

STUDIES OF THE BEHAVIOR OF LUNULATED AND SALVIN'S ANTBIRDS

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From the high green wall of the Andes to the great yellow Río Madeira, in the 2000 kilometers of Amazonian forest from Ecuador and Perú one third of the way across Brazil and Bolivia, live two little-known antbirds of the genus *Gymnopithys*. Plump, short-tailed birds slightly smaller than House Sparrows (*Passer domesticus*), Salvin's Antbirds (*Gymnopithys salvini*) have been known from over 150 skins in museums and Lunulated Antbirds (*Gymnopithys lunulata*) from seven or so specimens. The collectors, mostly nonbiologists, recorded nothing of their habits.

The other three species of the genus *Gymnopithys* follow swarms of army ants and snap up arthropods flushed by the ants (Willis 1967). In late 1965 and early 1966 I visited eastern Ecuador and Perú and western Brazil to study birds that follow the ants. I found that both Salvin's and Lunulated Antbirds are "professional" ant-followers, dependent on army ants to flush their food. In behavior, they proved to be remarkably similar to other species of the genus. However, certain peculiarities of their social organization throw new light on the general question of the roles of aggression and submission in behavior.

THE ANTBIRDS

Male Salvin's Antbirds are a soft "gray-flannel" bluish-gray, with black eyelines between white superciliaries and throats, and have white-barred blackish tails. Females are ochraceous or reddish-brown, rather like some females in the distantly related antbird genus *Cercomacra*. The female Salvin's Antbird also has a black-barred russet tail, upperparts vaguely ocellated with russets and browns and blacks, and an indistinct dusky crown-patch.

The male Lunulated Antbird (fig. 1) is like a male Salvin's Antbird, but lacks the white bars on the tail. Females are quite different from female *salvini*, being soft or pastel browns with white throats and superciliary lines as in the males. The upperparts and inner webs of the tail feathers are marked with crescentic grayish-white lunulations.

The similarity of males and the nearly complete allopatry of the two forms (fig. 2) sug-

gest that they may be conspecific. Indeed, the Río Ucayali is the most likely dividing line between their ranges, so that at Sarayacu and Lagarto on the Ucayali specimens of *lunulata* may have come from west of the river and specimens of *salvini* from east of it. However, the Ucayali is a meandering river, forming oxbows and cutoff channels; the occasional transfer of large sections of land from one side to the other should surely allow these birds to meet and hybridize if they can do so. Behavioral characteristics suggest that they are separate species. However, their ecologies are so similar that I doubt they can coexist over more than a very narrow zone where their ranges meet. Perhaps they meet in the fashion of Eastern and Western Meadowlarks (*Sturnella magna* and *S. neglecta*), with interspecific territoriality and little or no hybridization (Lanyon 1957), but more study is needed along the Ucayali.

Now that the male of *lunulata* is known, we can discount certain suggestions advanced (Zimmer 1937) when only three females were known. The species is not the female of or a hybrid with the White-cheeked Antbird (*Gymnopithys leucaspis*), which dominates it at swarms of ants in eastern Ecuador. The White-cheeked Antbird and its relatives, the Bicolored Antbird (*G. bicolor*) northwest of the Andes and the Rufous-throated Antbird (*G. rufigula*) northeast of the Río Negro, form a superspecies or subgenus quite distinct from the *lunulata-salvini* subgenus. The Lunulated Antbird is not a hybrid or form of the Scale-backed Antbird (*Hylophylax poecilonota*), even though the females of both show similar lunulated patterns. Zimmer suggested that the resemblance might prove to be significant, but it is significant ecologically rather than taxonomically. Lunulated and Scale-backed Antbirds are very similar in their ways of foraging whenever dominant competitors are present; perhaps the similar female patterns are related to interspecific competition or predation.

Both Zimmer and Hellmayr (1924) mention that Lunulated and Salvin's Antbirds have pale bases to the dorsal feathers, forming con-

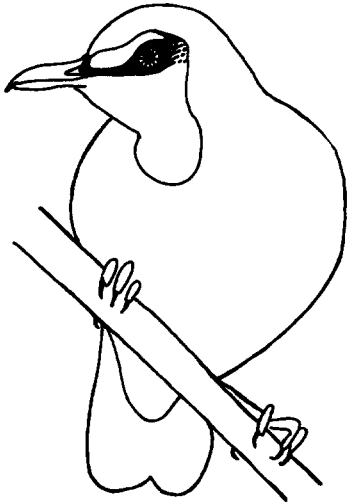


FIGURE 1. Male Lunulated Antbird, "investigating" the observer, to show the head shape and pattern.

cealed dorsal patches like those in *Gymnophrys rufigula* and many other antbirds. However, the specimens I have examined (5 *lunulata*, 137 *salvini*) show at most slight pale edges to the bases of a few dorsal feathers. In life, these birds do not show light patches by spreading the dorsal feathers at

the opponent as do antbirds with significant dorsal patches.

THE ARMY ANTS

From México to Argentina the two important species of army ants for birds are *Eciton burchelli* and *Labidus praedator*. These ants form wide swarms, flowing by the thousand over the leaf litter and tangles near or above the ground, and flush hundreds of arthropods each hour. There are many species of birds that depend on prey flushed by the ants, and dozens of other "semi-professional" and "amateur" species of birds regularly or occasionally follow the ants. No bird, so far as is known, regularly eats the ants themselves.

Eciton burchelli is a brown-and-yellow ant, a centimeter or so long, that swarms predictably and is very important for birds. *Labidus praedator*, a small black ant, flushes smaller prey and swarms unpredictably, so that it is less important for inveterate ant-followers (Willis 1966a). In Amazonia a big black-and-yellow army ant (*Eciton rapax*) also forms straggling swarms that occasionally attract birds.

Rettenmeyer (1963) and Willis (1967) give other information on the ants. For general sur-

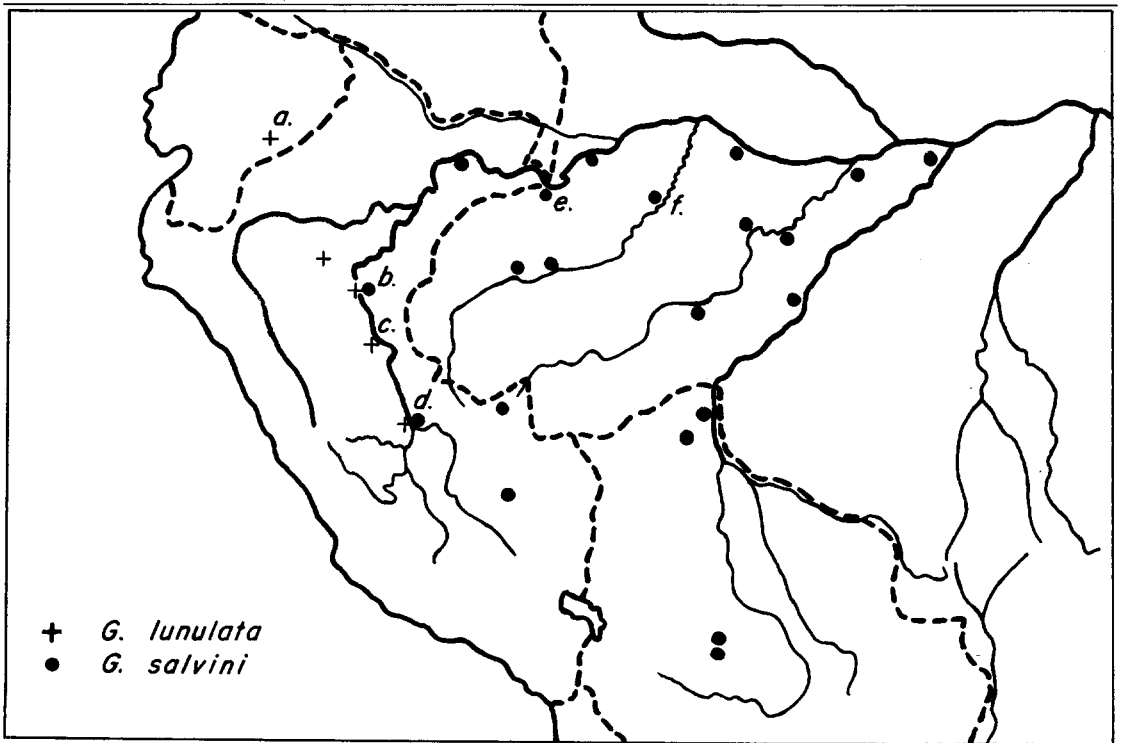


FIGURE 2. Localities where Lunulated and Salvin's Antbirds have been recorded. Both are known from Sarayacu (b) and Lagarto (d) in eastern Perú. I observed Lunulated Antbirds at Putuimi (a) in Ecuador and Yarinacocha (c) in Perú, Salvin's Antbirds at Benjamin Constant (d) and Carauari (e) in Brazil.

veys of the ant-following habit among birds, Chapin (1932) and Johnson (1954) are useful references.

STUDY AREAS AND HABITATS

I found Salvin's Antbirds in the forests at Carauarí (4° 52' S, 66° 54' W) and at Benjamín Constant (4° 22' S, 70° 02' W). At Carauarí I studied seven, five, seven, and seven *salvini* at four successive swarms of one colony of *Eciton burchelli*, 18 to 21 March, for a total of 29.3 hours; families of three birds each were observed briefly near folded swarms, i.e., swarms that have stopped hunting activities and are retreating, of *Labidus praedator* on 14 and 16 March. Two birds, seen in the evenings, were wandering away from ants. At Benjamín Constant I found three, two, six, and four *salvini* at four raids of *Eciton burchelli* on 16 to 18 April, and watched them for 9.7 hours.

Much of the region where Salvin's Antbirds live (fig. 2) was once the southern part of a great Amazonian Sea, so that the land is flat and the soil deep. At Carauarí there are swampy areas here and there, as befits an area laced with the oxbow lakes and meanders of the nearby serpentine Río Juruá. At Benjamín Constant the deep and fast Solimões drains the forests well, even though rainfall is 2742 mm per year. Epiphytes and moss are frequent and the undergrowth rather lush, as is usually the case in wet forests in areas without strong dry seasons. The forests at Carauarí seem somewhat less lush, despite the swampy areas and a rainfall of 2534 mm annually. To the south, *salvini* lives in forests with lower rainfall and in areas with a strong southern-hemisphere dry season (at or after the midyear). Presumably it there occupies the relatively open lower levels of the epiphyteless forests usual in a lowland tropical area with a strong dry season.

I found Lunulated Antbirds in forests at Putuimi (2° 39' S, 77° 28' W), on the meandering but incised Río Cangaima in eastern Ecuador, and on the Yarinacocha-Cashibococha Trail (8° 15' S, 74° 45' W), between two large oxbow lakes near the Ucayali River in central Perú. At Putuimi I watched one to three *lunulata* (one male and two females) at seven swarms of one colony of *Eciton burchelli* for a total of 25.1 hours and a pair at a swarm of *Eciton rapax* for one hour, between 26 November and 3 December 1965. At Yarinacocha I watched one to 10 (mean, 5.2) Lunulated Antbirds at 21 swarms of *Eciton burchelli* for 66.4 hours and one to three at two swarms of *Labidus praedator* for 1.2 hours, between 22 December 1965 and 3 January 1966. Four birds were wandering away from swarms of ants.

