5	
Flycatcher, Acadian	2+	1-	3	3	3	3	2	2	u	c	c	a	a	4	m4	

a—Foraging method: 1, moderately intent; 2, very intent; 3, looks widely.

b—Food source: 1, green foliage; 2, dead material; 3, both and air.

c—Family structure: 1, clans formed; 2, pairs; 3, solitary.

d—Chirping notes: 1, frequent; 2, occasional; 3, rare.

e—Initial alarm: 1, noisy; 2, sometimes noisy; 3, quiet.

f—Subsequent tameness: 1, rapidly tame; 2, slowly tame; 3, tends to flee.

g—Leader?: 1, leads or is followed; 2, follows.

h—Persistence: 1, high per cent with flocks; 2, moderate or low.

i—Frequency in flocks: c, common; u, uncommon; r, rare.

j—General abundance on Barro Colorado: c, common; u, uncommon; r, rare.

k—Forest type used: c, forest; u, vines and tangles; r, second growth.

l—Foraging height: a, low; g, high.

m—Flock type joined: a, antwren; g, greenlet.

n—Taxon: 1, antbirds; 2, furnariids; 3, manakins; 4, flycatchers; 5, songbirds.

o—Rank in Barro Colorado alliances: 1-20, antwren alliances; g1-g8, greenlet alliances; m1 to m9, migrants.

+ or - means tending higher or lower; in many cases 1 is higher than 3 and 3 is lower than 1, in a closed triangular series.

APPENDIX 2¹

- Accipiter* spp.—see Hawks
- Antbird, Bicolored (*Gymnopithys bicolor*)—4ff.
- Dot-backed (*Hylophylax punctulata*)—2
- Chestnut-backed (*Myrmeciza exsul*)—20, 50, 51, 110, 111, 112, 116, 130, 133, 134, a1
- Lunulated (*Gymnopithys lunulata*)—28
- Ocellated (*Phaenostictus mcleannani*)—18, 20, 27, 28, 42, 76, 78, 106, 110, 111, 112, 115, 116, 119, 120, 122
- Rufous-throated (*Gymnopithys rufigula*)—33
- Scale-backed (*Hylophylax poecilonota*)—97, 98
- Spot-backed (*Hylophylax naevia*)—2, 93, 95
- White-bellied (*Myrmeciza longipes*)—116
- Antbirds (Formicariidae)—74, 132
- Antpitta, Streak-chested (*Grallaria perspicillata*)—116
- Antshrike, Cinereous (*Thamnomanes caesius*)—143
- Dusky-throated (*Thamnomanes ardesiacus*)—143
- Slaty (*Thamnophilus punctatus atrinuchus*)—20, 48, 52, 54, 69, 76, 77, 78, 110, 112, 122, 127, 128, 129, 134, a1
- Ant-Tanager, Red-crowned (*Habia rubica*)—76, 77, 78, 127, 128, 145
- Red-throated (*Habia fuscicauda*)—64, 76, 77, 78, 100, 101, 127, 128, 143, 146
- Antthrush, Black-faced (*Formicarius analis*)—116
- Antvireo, Dot-crowned (*Dysithamnus puncticeps*)—129, 132, a1
- Antwren, Brown-bellied (*Myrmotherula gutturalis*)—129
- Checker-throated (*Myrmotherula fulviventris*)—110, 113, 128, 129, 134, 142, 143, a1
- Dot-winged (*Microrhopias quixensis*)—6, 7, 127, 130, 132, 134, 136, a1
- Fulvous-bellied (see Checker-throated)
- Gray (*Myrmotherula menetriesii*)—146
- Long-winged (*Myrmotherula longipennis*)—146
- Rufous-tailed (*Myrmotherula erythrura*)—129
- Stipple-throated (*Myrmotherula haematonota*)—129
- White-eyed (*Myrmotherula leucophthalma*)—129
- White-flanked (*Myrmotherula axillaris*)—78, 110, 126, 127, 128, 129, 133, 136, 142, 145, 146, a1
- Apodidae—see Swifts
- Automolus ochrolaemus*—see Foliage-gleaner, Buff-throated
- Baryphthengus ruficapillus*—see Motmot, Great Rufous
- Becards (*Pachyramphus* spp., *Platypsaris* spp.)—132
- Blackbirds (Icteridae)—135
- Bluebird, Eastern (*Sialia sialis*)—142
- Bucconidae—see Puffbirds
- Bushtit (*Psaltriparus minimus*)—138
- Buteogallus anthracinus*—see Hawk, Common Black
- Capella gallinago*—see Snipe, Common
- Chickadees (*Parus* spp.)—135
- Contopus* spp.—see Pewees, Wood
- Cotingas (Cotingidae)—132, 140
- Cuckoo, Squirrel (*Piaya cayana*)—110, 111, 113
- Cyphorhinus phaeocephalus*—see Wren, Song

¹ symbol: a = appendix number.