The antbirds at Putuimi were in the irregular and somewhat vine-tangled high-to-secondary forest near

the river and airstrip. The Jívaro Indians have many clearings for manioc and other crops nearby; most of the forests of eastern Ecuador seem to be in various stages of secondary succession. However, some patches of forest at Putuimi had giant trees and seemed relatively mature. Epiphytes and lush ground vegetation were common, suggesting an annual rainfall of over three meters. Here near the climatic equator the dry seasons are not pronounced. At Yarinacocha the forest looks like second growth 40 to 100 years old, with vine tangles and a low canopy. The Cashibo Indians and other Peruvians have clearings here and there. Streams are sluggish, but swamps occur mainly along the nearby lake of Cashibococha. The southern-hemisphere dry season must be fairly severe at midyear; there are few epiphytes and mosses, and few lush plants in the rather cluttered undergrowth.

I was unable to find Lunulated Antbirds at nearby locations in the rolling foothills of the Andes of eastern Ecuador (Yaapi, 2° 51' S, 77° 56' W) or Perú (San Alejandro, 8° 50' S, 75° 14' W). Possibly *lunulata* is restricted to swampy lowland forests in flat regions once covered by the western arms of the great Amazonian Sea. At present, the smaller silt-laden rivers emerging from the Andes dump most of their burden in this lowland region, which forms a great crescent from Colombia into Bolivia. Obstructed by the silt, the yellow rivers meander snakelike across the plains. Lunulated Antbirds have been found only in the central half of this lowland crescent, perhaps because they are replaced by the dominant *Gymnopathys leucaspis* from Ecuador north and by *Gymnopathys salvini* from the Ucayali south and east.

VOICE

Salvin's and Lunulated Antbirds are so like Bicolored Antbirds (Willis 1967) in their calls that I shall use the same terminology for all three. Birds of such related genera as *Rhegmatorhina* have similar calls, for these antbirds have diverged more in morphology than they have in voice. Compared with the species of *Rhegmatorhina* and with *Gymnopathys bicolor* and its relatives, *salvini* and *lunulata* have soft or faint calls.

Chirring. Lunulated and Salvin's Antbirds utter a faint buzz or *chirrrr* when disturbed by the observer or other animals. The Chir of *salvini* was fainter and less deep than that of the Hair-crested Antbirds (*Rhegmatorhina melanosticta*) foraging with it at Carauarí and Benjamín Constant, but I often could not tell which species was Chirring. At Putuimi, the Chir of *lunulata* was fainter and less deep than that of *Gymnopathys leucaspis*, but was otherwise rather similar.

Chipping. Alarmed or excited Lunulated and Salvin's Antbirds utter a soft but sharp

chip! The Chipping is sometimes doubled or tripled to *chip-ip!* or *chip-ip-ip!*, and once reached 13 notes in a row for a Lunulated Antbird fleeing a hawk. However, these birds normally single-chip rather than double-chip as do *Gymnopithys leucaspis* and its close relatives.

Keening. Both *lunulata* and *salvini* utter a short, thin *teeeeer!* whistle when Freezing in alarm. The note, occasionally doubled or tripled, is shorter than Keening in other species of *Gymnopithys*.

Singing. In Song, Lunulated and Salvin's Antbirds differ as much as do sympatric species in this and related genera. However, the songs of both species resemble those of related species, even ones that occur sympatrically with them. It is convenient to divide the wide spectrum of songs into Loud-songs, Why-songs, Faint-songs, and Serpentine-songs, as I did for *Gymnopithys bicolor*.

The Loud-song of *lunulata* is a rapid *TWEE'E-E-E-EE—EE, WHEEF, WHEEF, WHEEF!* or similar series of short whistles, descending in pitch and slowing from the rapid start into a series of harsher, terminal flourishes. The Loud-song of *salvini* is a *WHIEEHHHH, WHIEEH, WHIEEHH, WHIEEHHT!* or similar series of one to 10 sibilant whistles at two per second, descending in pitch and becoming longer and harsher after a long first note. Loud-songs are most commonly used when mates are separated from each other, when birds search for a swarm of ants, and when birds have been expelled from a swarm by dominant competitors. When birds quarrel with each other, the terminal notes of a Loud-song are one to 10 or so harsh *WHYYYYYYH!* noises or "Snarls," forming Why-songs. In *salvini* the Snarls descend in pitch and are very long and sibilant. In *lunulata* the Snarls are shorter and do not descend noticeably. To Loud-sing, the bird opens its beak and extends the head upward, but the shaking of the body with each note is often the only other sign that the bird is singing.

Faint-songs, faint and brief versions of the Loud-songs, are chirping little series most frequently used when several competing birds are occupying their own corners of a swarm of ants. *Whe-e-e, wheep!* is a common version for *lunulata*. The singer has its bill closed or nearly so and looks around casually, so that the shaking of the body with the notes is often the only sign a bird is Faint-singing. One male Lunulated Antbird lowered his tail 10 degrees for each Faint-song. *Whieh, whihhh!*

or similar, sibilant descending series are Faint-songs for *salvini*. Louder and longer series, often with snarling terminal notes if birds are feuding, bridge the gaps between the loudest Loud-songs and Why-songs and the shortest Faint-songs in both *lunulata* and *salvini*.

Serpentine-songs, faint ditties when a bird leads its nearby young or mate, are variable series of Faint-songs and Grunting or Chirping notes. Lunulated Antbirds generally repeat Faint-songs again and again when Serpentine-singing, but at times a faint *chup* or two alternates with the Faint-songs. Salvin's Antbirds commonly alternate series of *chup, chup-up-up-up* Grunts with Faint-songs. Oddly, when a Salvin's Antbird Serpentine-sings the component Faint-songs are often like the Faint-songs of a Lunulated Antbird: *whe-e-e, whee*. At other times, the Faint-songs of the two species are different.

Snarling. Snarling hisses or blasts of noise, like those at the ends of Why-songs, are sometimes given when these birds argue with each other. The Snarling of *lunulata*, associated with a striking Challenging display, is a long and hissing *WHIAHHHH'AHHHHH!* Compared with the Snarls of Bicolored Antbirds, the Snarls of Lunulated Antbirds are generally broken, tinny, faint, slow, and very long. Moreover, *lunulata* rarely gives more than three Snarls at a time. Separate Snarling is uncommon among Salvin's Antbirds, for moderately loud Why-songs can be rather snarly and generally replace pure Snarling. I recorded one sequence of seven Snarls, however. Unlike Why-singing, a sequence of Snarls stays at much the same pitch instead of descending and slowing. Each Snarl is a harsh *WHAHHH!*, associated with a slight or moderate Challenging display whether it ends a Why-song or is given separately. Compared with the Snarls of *lunulata*, the Snarls of *salvini* are rapidly uttered, variable in length, and unbroken.

Bugling. When Salvin's Antbirds chase competitors of their own species, they give musical *pee'lee'lee* or *too-loo-loo-loo* whistles. In similar encounters, Lunulated Antbirds give a very similar *pee-bee-beep* or *pee-lee-lee*. Usually there are two to five notes, uttered at five or six notes per second, and similar to a chickadee's call. Compared with Bugling in Bicolored Antbirds, the Bugling is very fast, faint, and includes only a few notes.

Hissing and Snapping. When a Lunulated or Salvin's Antbird supplants another, it sometimes snaps the bill once (rarely two or more times) and gives a hissing *chiahh!* The latter

may be a faint and brief form of Snarling. Many supplantings are silent or marked only by Snapping.

Peeping. Young Lunulated Antbirds commonly peep a faint *hee-hee-hee, wheeeee!* or similar series of two to six or so whistles. The first notes are fast but do not descend much in pitch or speed; the last note or notes are long. On a few occasions the first note was the longest, making the Peeping sound like that of young Bicolored Antbirds. Older young Lunulated Antbirds give Peeping Songs, intermediate between Loud or Faint-songs and Peeping. One young gave a rapid, trilly *he'e'e'e, he'e'e, he'e'e!* Another kind of Peeping is a soft *per-per-per-per-per!* series, uttered when a parent is about to feed the young. The Peeping of young Salvin's Antbirds is commonly a long and rather hissing *wheeeeieeh, peeeeieeh!* or *heee peee peie peie!* series. Older young give Peeping Songs, and most versions are clearly related to the adult song.

Squeaking. When fed, young *lunulata* give rough *chiahhh* Squeaks over and over. Squeaking is so widespread among young birds that young *salvini* probably Squeak when fed.

Growling. A female Lunulated or Salvin's Antbird growls a series of *chauhh* notes as her mate tries to feed her or holds food out of her reach. In the related Bicolored Antbirds, males Growl if a female refuses food; perhaps male Growling occurs in Lunulated or Salvin's Antbirds.

Chirping. A male Lunulated or Salvin's Antbird chirps *heu* softly as he approaches his mate, especially during courtship feedings. Mates following each other about a swarm also Chirp or Grunt *eup* to each other.

Grunting. When I approached tame Lunulated or Salvin's Antbirds, they often called *chup* faintly. Similar Grunts greet competitors, especially small or subordinate ones crowding a foraging bird. In Bicolored and other antbirds, Grunting is normally a reaction to a nearby supplantable competitor. A similar sound, punctuating Serpentine-songs in both Lunulated and Salvin's Antbirds, may be a form of Chirping. In these species Grunts and Chirps are difficult to distinguish.

Whimpering. A Lunulated Antbird being supplanted by another sometimes emits one or two faint *hee* or *kweeh* whistles, each a tiny squeak. Submissive Salvin's Antbirds give a slightly longer *wheeeh!* Probably Whimpering is related to Faint-singing, as it differs between these species in the way the first notes of their Faint-songs differ. In Bicolored Antbirds a distinctive Whimpering grades into

Faint-singing when the subordinate bird escapes from the dominant one.

BASIC POSTURES AND MOVEMENTS

The Standard Posture for both Lunulated and Salvin's Antbirds (fig. 3a, d) is like that for Bicolored Antbirds (Willis 1967). Although the latter are larger and heavier, the former have shorter legs and hence stand equally close to the perch. All are adept at clinging to slender vertical saplings, common near the ground in tropical forests. Lunulated and Salvin's Antbirds cling much as does the Bicolored Antbird: the upper leg is flexed, the lower leg extended, and toe II on the lower foot angles 20 to 40 degrees above the closely appressed toes III and IV.

The various simple movements are about the same as in Bicolored Antbirds. The tail is "flicked," or lowered to as much as 80 degrees below the line of the body and jerked back suddenly to near that line, when either *lunulata* or *salvini* is excited. Such compound movements as yawing and pitching on or around a perch, pivoting or reversing along a perch, and hopping from perch to perch or on the ground are performed easily in much the same ways as in Bicolored Antbirds. Lunulated and Salvin's Antbirds side-step up or down or along a perch much more readily than do Bicolored Antbirds. Both *lunulata* and *salvini* flit from one perch to another more readily than does *bicolor*, and hop less frequently than it does. The flight of Lunulated and Salvin's Antbirds is sudden, quiet, rapid, somewhat fluttery, and direct. Their larger relatives jump to start flight, so the course of a bird often starts with an upward parabola. Lunulated and Salvin's Antbirds hop to start flight at times, but their flights often start so directly that wings and legs must contribute about equally to take-off. Despite the greater mobility of these small antbirds, their momentum is not as great as that of their larger relatives; the latter dart at each other or at prey much more forcefully and rapidly than does *lunulata* or *salvini*.

WANDERING

I never saw Lunulated or Salvin's Antbirds foraging away from ants. Several birds seen away from ants in the late afternoon were wandering as if the ant swarm they had been following had folded. One male Lunulated Antbird sang and wandered between preening sessions, but did not keep up a definite direction of travel. Other birds, especially ones seen earlier in the day, wandered in one direction as if looking for ants. A wandering pair of *salvini* at Carauari moved in a zigzag in one general direction as the couple Serpentine-sang and led a young bird ahead of me but circled back periodically to Chirr at me.

A wandering antbird generally travels through the low vegetation or through the more open upper levels of the undergrowth, 0.5 to three meters above the ground. It

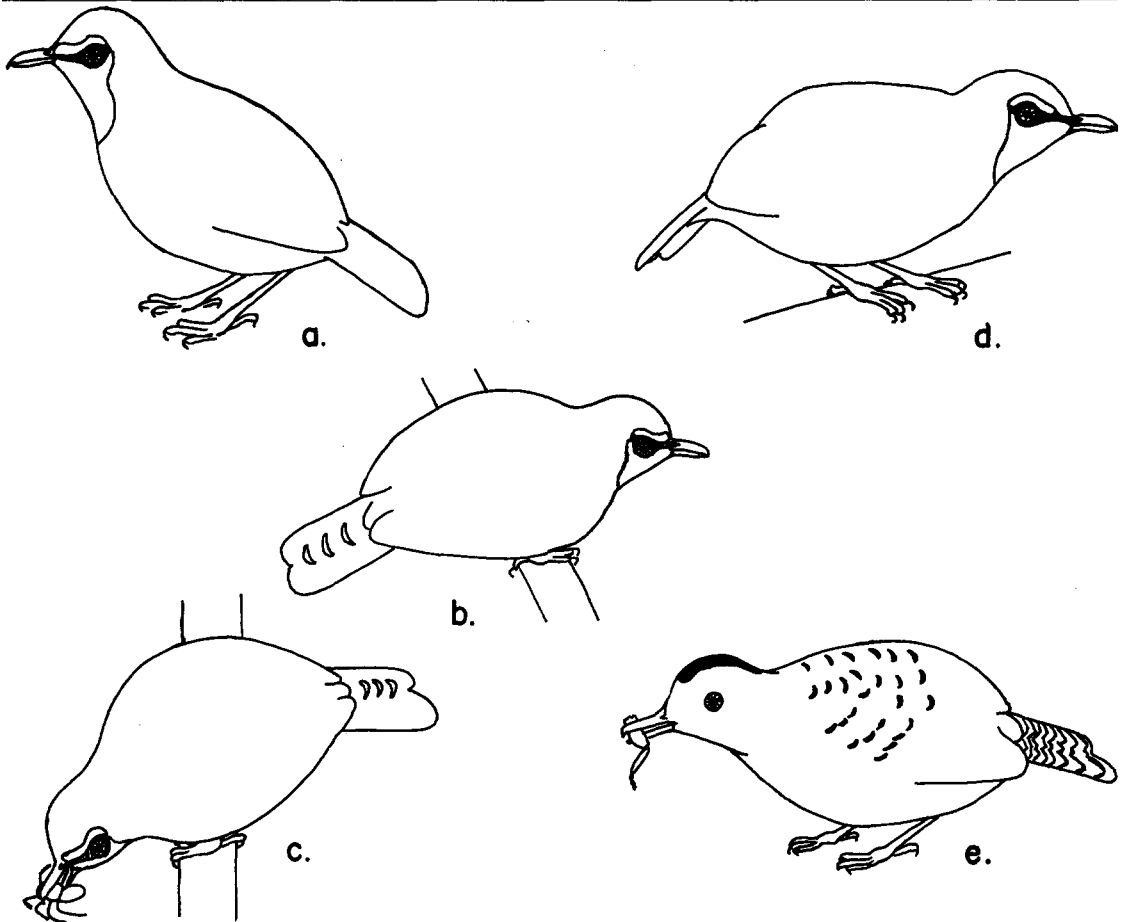


FIGURE 3. Foraging Lunulated and Salvin's Antbirds, from field sketches: (a) male Lunulated Antbird in somewhat upright or domineering pose, close to the Standard Posture; (b) female in a low and submissive pose, after supplantings by larger antbirds; (c) female yawning downward to shake and chew prey; (d) male Salvin's Antbird in rather low or submissive pose, close to the Standard Posture, after being supplanted; (e) female dissecting prey on the ground.

flutters from one vertical sapling or sprout to another, one to 15 meters at a flight, and alights precisely and easily. It looks about at each stop, but it seldom cocks the head as if looking for prey.

In the fashion of other habitual ant-followers, these antbirds readily follow trails of ants from bivouacs and find swarms. They chirp softly, flick their spread tails, look down at the ant trail from each low stop, and Faint-sing. When a swarm or branch of a swarm folds, the antbirds wander about, then move back along the retreating ant trail to the bivouac or until they find a new active branch. Once several Salvin's Antbirds loafed and wandered, Serpentine-singing, around an inactive ant bivouac rather than strike out and forage on their own; such reluctance to leave inactive ants or a folding swarm is characteristic of the habitual ant-follower.

FORAGING

When larger competitors are absent, Lunulated and Salvin's Antbirds forage low over swarms of ants in much the same way as do Bicolored Antbirds. Much of the time Lunulated Antbirds are between 0.1 and 0.7 meters above the ants, rarely as much as three or four meters up (figs. 4, 5); Salvin's Antbirds forage at similar levels. Generally, they are on the slender vertical saplings or sprouts or on the horizontal fallen limbs so common near the ground in a tropical forest (table 1). When the angle of the perch is 45° or more, the diameter is seldom over three centimeters; there were 27 records of Lunulated Antbirds clinging to perches under 1 cm in diameter, 19 of perches of 1 to 2 cm, 15 of perches to 3 cm, 4 to 4 cm, 1 to 5 cm, 2 to 6 cm, 1 to 7 cm, and 2 for pole-sized perches; for Salvin's Antbirds, there were 17 records of

TABLE 1. Records of perch angles for Lunulated and Salvin's Antbirds.

Angles	Lunulated Antbirds		Salvin's Antbirds	
	Records	Per cent	Records	Per cent
0-20°	23	20.8	5	13.5
25-40°	11	9.9	4	10.8
45-60°	15	13.5	3	8.1
65-80°	10	9.0	5	13.5
85-100°	52	46.8	20	54.1
Total	111	100.0	37	100.0

perches to 1 cm, 5 records to 2 cm, 1 record to 3 cm, and 1 record of a bird on a big pole.

As they perch, these antbirds pitch and yaw, pivot and look about, or cock their heads quietly for minutes at a time. They can be very inconspicuous at such times, for they hide behind sprigs of vegetation and move suddenly if they move at all. Unlike their more-volatile, larger relatives, they are likely to hide at one spot for long periods. However, they are quick to shift to new sites if foraging is poor or if larger birds supplant them. At such times they often ascend to one or two meters above the ants, faint-sing and wander, and drop in quickly at unoccupied sites.

Most of the prey is captured by sallying to the ground (table 2). The bird leaps or leap-flutters after a fleeing arthropod and bounces back up to a perch with it so rapidly that the army ants rarely have a chance to counter-attack. Compared with Bicolored Antbirds, Lunulated and Salvin's Antbirds are reluctant to sally long distances. Instead, the small antbird often flits inconspicuously to a perch close to the arthropod as it dives under cover, waits a few moments until the ants flush it again, and then sallies at very close range. One female sidestepped down a vertical sap-

ling, hopped to peck the prey off the ground, and hopped back rather than fly down and back. Often Lunulated and Salvin's Antbirds peck or lunge at the prey from a nearby perch rather than sally for it (table 2). These behavior patterns, and the reluctance of these species to go on prolonged hop-flutter-pivot chases of a fleeing arthropod, make them very hard to detect at swarms of ants.

At times the antbird yaws or pitches and pecks the prey out of the air or off a low liana or stem. Conspicuous sallies above the ground are infrequent; usually the bird flies to near the prey, waits a moment, and pecks it as inconspicuously as possible.

The prey of Lunulated and Salvin's Antbirds were generally too small to be identified from a distance. The largest prey items were about 1.5 times the length of the exposed bill, or about 22 mm. Crickets, roaches, and spiders were taken by *lunulata* and spiders by *salvini*. I never saw them eat army ants or adult ants of any sort. However, in upper Amazonia there are several kinds of ants that, when the army ants approach, grab their white larvae and rain down from canopy nests or boil up from ground nests in frantic races to escape. Both Lunulated and Salvin's Antbirds quickly dart to such places and peck rapidly, tossing each adult ant and eating its white larva, as if working on assembly lines. One female Lunulated Antbird at Putuimi Chirred as she picked up 21 ant larvae near me, while more-timid large antbirds watched us both but would not come near me. At Yarinacocha a male and a young male *lunulata* got 47 larvae at an ant exodus near me. A male Salvin's Antbird at Carauari fed his mate twice and pecked off 13 other ant larvae before the female joined him along the ant line. A male at Benjamín Constant waited patiently for a larger Hair-crested Antbird (*Rhegmatorhina melanosticta*) to stop eating and leave, then picked up the two last larvae of the exodus.

At times large prey is chewed and shaken repeatedly as the bird yaws downward from a vertical perch (fig. 3c) or holds its head down on a horizontal perch. Occasionally, the bird flutters off with prey, takes it

TABLE 2. Attempts at prey capture by Lunulated and Salvin's Antbirds.

Bird, place, motion	Competition ^a	Location of Prey						Total	
		Ground, root	Stem, Liana, limb	Log, trunk	Foliage	Trash	Unspecified		
Lunulated Antbird									
Ecuador	S ^b	No	36	2	2	1	3	1	45
	L ^c	No	14	2	15				31
	T ^d	No	2						2
	S	Yes	7	10	1	6	1	1	26
	L	Yes	2	8	1	1	1		13
Perú	S	Yes	8	3			1		12
	L	Yes		1	2		1		4
	S	No	233	2	7	8	3	4	258 ^e
	L	No	40	5		15	2	3	65
	T	No	1						1
Salvin's Antbird									
Brazil	S		24		3	3	1	1	32
	L		2		2	23 ^f			27

^a Competing larger antbird within two meters horizontally. ^b Sallying. ^c Lunging. ^d Leaf-tossing. ^e Includes one sally into the air. ^f A sequence of 21 captures of black ant larvae, from a single palm spine, is included.

TABLE 3. Supplantings and displacings of and by Lunulated and Salvin's Antbirds.

Other species	Lunulated Antbirds				Salvin's Antbirds			
	Putuimi		Yarinacocha		Carauari		Benj. Constant	
	Sup.	Displ.	S	D	S	D	S	D
Own species	5	2	383	24	66	2	8	
White-ch. Antbird	5	1						
Hair-cr. Antbird					5	3	4	3
Reddish-w. Bare-Eye	1					3		
Black-sp. Bare-Eye			34	12				
Sooty Antbird	11	6			4		3	1
Spot-backed Antbird ^a		1						
Scale-b. Antbird ^a			6	3	1			
Black-faced Antbird ^a			1					
White-ch. Woodcreeper			8 ^b					
Plain-brn. Woodcreeper					1		0 ^b	
Total	22	10	432	39	77	8	15	4

^a Subordinate (*Hylophylax naevia*, Spot-b. Antbird; *Hylophylax poeilonota*, Scale-b. Antbird; *Myrmoborus myotherinus*, Black-f. Antbird) rather than dominant to Lunulated or Salvin's Antbirds. ^b Excludes one reverse supplanting of the woodcreeper by the smaller antbird (see text).

to the ground, shakes and chews it, drops it to the ground (fig. 3e) and looks at it periodically, then takes it up again. The prey is not held by the foot or hammered against objects. Dissecting prey is less common than it is for Bicolored Antbirds and other large birds that capture many large prey items.