- Dendrocincla fuliginosa*—see Woodcreeper, Plain-brown
Dendrocolaptes certhia—see Woodcreeper, Barred
 Dendrocolaptidae—see Woodcreepers
Dendroica spp.—see Warblers
Dysithamnus puncticeps—see Antvireo, Dot-crowned
Empidonax virescens—see Flycatcher, Acadian
Eucometis penicillata—see Tanager, Gray-headed
 Euphonia, Fulvous-vented (*Euphonia fulviventris*)—130, a1
 Flatbill, Olivaceous (*Rhynchocyclus olivaceus*)—132, a1
 Flycatcher, Acadian (*Empidonax virescens*)—110, 133, a1
 Bentbill (*Oncostoma cinereigulare*)—131, 135, 136, a1
 Black-tailed (*Myiobius atricaudus*)—131, 138
 Dusky-capped (*Myiarchus tuberculifer*)—132, 133, 138, a1
 Great Crested (*Myiarchus crinitus*)—133, a1
 Ochre-bellied (*Pipromorpha oleaginea*)—131, a1
 Olivaceous (see Dusky-capped)
 Ruddy-tailed (*Terentropicus erythrurus*)—9, 110, 113, 131, a1
 Sulphur-rumped (*Myiobius sulphureipygeus*)—131, 138
 Yellow-margined (*Tolmomyias assimilis*)—132, a1
 Flycatchers—see Tyrant Flycatchers
 Foliage-gleaner, Buff-throated (*Automolus ochrolaemus*)—130
 Forest-falcon, Barred (*Micrastur ruficollis*)—140
 Forest-falcons (*Micrastur* spp.)—28, 140
 Formicariidae—see Antbirds
Formicarius analis—see Antthrush, Black-faced
 Furnariidae—see Ovenbirds
Glaucidium spp.—see Owls, Pygmy
Glyphorhynchus spirurus—see Woodcreeper, Wedge-billed
 Gnatcatcher, Tropical (*Polioptila plumbea*)—130, a1
 Gnatwren, Long-billed (*Ramphocaenus melanurus*)—130, a1
 Goldfinches (*Spinus* spp.)—79
Grallaria perspicillata—see Antpitta, Streak-chested
 Greenlet, Gray-headed (*Hylophilus decurtatus*)—126, 127, a1
 Greenlets (*Hylophilus* spp.)—126, 127
Gymnopithys spp.—see Antbirds
Habia spp.—see Ant-Tanagers
Harpagus bidentatus—see Kite, Double-toothed
 Hawk, Common Black (*Buteogallus anthracinus*)—20
 Semiplumbeous (*Leucopternis semiplumbea*)—75, 84
 Tiny (*Accipiter superciliosus*)—140
 White (*Leucopternis albicollis*)—84
 Hawks (Accipitridae, Falconidae)—140
Helmitheros vermivorus—see Warbler, Worm-eating
Heterospingus rubrifrons—see Tanager, Sulphur-rumped
 Hummingbird, Hermit (*Phaethornis* spp.)—28, 78
 Hummingbirds (Trochilidae)—74
Hylocichla spp.—see Thrushes and Veery
Hylophilus spp.—see Greenlets
Hylophylax spp.—see Antbirds
 Icterids (Icteridae)—74, 135

- Kite, Double-toothed (*Harpagus bidentatus*)—20
 Leafscraper, Scaly-throated (*Sclerurus guatemalensis*)—110, 113, 126, 138
 Leafscrapers (*Sclerurus* spp.)—142
Leucopternis albicollis—see Hawk, White
Malacoptila panamensis—see Puffbird, White-whiskered
Manacus vitellinus—see Manakin, Golden-collared
 Manakin, Blue-crowned (*Pipra coronata*)—131
 Golden-collared (*Manacus vitellinus*)—131, a1
 Red-capped (*Pipra mentalis*)—110, 131, a1
 Manakins (Pipridae)—74, 131, 132, 139
Micrastur spp.—see Forest-falcons
Microrhophias quixensis—see Antwren, Dot-winged
Mniotilta varia—see Warbler, Black-and-white
 Motmot, Great Rufous (*Baryphthengus ruficapillus*)—20, 110, 113
 Motmots (Momotidae)—118
Myiarchus spp.—see Flycatchers
Myiobius spp.—see Flycatchers
Myrmeciza spp.—see Antbirds
Myrmotherula spp.—see Antwrens
Oncostoma cinereigulare—see Flycatcher, Bentbill
Oporornis formosus—see Warbler, Kentucky
 Ovenbirds (Furnariidae)—74, 130, 132
 Owls, Pygmy (*Glaucidium* spp.)—140
Pachyramphus spp.—see Becards
 Paridae—see Titmice
 Parrots (Psittacidae)—74, 126, 132
 Parulidae—see Warblers (Parulidae)
 Pewees, Wood (*Contopus* spp.)—133
Phaenostictus mcleannani—see Antbird, Ocellated
Phaethornis spp.—see Hummingbirds, Hermit
Piaya cayana—see Cuckoo, Squirrel
 Picidae—see Woodpeckers
Pipra spp.—see Manakins
 Pipridae—see Manakins
Pipromorpha oleaginea—see Flycatcher, Ochre-bellied
Platypsaris spp.—see Becards
Platyrinchus coronatus—see Spadebill, Golden-crowned
Poliophtila plumbea—see Gnatcatcher, Tropical
Psaltriparus minimus—see Bushtit
 Psittacidae—see Parrots
 Puffbird, White-whiskered (*Malacoptila panamensis*)—20, 110, 111, 113, a1
 Puffbirds (Bucconidae)—74, 118
 Ramphastidae—see Toucans
Ramphastos sulfuratus—see Toucan, Keel-billed
Ramphocaenus melanurus—see Gnatwren, Long-billed
 Redstart, American (*Setophaga ruticilla*)—a1
Rhynchocyclus olivaceus—see Flatbill, Olivaceous
Sclerurus guatemalensis—see Leafscraper, Scaly-throated
Seiurus spp.—see Waterthrushes
Setophaga ruticilla—see Redstart, American