Bill-wiping is performed much as in Bicolored Antbirds. Since Lunulated and Salvin's Antbirds eat large or messy prey only rarely, bill-wiping is not frequent during foraging.

To egest, the bird lifts the closed tail slightly.

One young Lunulated Antbird, spiraling up a low stem, held its wings tented out at the wrists and flashed them widely several times as it peered at the stem, then jabbed once. The flashing was not a balancing motion or necessary for the spiraling, and seemed a slow display of the outspread wings rather than a simple flitting. In the woodcreeper genus *Dendrocincla* (Willis, unpublished data) and in the mockingbird, *Mimus polyglottos* (Hailman 1960), wing-flashing is regularly associated with flushing prey. I wonder if wing-flashing may be a usual reaction when prey is hiding, but is used regularly only by a few species of birds.

One young Lunulated Antbird "anted," pushing a captured prey under the outstretched wing several times. The young antbird shook its plumage and champed the beak after anting. In related species, anting behavior seems a reaction to distasteful prey (Willis 1967).

Two Lunulated Antbirds at Putuimi, displaced by larger antbirds, turned to "thievery." In each case the subordinate bird moved back to the ant trail and sallied into it three times, tossing a homeward-bound army ant and eating its fragment of booty each time.

INTERSPECIFIC COMPETITION

Table 3 lists supplantings and displacings of and by Lunulated or Salvin's Antbirds. In supplantings, the Antbird is supplanted or takes the perch of another ("subordinate" bird) with snapping or a snapping hiss. In displacings the subordinate bird clearly moves out of the way of another. In general, larger birds supplant smaller ones. However, at Yarinacocha one Lunulated Antbird gave an outraged *pee'lee'lee!* attack and drove off a

startled, large White-chinned Woodcreeper (*Dendrocincla merula*) when it sallied for prey nearby. One Salvin's Antbird at Benjamín Constant surprised a large Plain-brown Woodcreeper (*Dendrocincla fuliginosa*) with a sudden attack. Generally, both woodcreepers ignored the small antbirds or supplanted them infrequently.

A foraging motion by a small bird is likely to bring a nearby large bird over to supplant it, even from distances as great as three and four meters. Large birds quickly move in from even greater distances and displace small birds if the latter capture several prey. When large birds take the best sites over the ants, Lunulated and Salvin's Antbirds forage by wandering about at the periphery and by variants of this method (table 4). Because of difficulties of observation in the tropical forest, the table underestimates the number foraging ahead of the swarm, moving to separate branches of a swarm, or deserting it; it overestimates the number foraging behind the swarm or near the observer, since I was generally behind the swarm. Occasionally a bird stayed near larger birds and was ignored; the many cases when the small antbird was supplanted or displaced are listed in table 3, as are any such cases that belong in other categories of table 4.

Foraging high over the ants is an important and easily quantified (figs. 4, 5; table 5) method of foraging when larger antbirds are "present," or within two meters horizontally. The change in foraging heights is similar to the change for Plain-brown Woodcreepers when antbirds exclude them from the low-central foraging zone at swarms (Willis 1966b). At Putuimi, where large antbirds of several species (White-cheeked Antbird,

TABLE 4. Records of foraging Lunulated and Salvin's Antbirds obviously excluded by larger birds.

Foraging method	Lunulated Antbird		Salvin's Antbird	
	Putuimi	Yarinacocha	Carauari	Benj. Constant
Deserts raid	—	—	—	2
Wanders about	26	7	5	6
Moves high	47	16	4	—
Moves ahead	6	—	1	—
Moves to side	18	5	5	4
To separate branch-raid	6	7	—	—
Behind swarm	18	5	4	1
Near observer	14	16	5	5
In as larger bird leaves	1	4	2	1
Hit-and-run (infiltrates)	4	—	—	—
Stays near large birds	3	3	4	3
Total	143	63	30	22

Gymnophithys leucaspis; Sooty Antbird, *Myrmeciza fortis*; Reddish-winged Bare-Eye, *Phlegopsis erythroptera*) dominated the ground levels, Lunulated Antbirds had to forage in high and peripheral sites much of the time. They were rare there; only three birds were seen at or near only one of the four colonies of *Eciton burchelli* I watched. At Yarinacocha only the uncommon Black-spotted Bare-Eye (*Phlegopsis nigromaculata*) and the open-foraging White-chinned Wood-creeper (*Dendrocincla merula*) interfered with

the foraging of the common Lunulated Antbirds. They generally ignored the wood-creeper, so that the Bare-Eye was the only opponent important enough to consider for the figures and tables. However, high intraspecific competition between the many Lunulated Antbirds sometimes forced the subordinate birds to forage on the periphery or above the swarm when no other species were present. Similar intraspecific exclusion of subordinate individuals is often seen among Bicolored Antbirds on Barro Colorado (Willis

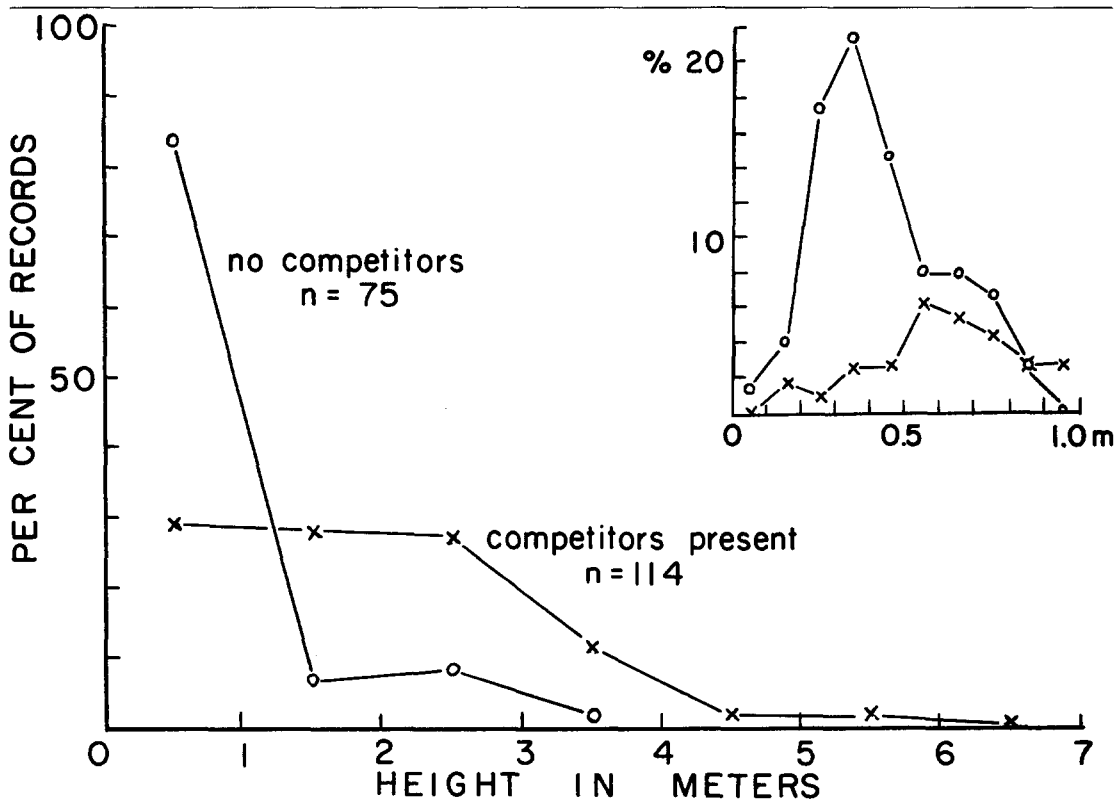


FIGURE 4. Estimated heights of perching for foraging Lunulated Antbirds at Putuimi, Ecuador, in relation to the presence of dominant large antbirds. The inset figure details heights below one meter.

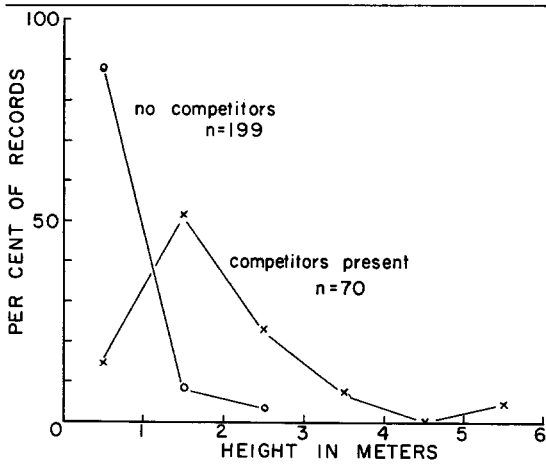


FIGURE 5. Estimated heights of perching Lunulated Antbirds at Yarinacocha, Perú, in relation to the presence or absence of the large Black-spotted Bare-Eye.

1967). At both Caruarí and Benjamín Constant moderate numbers of Salvin's Antbirds had to contend with low numbers of Reddish-winged Bare-Eyes, Sooty Antbirds, Hair-crested Antbirds, and White-chinned Woodcreepers; however, Salvin's Antbirds often managed to sneak in at unoccupied sites near the ground.

As noted earlier, inconspicuous foraging behavior is characteristic of Lunulated and Salvin's Antbirds, especially the former. Since small birds have to catch many prey items rather than wait for the infrequent large arthropod, one would expect them to be active and conspicuous. Many small antbirds, especially the smaller *Hylophylax naevioides* or Spotted Antbird, flutter about a swarm very conspicuously and actively. Lunulated and Salvin's Antbirds are so tame and unsuspecting toward a human that I doubt they are hiding from predators. They panic, Chip, and zip about actively if a hawk appears. I think it likely that both species, by their sneaky foraging, avoid attracting the attention of larger

competitors. The faintness of their songs and calls also may contribute to their inconspicuousness. I have shown (Willis 1967) that competitors of other species quickly move in when one plays a recorded song of an ant-following species, the Bicolored Antbird.

OTHER INDIVIDUAL BEHAVIOR

Periodically, Lunulated and Salvin's Antbirds loaf or preen in cover or over the ants, especially when large or dominant birds prevent their foraging. Generally, Lunulated and Salvin's Antbirds preen on horizontal perches, from 0.3 to two meters above the ground. Both readily interrupt preening to dash after prey, being less sedate than are Bicolored Antbirds and other large related species.

Both Lunulated and Salvin's Antbirds shake the whole body during preening and (less often) during foraging much more frequently than do Bicolored Antbirds. The body and wings are fluffed or extended, even the head feathers, before the bird shakes as vigorously as a dog after bathing. On one occasion a female Lunulated Antbird shook the body so often as she preened that she may have been bathing, though there was no water nearby unless it was in a knothole.

One Lunulated Antbird nibbled the tip of a leaf as if drinking raindrops.

On five occasions Lunulated Antbirds scratched the head over the wings; Salvin's Antbirds did so four times. Antbirds in general scratch over the wing, but many species also scratch under the wing at times.

I recorded full side-stretches (wing, leg, and tail on one side of the body), especially before returning to foraging at the end of preening sessions, for Lunulated Antbirds. This and other stretching movements (yawning, toe-standing, two-wing stretches) are so widespread among birds that they are to be expected for both Lunulated and Salvin's Antbirds.

Frequently a Lunulated or Salvin's Antbird twitches the rear half of the body or shakes the head as it forages, loafs, or preens. The twitching often includes a sudden flit of the wings and a brief spreading of the tail. At times such movements seemed part of a sequence of bill-wiping, Toe-looking, or other "displacement activities" after a bird was displaced by a rival, but usually twitching and headshaking were reactions to mosquitoes. One male Salvin's Antbird pecked at a mosquito after shaking his body. A female gave a flitting twitch every second or two and pecked between her legs frequently one day when mosquitoes were unusually bad.

When army ants attack its toes, a Lunulated Antbird pecks at the ants and tosses them through the air, Jitters from one foot to the other, shakes the foot,

TABLE 5. Attempts at prey capture by Lunulated and Salvin's Antbirds.

Species, place	Competition ^a	Height in meters														
		0.1	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9	1.0	2	3	4	5	
<i>lunulata</i>																
Ecuador	No	57	3	1	3	2	2	1			2	4	1	1		
	Yes	9									8	14	7	1		
Perú	Yes	8									5	3				
	No	260	1	2	2	2		2	4	2	2	16	5			
<i>salvini</i>																
Brazil	Yes	2					1			1	2	3				
	No	19			1					2		21 ^b				

^a Competing larger antbird within two meters horizontally. ^b A single series of 21 black ants with larvae.

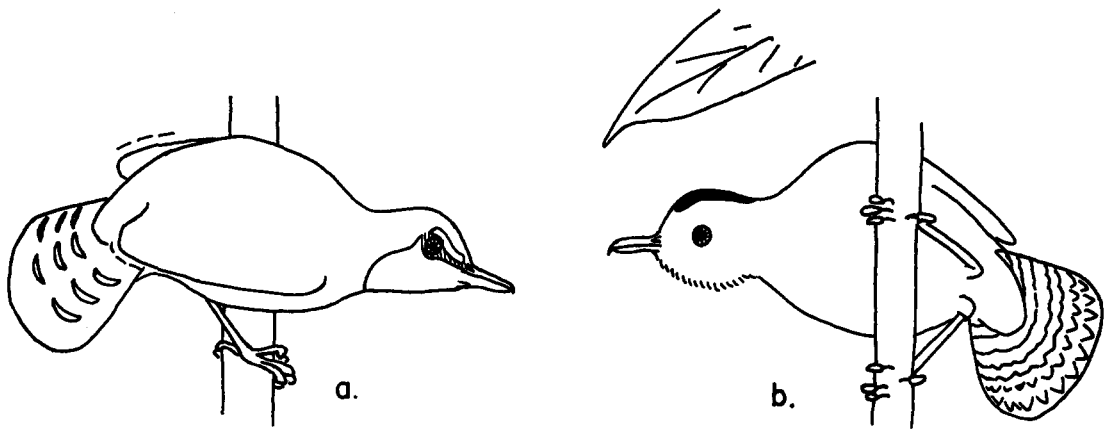


FIGURE 6. Reactions to danger, from field sketches: (a) Panicking, chipping female Lunulated Antbird; (b) female Salvin's Antbird, near young, Mobbing observer.

and flees. These reactions are similar to those of ant-disturbed Bicolored Antbirds, and are to be expected in Salvin's Antbirds.

REACTIONS TO DANGER

Lunulated and Salvin's Antbirds Freeze and Keen at uncertain or distant danger. The movements, including crouching on the perch, resemble those in Freezing Bicolored Antbirds (Willis 1967). The loud calls of martins (*Progne chalybea*) above the treetops, the sharp alarm calls of Plain-brown Woodcreepers (three times), a chattering alarm from a White-chinned Woodcreeper, the *stool* alarm call of a Buff-throated Woodcreeper (*Xiphorhynchus guttatus*), the sudden appearance of a young Double-toothed Kite (*Harpagus bidentatus*), the sound of large wings in the canopy, my slapping at mosquitoes, Chipping notes from another Lunulated Antbird, and supplanting by a female *lunulata* all evoked Keening and Freezing from Lunulated Antbirds.

As in Bicolored Antbirds, Chipping and hyperactive Panicking are the reactions to more obvious danger. The Panicking Lunulated or Salvin's Antbird sleeks the body, flexes the femora as it extends the next two joints of each leg, and extends the neck and head (fig. 6a). It thus angles the body downward in front. It flicks the spread tail rapidly. It darts from perch to perch or into cover with sharp *chip!* notes. Unlike the more-sedate Bicolored Antbirds, Lunulated and Salvin's Antbirds often flit the wings as they flick their tails and reverse, pivot, or zip from one perch to another. One preening Lunulated Antbird stopped and looked about when another one Chipped.

A female crouched and looked about when two others Chipped. Chipping by one or two birds started the spread of a Keening Freeze and then a Chipping Panic among several on another occasion. One male Chipped at the rate of eight Chips in 10 seconds during that Panic. The Chipping and other notes of an antshrike (*Pygiptila stellaris*) overhead started a Chipping panic on another occasion. A Chipping panic followed Keening when a kite (*Harpagus bidentatus*) flew up. A woodcreeper's (*Dendrocincla fuliginosa*) sharp alarm calls at monkeys startled a *chip!* from one Lunulated Antbird, and the Chipping and Panicking of a female Scale-breasted Antbird (*Hylophylax poecilonota*) started another Chipping. One female Chipped often as she worked an exodus of black ants near me, but she soon became less timid and stopped her flitting, flicking, Chipping, and zipping about.

Lunulated and Salvin's Antbirds, like related antbirds, Mob and Chirr at the observer when he first appears. One Lunulated Antbird Chirred when a tayra (*Eira barbara*) loped by. Squirrel monkeys (*Saimiri sciurea*), passing as low as two meters overhead, started several Chirring at Yarinacocha. If parents are with a young bird, they Mob the observer and Chirr persistently.

A female Salvin's Antbird at Caruarú fluffed out her throat and cheeks and spread her tail as she Chirred at me from two meters above the ground between me and a young bird as I followed them (fig. 6b). Throat-fluffing is the most characteristic movement of Mobbing in related antbirds. In both Lunulated and Salvin's Antbirds, throat-fluffing displays conspicuously colored areas. The female Salvin's Antbird showed other Mobbing movements: the femora were flexed, the neck extended, and she stared at me with one eye.

Other Mobbing Salvin's Antbirds show other characteristic movements, swinging around and around a vertical perch or revers-

ing frequently so that one eye and then the other is toward the opponent. These birds lack the conspicuous bare faces that related antbirds display by such movements, but they go through the motions anyway.

Mobbing Lunulated and Salvin's Antbirds flick the tail little; tail flicking probably indicates an admixture of Panicking in the many cases where Mobbing antbirds of these or related species perform it. Such Lunulated and Salvin's Antbirds often alternate Chipping and Chirring or give a mixed *chip-urrrrr!* call.

Neither species Mobs or Chirrs as persistently as do related species of antbirds. Both, especially Lunulated Antbirds, are very quick to accept the observer by closing their tails, stopping Chirring, and returning to foraging almost underfoot. They persistently keep behind cover, and they flit their wings and flick their half-closed tails or silently desert the area if pressed too closely, but they are remarkably easy birds to study compared with their larger relatives.

In general, the larger an ant-following antbird is, the more persistently it Mobs or Panics before the observer. In Bicolored Antbirds the lower an individual is in its intraspecific peck order, the more rapidly it becomes tame (Willis 1967). Small species may have less to fear from predatory mammals than do large species, but the rule that subordinate birds become tame quickly applies intraspecifically in the absence of differences in size. The major factor in tameness in these antbirds is probably the food advantage. Foraging near the observer gives a bird that is low in the peck order protection from attack by dominant birds. Theoretically, birds low on peck orders should not call repeatedly, as dominant competitors might be attracted. However, this possible contributing factor is probably unimportant: Chirring is an inconspicuous sound except at close range, and birds generally disperse rather than congregate when Chirring starts.

A semitame Lunulated or Salvin's Antbird performs throat-ruffing and wing-flitting but continues to forage near the observer. It Grunts (or Chirps?) at intervals as it wanders around. One male Salvin's Antbird was ignoring me but Chirred after a Hair-crested Antbird stumbled on us and started to Chirr. One young Lunulated Antbird flew up near me and peered intently, then returned to foraging. At times others (fig. 1) showed signs of "investigating" behavior, but generally they accepted me without going through the process of looking me over from close range.

At Yarinacocha, Lunulated Antbirds foraged

at the edges and in isolated clumps in a clearing caused by a species of sapling, one that either poisons vegetation below it or has ants that cut out the plants for it. The antbirds Chipped and showed other signs of Panicking. They darted up to four meters to capture food rather than work from isolated saplings. These birds generally avoid open undergrowth and paths. I never saw either species outside the forest. Large rivers, such as the Amazon and Madeira, bar their spread (fig. 2).

INTRASPECIFIC AGONISTIC BEHAVIOR

As in an earlier paper (Willis 1967), I shall use "agonistic behavior" to refer to such competitive behavior as fighting, supplanting, aggressive and submissive display. Interspecific agonistic behavior, which is usually confined to Snap-hiss supplantings but at times goes as far as spread Challenges and Bugling, has already been discussed.

Once two male Salvin's Antbirds had a brief fluttering scuffle on the ground, their wings outspread, as one supplanted the other four times. Once, as a female supplanted another several times, there was a brief scuffle. I doubt that fighting is frequent in either species, although I am surprised that I saw two brief fights between Salvin's Antbirds in only 76 recorded encounters (table 3) and none between Lunulated Antbirds in 414 encounters. In Bicolored Antbirds (Willis 1967) there was a fight every 400 encounters or so.

Submissive behavior is difficult to observe unless one can work with birds over periods of several weeks, so that they become very tame. The problem is that dominant birds are wary and will not persecute a subordinate bird enough to start its submissive behavior if the observer is nearby. Even though Lunulated and Salvin's Antbirds became tame quickly, I observed only low-intensity submissive displays. Possibly submissive behavior is rare in both species.

Lunulated Antbirds commonly turn the back to a dominant opponent and take rather low "cringing" poses, with necks retracted and legs flexed. These activities resemble the lowest intensities of the Cringing display in Bicolored Antbirds; perhaps Lunulated Antbirds have strong Cringing displays, with wing-fluttering and similarly humble postures, when the birds are tame.

Subordinate Salvin's Antbirds also turn the back to the opponent and take somewhat low poses (fig. 3d). One male turned his back to a passing opponent even though he had to face me to do so, causing him to Chirr. As

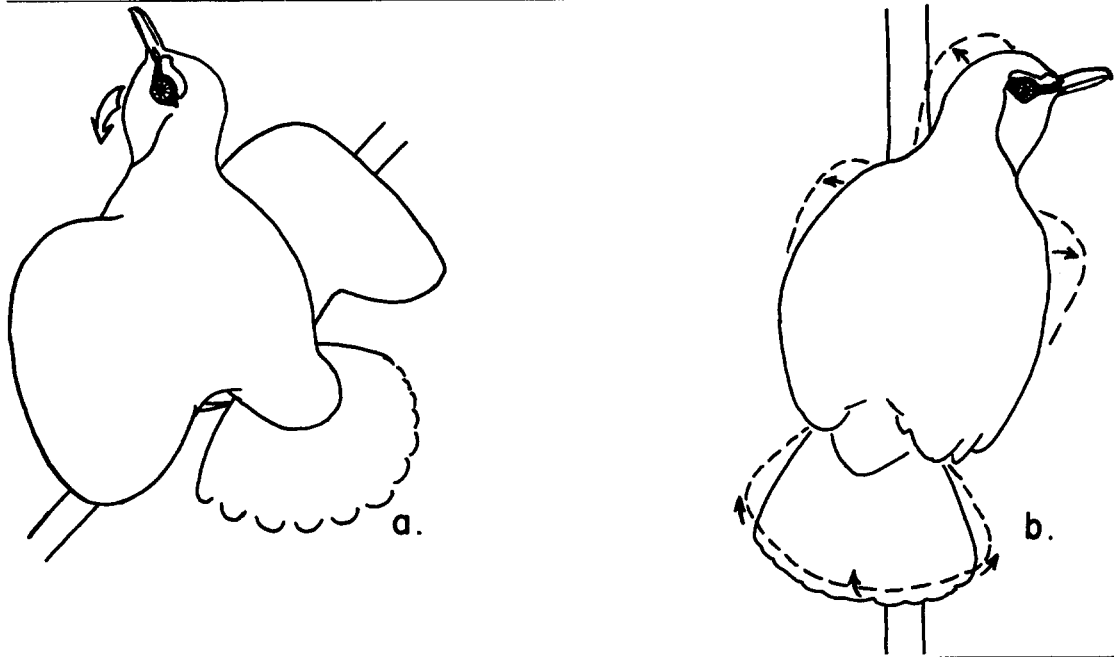


FIGURE 7. Aggressive display in Lunulated Antbirds, from field sketches: (a) high-intensity Challenging, with wing-flapping and head-bobbing; (b) medium-intensity Challenging; dashed lines and arrows show next higher intensity.