- Sialia sialis*—see Bluebird, Eastern
 Snipe, Common (*Capella gallinago*)—26
 Spadebill, Golden-crowned (*Platyrinchus coronatus*)—132, a1
Spinus spp.—see Goldfinches
 Swifts (Apodidae)—126
Tachyphonus spp.—see Tanagers
 Tanager, Gray-headed (*Eucometis penicillata*)—9, 20, 110, 111, 112
 Plain-colored (*Tangara inornata*)—140, 141
 Sulphur-rumped (*Heterospingus rubrifrons*)—128, a1
 Tawny-crowned (*Tachyphonus delattrei*)—128
 White-shouldered (*Tachyphonus luctuosus*)—127, a1
 Tanagers (Thraupidae)—74, 126
Tangara inornata—see Tanager, Plain-colored
Terentotriccus erythrurus—see Flycatcher, Ruddy-tailed
Thamnomanes spp.—see Antshrikes
Thamnophilus punctatus atrinuchus—see Antshrike, Slaty
 Thraupidae—see Tanagers
 Thrush, Gray-cheeked (*Hylocichla minima*)—110, 111
 Hermit (*Hylocichla guttata*)—142
 Swainson's (*Hylocichla ustulata*)—110, 111
 Wood (*Hylocichla mustelina*)—133
 Thrushes (*Hylocichla* spp.)—83, 110, 111, 113, 121, 122
 Titmice (Paridae)—135
Tolmomyias assimilis—see Flycatcher, Yellow-margined
 Toucan, Keel-billed (*Ramphastos sulfuratus*)—57
 Toucans (Ramphastidae)—126, 132, 140, 145
 Trochilidae—see Hummingbirds
 Troglodytidae—see Wrens
 Trogon, Black-throated (*Trogon rufus*)—20, 132, 145
 Trogons (Trogonidae)—74, 132, 140
 Tyrant Flycatcher (Tyrannidae)—74, 132, 133, 138
 Veery (*Hylocichla fuscescens*)—110
 Vireo, Red-eyed (*Vireo olivaceus*)—a1
 Warbler, Bay-breasted (*Dendroica castanea*)—133, a1
 Black-and-white (*Mniotilta varia*)—133, a1
 Canada (*Wilsonia canadensis*)—110, 111, 113, 133, 134, 138, a1
 Chestnut-sided (*Dendroica pensylvanica*)—133, a1
 Kentucky (*Oporornis formosus*)—110, 133, 134, 135, a1
 Worm-eating (*Helmitheros vermivorus*)—129
 Warblers (Parulidae)—133, 135, 142
 Waterthrushes (*Seiurus* spp.)—133, 142
Wilsonia canadensis—see Warbler, Canada
 Woodcreeper, Barred (*Dendrocolaptes certhia*)—102, 110, 112
 Black-striped (*Xiphorhynchus lachrymosus*)—50, 130, a1
 Buff-throated (*Xiphorhynchus guttatus*)—110, 122, 130, a1
 Plain-brown (*Dendrocincla fuliginosa*)—18, 20, 27, 50, 110, 111, 112, 121, 122,
 131, a1
 Wedge-billed (*Glyphorhynchus spirurus*)—128, 129, a1
 Woodcreepers (Dendrocolaptidae)—133
 Woodpeckers (Picidae)—74, 132, 145

- Wren, Song (*Cyphorhinus phaeocephalus*)—128
Wrens (Troglodytidae)—147
Xenops, Plain (*Xenops minutus*)—129, a1
Xiphorhynchus spp.—see Woodcreepers

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