I approached two other males, the nearer one gave wing-quivering in bursts, pitched and reversed, flicked his closed tail, and fled from his spread-tailed opponent. On two occasions juveniles supplanted by adults wing-fluttered, but they may have been begging. However, wing-fluttering in juvenile fashion is characteristic of high-intensity submissive display in many related species.

The aggressive or "challenging" display of Lunulated Antbirds (fig. 7a) is even more spectacular than the rather similar display of Bicolored Antbirds. The Challenging Lunulated Antbird jerks its body upright, spreads the tail widely and even raises it above the line of the body. The wings are spread and flap slowly up and down, once or twice a second. The head is thrown up and down at about the same rate, but out of synchrony with the wings, so that the bird seems a disjointed puppet. As it semaphores the head and wings, it Snarls loudly one or more times. Each long Snarl is broken in the middle, apparently when movements of the head interfere with sound production. I am not sure whether the two parts of each Snarl coordinate with particular positions of the head or not. In one case I recorded that the Snarl was given each time the head was thrown downward, but the movements are so fast I may have had the timing wrong. Ordinarily, the Challenging display includes one to four

wing-wavings and head-bobbings. At times the wings are held rigidly outstretched rather than waved. The Challenging bird performs head-bobbing, displaying its puffed-out white cheeks and throat, even if it Challenges with back to the opponent; in this case, the head is turned to the side as the bird looks back at the opponent.

At low intensities of Challenging, a Lunulated Antbird merely spreads the tail slightly and glares at the opponent. Between the poses at low and high intensity are a spectrum of postures, with the body of the bird more and more upright and the wings and tail increasingly spread (fig. 7b). An upright posture with wings out at the wrists is very common. Brief Snarls are often given from low- or medium-intensity Challenging poses. One female stabbed her beak skyward for each Snarl and returned the head to horizontal between and after the Snarls. Challenging is thus a graded display, as in related antbirds.

Bugling is given from various intensities of the Challenging position, either while the bird is perched or when it is flying. Bugling is generally associated with a supplanting or a series of supplantings. Lunulated Antbirds perform Challenge-flying, with outspread wings flapping slowly and the tail spread, in much the same way as does the Bicolored Antbird. However, they are so light and fast that the mixture of Challenging and flight

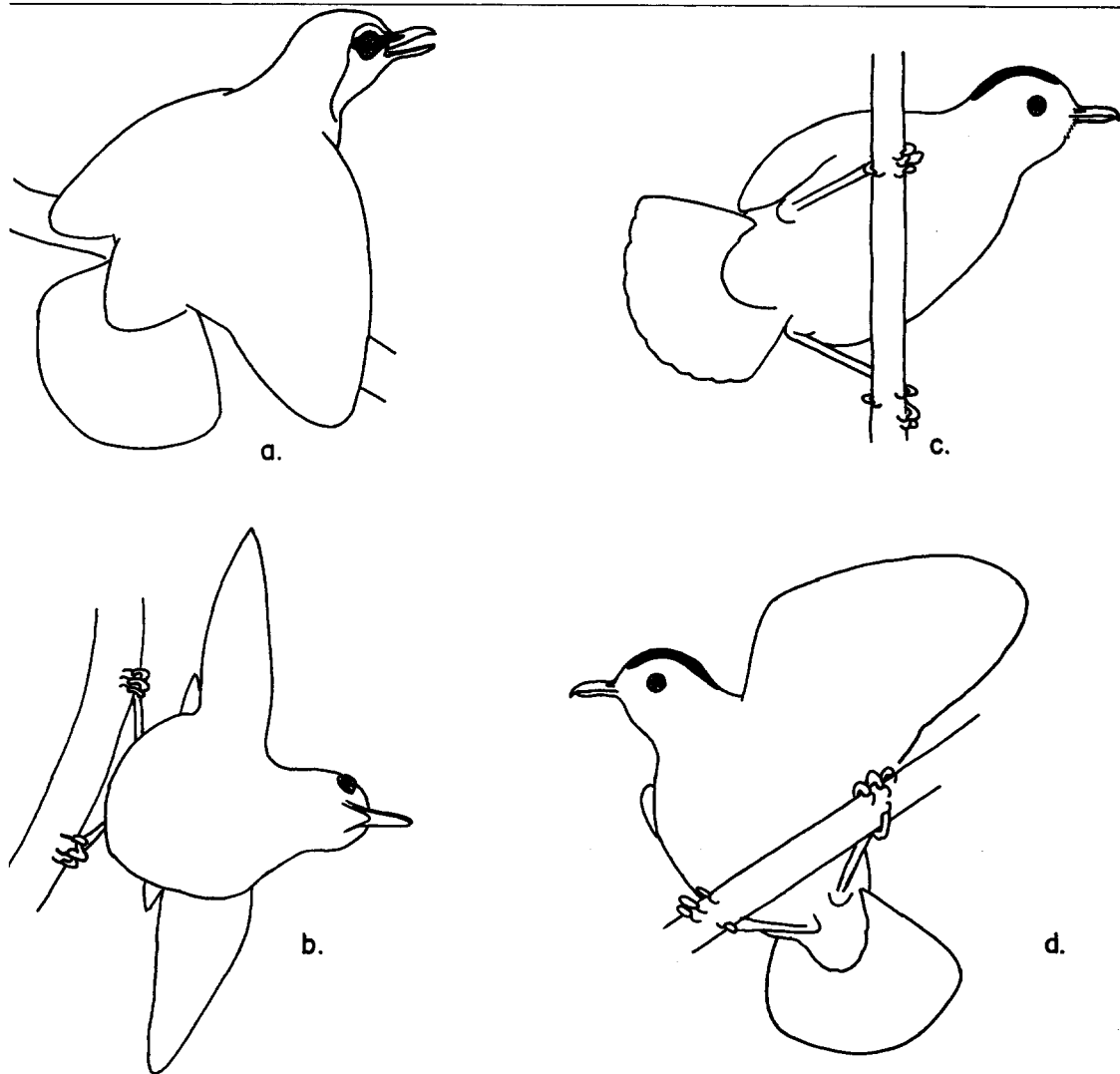


FIGURE 8. Aggressive display and chases of Salvin's Antbirds, from field sketches: (a) male Challenging at moderate intensity; (b) female, wings outspread, alighting momentarily while supplanting another; (c) challenging female, starting to Mob the observer after chasing another female past him; (d) one-wing-out pose of female, defeated in series of supplantings but still showing Challenging.

does not interfere with flying as much as it does in Bicolored Antbirds. Ordinarily, as in Bicolored Antbirds, Challenging drops to a level close to the Standard Posture before a bird darts at another. Otherwise, the extended wings and legs of Challenging interfere with leap-fluttering at the opponent.

The bowing motions of high-intensity Challenging present the white throat very strongly. The throat is fluffed and the head slightly extended for the display, two movements opposite to Challenging movements in Bicolored Antbirds. The latter generally follow a "rule of angles," in which angles at the extremities are closed and angles toward the center opened during aggressive display and vice versa for submissive display (Willis 1967).

Head-extending may be considered a movement at an extremity, in which case Lunulated Antbirds are not following the rule completely. However, the main movement seems to be neck-extending rather than head-extending. Throat-fluffing, which also occurs in Challenging in the similarly bright-throated *Gymnopithys rufigula*, is possibly an exception to the rule of angles. However, both Lunulated and Salvin's Antbirds seem to puff the throat and lower cheeks with air rather than fluff the feathers directly. Sleeking the neck feathers also contributes much to the spread-throated appearance.

Salvin's Antbirds use Bugling Gantlets (Willis 1967: 57) or supplanting series frequently and Snarling Challenges infrequently.

I have seen only low- and medium-intensity Challenging. The latter (fig. 8a) resembles the medium-intensity display in Lunulated Antbirds: the bird jerks upright, spreads the tail widely, fluffs or expands the body and throat, extends the neck, and Snarls at the opponent. The bends or tips of the wings are often spread. One Challenging Salvin's Antbird expanded the body, perhaps by inflation, before compressing it to dart at the opponent. Another female had her body expanded as she alighted near me after a chase (fig. 8c). Possibly wing-spreading, wing-waving, and head-bobbing are used in high-intensity displays, but these must be less frequent than in Lunulated Antbirds.

In the frequent and musical Bugling Gantlets and Challenge-flights of Salvin's Antbirds, alighting birds sometimes hold one or both wings out (fig. 8b and d). These birds often have the throats, cheeks, and bodies fluffed out and perhaps inflated. The whole head of one Challenging male seemed ruffed. As in Lunulated Antbirds, Challenging seems to interfere very little with flying.

Lunulated Antbirds use Challenging as an "insubordinate" reaction, before fleeing from a dominant opponent, surprisingly frequently. A possible reason for this is discussed later, under the behavior of young birds. Oddly, the dominant bird rarely explodes into attack at such insubordination, but simply forages toward the insubordinate bird until it comes down from the Challenge, turns its back, and silently steals away. A Bicolored Antbird, encountering a Challenging subordinate bird, would trounce it with violent Challenging and supplanting (Willis 1967). Perhaps a quiet reaction to insubordination is less likely to attract large competitors. Another possibility, that the insubordinate birds are young, is discussed later.

Lunulated Antbirds are very quiet about their disputes compared with Bicolored Antbirds. One can listen for hours near several Lunulated Antbirds and hear only a few Snarls or Bugling Challenge-flights, even though birds foraging near each other have a strong peck order and are supplanting and displacing each other frequently. Occasionally, there is a flurry of four or five snapping and hissing supplantings as a brief Gantlet, or a chip or two as a supplanted bird departs, but mostly the birds are inconspicuous. Males and females spread their tails and glare back and forth, but they are rather tolerant as long as the opponent stays more than two or three meters off. Since they often hide in low vegetation or wander about the periphery of a

swarm, excluded from the center by larger antbirds, they have many opportunities to avoid each other without resorting to strong agonistic interactions. The tolerance is less when a new bird arrives at a swarm, and there may be Bugling-Snarling-Challenging-supplanting-Chipping-Whysinging-Loudsinging "Arrival Outbursts" at such times. Twice I recorded loud outbursts of Why-singing, one ending in Loud-songs from a departing bird. However, new birds are accepted into the local peck order much more quickly than would be the case among Bicolored Antbirds; and outbursts do not spread to neighboring birds or last as long. Once a Lunulated Antbird moved ahead of the swarm 20 meters before answering distant Loud-songs; but even the less-inhibited Bicolored Antbird sometimes behaves similarly.

Salvin's Antbirds seemed more like Bicolored Antbirds in the outspoken conspicuousness of their disputes. Noisy arrival outbursts, with Gantlets and Challenge-flights with Bugling, were frequent and prolonged compared with Lunulated Antbirds. I saw rather little insubordinate Challenging, although one supplanted bird Bugled as it fled. However, snarling displays were even less common than in Lunulated Antbirds, being replaced by faint Why-singing (rather snarly in *salvini*) and by Bugling chases. Moreover, Salvin's Antbirds soon became quiet and sneaky about their feuding if no new antbirds appeared. In a typically quiet interaction, a female *salvini* alighted above another and both gave a faint *pee'lee'lee* Bugle with very little wing or tail spreading. The upper bird supplanted the lower, and both moved about with tails spread and wings tented out at the wrists.

As in interspecific agonistic behavior, Lunulated and Salvin's Antbirds defeated by others of their own species wander about, often at one to two meters above the ground, Faint-singing, and drop or sneak in at unoccupied spots at or near the swarm.

Salvin's and Lunulated Antbirds often bill-wipe, champ the bill, look at the toes, flit the wings, flick the tail, or shake the body if dominant opponents pass by, supplant them, or stay and ignore Challenges. Probably these are "displacement activities." At times the twitching and head-shaking at mosquitoes seemed more frequent as birds foraged near each other than when a bird foraged alone. The foraging of subordinate birds was inhibited when birds worked near each other, and Grunting notes and Faint-songs were rather frequent. Subordinate birds usually

Faint-sang and dominant ones Grunted, but at times both Faint-sang or were quiet.

In Bicolored Antbirds the pair on its own territory dominates other birds at swarms of ants but permits them to stay (Willis 1967). Probably Lunulated and Salvin's Antbirds have the same type of territoriality, for I saw two pairs foraging together on many occasions even though the birds were breeding at the seasons I visited them. There were, of course, major or minor squabbles between competing pairs. Generally, females feuded with females or supplanted their own mates, while males feuded with males. Different pairs tended to move to different ends of branches of a swarm of ants, as is the case for Bicolored Antbirds. Except for greater tolerance of others and quieter feuding, especially in Lunulated Antbirds, competing pairs seemed remarkably like Bicolored Antbirds in their relationships. Of course, one cannot prove territoriality in birds like these without following marked individuals from one territory to another to see if there is a reversal of dominance.

Female Lunulated and Salvin's Antbirds always supplanted their mates, never the reverse. Birds of a pair converse with faint Chirping or Grunting notes and short Faint-songs. They sometimes forage a meter or two apart, but closer approach is permitted only for courtship feedings. In this respect these species are like other species of *Gymnophithys* and *Rhegmatorhina* and unlike *Phaenostictus*, *Phlegopsis*, and *Skutchia*, which tolerate the foraging mate within a centimeter or two. A preening female Lunulated Antbird gaped as a male alighted one meter off, supplanted him with beak open for a hiss and snap, then supplanted him again after jittering as ants attacked her on his perch. On another occasion, a female supplanted her mate, but then the two flicked their tails and pivoted about as they stood facing the same way about one body-width apart; he soon flew off. Although males and females preened together at times, they stayed a meter or more apart.

REPRODUCTIVE BEHAVIOR

Adult female Lunulated and Salvin's Antbirds generally had mates, except for one lone female *lunulata* at Putuimi. Female Bicolored Antbirds gain mates when about six months old, since there is a surplus of males (Willis 1967). There were some seemingly unmated male Lunulated Antbirds in Perú and Salvin's Antbirds in Brazil, suggesting a surplus of males in these two species.

Probably the pair bond is formed and main-

tained by courtship feeding, which is the pairing and precopulatory ritual in many genera of antbirds. Male Lunulated Antbirds carry food about, flick their partly spread tails, and repeat *ih'e'e'e'e'e*, *whEEP* and Chirps or Grunts as Serpentine-songs. The male eats the food himself if no female is present. If she is near, she looks up and flies to him. He flies to her and gives faint *cheu* notes over and over as he bends down. She Growls a few times and refuses his food or takes it. Usually the two are about one body-width apart for the feeding. He usually flutters away as she holds her head down and chews the food (fig. 3c). Once a female flew to the male, he hopped away from her repeatedly, and he fed her and champed the bill as she flew off with the prey. Another time there was much nibbling back and forth, perhaps removing fragments of prey from each other's bill, before the male flew off. Once a male held an insect until the female was 0.5 meter off; when he ate it, she supplanted him vigorously. Another female overbore her mate before taking the food from him; she flew and he stood, looked about, and then wiped his bill energetically.

Male Salvin's Antbirds feed their mates in much the same fashion. The Serpentine-song, with *wh-e-e-e*, *whEE* and *cheu* notes alternating, is often like that of Lunulated Antbirds. Once a male *salvini* gave a *whEEP whEEP whEEP chu-uc-uc-uc* Serpentine-song, more like the usual Faint-songs of the species. The male Chirps *cheu* as he feeds the female, and she Growls several times. In one feeding she flitted the wings and flicked the tail, pivoting often. Wing-flitting by males and females is so regular in courtship feeding in Bicolored Antbirds that I may have overlooked it in Salvin's and Lunulated Antbirds. However, these two species flit the wings at other times much more than do Bicolored Antbirds. Both male and female Salvin's Antbirds spread their tails at one feeding; they had just been feuding with another pair, and were probably mixing aggressive display with their courtship. Once a female supplanted her mate as he stood near her and Chirped after she ate his present. A male and female Salvin's Antbird exchanged a larva of a black ant back and forth three times before she ate it; repeated exchanges generally occur only in abnormal male-to-male feedings in Bicolored Antbirds.

Males lead their mates to swarms by Serpentine-singing. The female may tag along behind or alternate the lead with her mate. Early one morning at Putuimi a female Lunulated Antbird sang loudly when the male sang off northeast of the swarm; he quickly moved

in and joined her. Mated Bicolored Antbirds often call similarly, especially when the male first comes off the nest after incubating all morning. Once at Yarinacocha a male Lunulated Antbird Loud-sang at a swarm until his mate answered, then flew over and preened with her.

BREEDING SEASONS AND MOLTS

In Bicolored and other ant-following antbirds on Barro Colorado, breeding is restricted to the northern rainy season, May to November, when there are large numbers of arthropods in the leaf litter (Willis 1966a). By analogy, such southern ant-following antbirds as Lunulated and Salvin's Antbirds should nest in the southern rainy season, October to May. Near the equator, where both northern and southern rainy seasons spread rainfall over much of the year, breeding should be less restricted. Specimens of Lunulated and Salvin's Antbirds in various museums (AMNH, American Museum of Natural History; CM, Carnegie Museum at Pittsburgh; CMNH, Chicago Museum of Natural History; JM, Museo Nacional Javier Prado, Lima; LSMZ, Louisiana State University Museum of Zoology, Baton Rouge; MCZ, Museum of Comparative Zoology at Harvard; PANS, Philadelphia Academy of Natural Sciences; specimens examined courtesy of the curators of the Departments of Ornithology) add to my field notes on breeding seasons and molts.

There are few specimens or data to show breeding seasons for Lunulated Antbirds. Young out of the nest were common at Yarinacocha in late December and early January. Some young, nearly in adult plumage, probably came from nests started in late October. Both known male specimens (JP-1295, Pucallpa, 15 May 1953; LSMZ-42856, Yarinacocha, 9 April 1965) are molting from juvenal to adult plumage. One female (AMNH-239153, Lagarto, 24 March 1928) is molting from juvenal to adult plumage. Dates of nesting, approximately October to April, coincide with the southern rainy season. The other two specimens I have seen (LSMZ-42772, Yarinacocha, 2 April 1965; CMNH-185631, Yarinacocha, 29 May 1946) are adult females and not in wing molt. I have not seen the females from Sarayacu on the Ucayali or Yurimaguas on the Huallaga. The season of adult molt is unknown.

Young Salvin's Antbirds were following their parents at Caruarí in March and at Benjamín Constant in April. Thirty-four juveniles from various parts of the range span dates from 27 January (Hyutanaã, Río Purús, CM-87565)

to 14 October (Arimã, Río Purús, CM-93735), the latter bird very advanced in molt. According to these data, fledglings leave the nest from December to August, in the rainy season and first part of the dry season. Bicolored Antbirds, which start nests only in the rainy season, lose so many early nests to predators that young out of the nest are common only in the last months of the rainy season and first months of the dry season (Willis 1967). Most juvenile Salvin's Antbirds were collected in the dry season, May to August, but this is also true for adults; most collectors in this region have avoided the rainy season.

Molt in Salvin's Antbirds peaks in dry periods, September to the south and March to the north. Possibly the few molting southern adults taken in January are first-year birds, as otherwise records run from late July to November. To the south, molt alternates with the breeding season rather than peaking at its close or at its start. More data are needed from different southern regions, since local differences may be obscuring the seasonal pattern. In the related genus *Rhegmatorhina*, molt peaks at the start of breeding in two species living between the Madeira and Tapajoz, while two related species across these rivers are in molt about the end of the breeding season. To the north, along the Amazon, many Salvin's Antbirds taken in February to May were molting, and only a few were molting in August to October. Young are out of the nest during the main period of molt, but it may be that northern birds nest mainly in the wet periods before the start and center of the year and molt in drier periods in between.

The young male Salvin's Antbird is brown, with a wingbar formed by the buff tips and subterminal black bars of the greater coverts. The other coverts are faintly tipped with brownish-buff, forming indistinct wingbars. There are also whitish-buff tips and black subterminal bars on the brownish-black tertials and secondaries. The brown upper tail coverts have broad, black subterminal bands.

There are white bars on all the inner webs and slight white bars on the outer webs of the outermost tail feathers, much as in the adult male; however, the feathers are brownish at the edges rather than bluish as in the adult, and there are usually five or six white bars per feather rather than seven or eight as in the adult. Zimmer reported (1937) and marked on the label of one changing young male (AMNH-137108, Todos Santos, Bolivia) "left outer rectrix marked as in *G. lunulata*." This rectrix, the last battered one of the juvenal plumage, is indeed marked as in *lunulata* juveniles and adult females. However, the resemblance is normal and not a sign of hybridization; this is also true for the white-barred juvenal tail feathers I saw on changing male Lunulated Antbirds at Yarinacocha.

The young male Salvin's Antbird soon molts into a plumage like that of the adult. Blue feathers cover the belly as white feathers replace brown ones on the throat, leaving for a time a brown breast-band. The superciliary line becomes white, the face changes from brown to black, and finally the crown and back become blue. On the wings the marginal coverts are replaced first and the greater coverts last. As the front edges of the wings become blue, the brown-edged juvenal primaries are replaced by blue-edged adult feathers, starting with the innermost. As or before the primaries are replaced, the innermost and the outermost secondaries are changed. The last brown juvenal feathers are likely to be scattered ones on the scapulars, crown, rump, and breast-band. The last juvenal tail feathers are generally the outermost. The last juvenal wing feathers are the alulars, the outermost primaries, the centermost secondaries, and the outermost greater primary coverts. In general, the ventral feathers are replaced first, the dorsal ones next, and the wing and tail feathers last. However, there are some individual differences in sequence of molt among the 25 molting young males examined.

On specimen labels and in faunal lists, birds starting the juvenal molt are usually called "juveniles" and birds completing it "immatures." While one can justify changing the name as soon as the young bird passes the midpoint of molt, the term "immature" gives the impression that there is a distinctive first-year or immature plumage. Possibly the first plumage is paler, but these "immatures" and older males are so similar that I have not been able to discover an infallible way of telling them apart.

Young female Salvin's Antbirds are brown, with a reddish or cinnamon cast to the breast-band and feathers of the upperparts. The throat feathers and bases of the ventral feathers are dull bluish. The wing coverts are blackish, with buff edgings; the greater coverts have only small buff tips, in contrast to the prominent wingbar of the juvenal male. The tertials are much as in the adult female, but darker. The other remiges are also darker, but their paler-brown leading edges and tips contrast more than in the adult. The tail is a paler cinnamon than in the adult, and there are five or six black bands rather than seven or eight as in the adult. In specimens the bill of the young female is blacker than the bill of the adult female. In the nine young females examined, the sequence of molt is like that of young males. Molt is complete, so first-year females look like older females; there may be slight differences.

The young female Lunulated Antbird (AMNH-239153) has duller-brown feathers above and below than does the adult female. The young female lacks the white superciliary and bib, although the superciliary is a lighter brown than is the crown. The feathers of the underparts are dull brown, with white shaft streaks on the breast and very faint mottling (buffy tips, blackish subterminal bars) posteriorly. The tail is a darker brown than in the adult, and the bars on the inner webs are buffy rather than whitish. There are a few lunulated (buff-white tips, black subterminal bars) back feathers, but most fray so much at the tips that they seem brown; the upper tail coverts are strongly lunulated.

The two male specimens and the many young males

I saw at Yarinacocha showed a molt sequence like that in young Salvin's Antbirds. The young male *lunulata* looks much like the young female, being brown with pale gape angles, and has a brown tail barred or lunulated with five or six whitish bars. The gape is yellow in both sexes. In the young male the wing coverts and secondaries are edged or tipped with whitish, based by blackish subterminally; the edgings of the greater and median coverts form two more or less conspicuous wing bars. There are even more lunulated feathers on the back than in the young female. However, the best way to distinguish the young male from the young female in the field is the presence of new blue feathers of the adult plumage, appearing while the young male is still being fed by his parents.

Possibly the young male has a pale plumage his first year, especially at the whitish tips of the secondaries and tail feathers. One young male at Yarinacocha definitely had new blue feathers with blackish subterminal bands on his back, unlike the adult male. However, the two specimens and other young males at Yarinacocha did not have banding on the new back feathers.

BEHAVIOR OF YOUNG

Many of the pairs of Lunulated Antbirds at Yarinacocha had young out of the nest in late December 1965. Generally, there were two young per pair, the usual number among tropical antbirds. One parent feeds each young bird and ignores the other young, as is generally the case in related species.

The brown, poorly flying smaller young hide in vine tangles and other dark places behind or ahead of the swarm of ants. The parent Faint-sings and Chirps repeatedly as it flies back or ahead with food to its young bird every few minutes. It flicks the tail and looks about if the young does not emerge. The young bird peeps loudly, then gives a fainter *per-per-per-per-per* and other peeping notes as the parent comes into sight. It finally Squeaks loudly as the parent feeds it. The young bird gapes, crouches low on the perch, and flutters its wing tips before (fig. 9), during, and after the feeding.

When a parent encountered me near the young, it Chirred volubly even if it had been

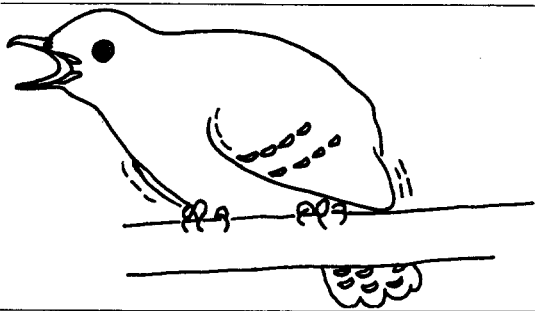


FIGURE 9. Begging young Lunulated Antbird, sketched at Yarinacocha.

ignoring me at the swarm a minute earlier. Often the parent led the young bird off to another tangle by giving a series of Faint-songs or Serpentine-singing. Parents soon became tame enough to feed young near me, however.

The dominance relationships of parent and young Lunulated Antbirds are very peculiar. Young that are feeding themselves all or part of the time and starting to molt into adult plumage dominate their own parents and most or all other Lunulated Antbirds at a swarm! One often sees a molting young bird move in on an adult male or female and supplant it without display. Older young, with white areas on the throat, consistently dominate browner and less-advanced young. In Bicolored Antbirds, dominance is a direct function of age unless a young bird gains a territory; young are supplanted by their own parents and by any other adults present, even low-ranking independent juveniles (Willis 1967). However, young Ocellated Antbirds (*Phaenostictus mcleannani*) scream and wing-wave to supplant their own parents, so that the Lunulated Antbird is not unique.

As in Ocellated Antbirds, young Lunulated Antbirds that have left their parents lose some of their privileges. In a few cases, independent young supplanted adults; but often these young were the lowest birds in the dominance hierarchies. Probably young Lunulated Antbirds with their parents on the territory are protected by the status of their parents, and then dominate their parents to become the highest-ranking birds at a swarm. However, when two families are present, one family tends to replace the other at the best site at a swarm, so the young birds of the other family are technically below adults and young of the first family. Still, I rarely saw an adult bird supplant a young one directly; generally parents feud and replace each other, and the young birds then follow their parents.

The high status of dependent young may explain why Lunulated Antbirds use challenging in an insubordinate manner so often, without violent reactions from dominant birds. The shift from young-dominance to adult-dominance as the young become independent may be conditioned by family relationships and locality, as in Ocellated Antbirds. A parent must be unwilling to attack its own offspring for some time after they are independent; the screaming challenges of the independent young are ignored, but the young has to flee eventually even if it once dominated its parent. In an area where a young bird formerly dominated it, a trespassing adult

may hesitate to attack even though the parents of the now-independent young are no longer present. Long-term studies of banded Lunulated Antbirds are needed. Since the privileged local status of offspring lasts several years in Ocellated Antbirds, there may be similar relationships among Lunulated Antbirds.

Once a young Salvin's Antbird supplanted an adult male, suggesting that young also dominate their parents in this species. On another occasion an adult male supplanted a fluttering young bird. A female twice supplanted a young female, which then fluttered the wings as the adult female dissected prey on the ground nearby. Possibly the adult birds in these two cases were not the parents, however. Peeping of young resembled the peeping of young Lunulated Antbirds, but I had little opportunity to watch young *salvini* and did not hear or see a feeding. I saw a male carry a spider toward a hidden young bird at Benjamín Constant on 17 April.

The prevalence of clearly aggressive challenging of the "nose-thumbing" type among subordinate Lunulated Antbirds had led me (Willis 1967) to question Tinbergen's suggestion (1959) that one can detect a conflict of "attack and escape drives" in a displaying bird by observing whether it flees or fights in a given situation. By this method, a display that is always followed by flight, like Challenging at a dominant bird, would be 100 per cent based on escape drive. This uncritically accepts the "militaristic" viewpoint on aggressive behavior: that aggressive behavior is forward acceleration in a competitive situation and submission is "appeasement" or rearward acceleration. The use of the term "appeasement behavior" by many ethologists to mean "submissive behavior" may well be an example of uncritical acceptance of the militaristic viewpoint.

Despite the militaristic viewpoint, aggressive behavior can lead to negative acceleration as quickly as to winning if the opponent is dominant; insubordinate Challenging leads to flight in both Lunulated and Bicolored Antbirds. To admit the possibility that one can lose by aggressive behavior, I prefer the "cybernetic" or "automotive" viewpoint of agonistic behavior: aggressive display, like the accelerator of a car, can send a bird backward or forward depending on the "gear" of the situation and hence leads to positive feedback; submissive display tends to give negative feedback, "braking" the competitive interaction whatever its gear. The gear of a situation is determined by outside factors,

which in Bicolored Antbirds include territoriality and the outcomes of previous interactions. I think this viewpoint, while it may still be too simple, leads closer to an understanding of the roles of aggressive and submissive behavior than does the overly simple and obviously incomplete militaristic viewpoint.

SUMMARY

Lunulated Antbirds (*Gymnopithys lunulata*) and Salvin's Antbirds (*Gymnopithys salvini*) persistently follow swarms of army ants and capture arthropods flushed by the ants low in the undergrowth of tropical forests from Ecuador and Perú east to the Río Madeira in Brazil and Bolivia. The two are mostly allopatric, and the large Río Ucayali in eastern Perú may separate their ranges. However, differences in songs and behavior suggest that they are separate species.

The most common foraging motion is sallying to the ground. In foraging, both species are very like other members of the genus *Gymnopithys* and related genera. However, Lunulated and Salvin's Antbirds are very inconspicuous when foraging. When larger species are present, the Lunulated or Salvin's Antbird hides behind cover or forages at the periphery of the ant swarm, above it, or in similarly poor sites. Both quickly become tame and forage near the observer. Their inconspicuousness, mobility, and tameness probably help them avoid supplantings by the many larger birds at swarms of ants in upper Amazonia.

In addition to Mobbing and Chirring at mammals, fear reactions include Freezing and Keening to uncertain or distant danger and Chipping and Panicking to nearby danger. The birds Jitter and peck-toss army ants that attack their toes. In all these respects, these birds are like other species of *Gymnopithys* and related genera.

Submissive behavior includes crouching, closing the tail, and uttering a faint whimpering call. The aggressive display is Challenging, as in related species of antbirds. Lunulated Antbirds Snarl vigorously as they jerk upright, extend the neck and puff out the white throat, spread the tail and raise it, and flap the head and outspread wings up and down energetically. In supplanting chases and Challenge-flights, musical Bugling calls are used. Salvin's Antbirds emphasize Bugling chases, and Snarling Challenges from a perch are not common. This antbird spreads the wings when it alights during supplanting chases, but the Snarling Challenges observed

were like low- or medium-intensity Challenging in *lunulata*: the bird jerks upright, spreads the tail and body and bright throat, and Snarls without waving the wings or head.

Adult females are generally paired. There was a surplus of adult males except in eastern Ecuador, where I saw only three Lunulated Antbirds. Males lead their mates to swarms by Serpentine-singing, or a bird at a swarm Loud-sings to its distant mate's songs and thus brings it in. As in related species, the pair bond is maintained by courtship feeding of the female.

Specimens and observations indicate that to the south these birds breed mainly in the southern rainy season, October to May, and molt mainly late in the southern dry season. To the north, where there are two rainy and two dry seasons each year, there is some evidence that the northern-hemisphere dry-wet cycle determines breeding and molt; but more data are needed.

Oddly, young Lunulated Antbirds supplant their parents. The data for Salvin's Antbirds are insufficient to determine whether they are like *lunulata* or like most related species, in which dominance is directly related to age unless territoriality intervenes. Possibly the frequent use of Challenging as a "nose-thumb-ing" gesture of insubordination in Lunulated Antbirds is related to a reversal of dominance after a young bird leaves its parents: independent young are tolerated, despite their Challenging, but are low in the peck order.

The prevalence of insubordinate Challenging suggests the inadequacy of the "militaristic" viewpoint of aggressive behavior. Instead, a "cybernetic" or "automotive" viewpoint seems better: aggressive behavior leads to positive feedback in a competitive situation, "accelerating" either flight or fight, depending on the "gear" of the situation; submissive behavior "brakes" the situation, or induces negative feedback, rather than being "appeasement."

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