ECOLOGY AND NESTING BEHAVIOR OF THE CHESTNUT-BACKED ANTBIRD (*MYRMECIZA EXSUL*)

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The Chestnut-backed Antbird (*Myrmeciza exsul*) is a dark-brown bird whose most striking characteristic is a patch of whitish-blue skin around each eye (fig. 1). The bare areas contrast in the male with blackish head and underparts (pictured in Austin 1961:200) and in the female with dark blackish-brown on the head. The normally concealed bends of the wing are white. (One captured bird also had one outer primary white. A specimen in the American Museum from Sucubtí, Darien, Panamá, has many white feathers on the crown, face, and back.) For three live birds, weights were 26.1–30.0 g (mean, 27.4 g) and cloacal temperatures, 41.5–42.3°C (mean, 41.9°); one bird had a bill (culmen) 21 mm long. The culmens of 116 adult Panamanian specimens in several museums range from 18.8 to 24.4 mm and average 21.4 mm.

Chestnut-backed Antbirds live near the ground in lowland tropical forests from eastern Nicaragua to the middle Magdalena Valley in Colombia, southward along the Pacific coast to Prov. del Oro in western Ecuador (Meyer de Schauensee 1966). As Slud (1960, 1964) and Skutch (1969) note, they usually occur alone or in pairs, and occasionally join wandering interspecific flocks of ant-following birds. When watched or disturbed even slightly, they "pound" their tails, beating them suddenly downward from as much as 30° above to some 50° below the horizontal.

We studied Chestnut-backed Antbirds, mainly on Barro Colorado Island, Panamá Canal Zone, during the years 1960 to 1971. Willis observed others at various other places in the Panamá Canal Zone from 1960 to 1971, at Golfito, Costa Rica (8° 38′ N, 83° 10′ W), in 1961, and at several places in Colombia from San Pedro (8°27′N, 76°18′W) to Remedios (7° 02′ N, 74° 41′ W) and El Tigre (4° 57′ N, 76° 30′ W) in 1962 and 1965. The Colombian birds (*M. e. cassini* and *M. e. maculifer*) have white spots on the wing coverts and the birds from western Costa Rica (*M. e. occidentalis*) have brighter colors, and hence were formerly considered separate species. They did not seem to differ from birds of the Canal Zone in voice and behavior.

HABITAT

Skutch (1969) found Chestnut-backed Antbirds mainly in wooded dells rather than on drier ridges at their upper altitudinal limit (about 1000 m elevation) in Costa Rica, and there is a tendency for them to avoid the heights of ridges, even on Barro Colorado. However, they are not such confirmed inhabitants of small valleys or very wet forests as are Dull-mantled Antbirds (*Myrmeciza laemosticta*). The latter tend to take over from them in very wet forests from Costa Rica to Ecuador, especially in ravines and on steep slopes where there are landslides. Chestnut-backed Antbirds extend into tropical dry forest in northwestern Costa Rica (Slud 1964), and into tropical rain forest at El Tigre in Colombia, but center in the tropical moist and wet forests of Holdridge's (1947) classification.

They usually live in fairly mature forest or at its edges, but persist in tall second growth or in small patches of forest on tiny Orchid Island near Barro Colorado, at El Recreo in Nicaragua (Howell 1957), and in pastures at Caucasia (8° 00′ N, 75° 13′ W) in Colombia. We have not found them singing in the extensive areas of low second growth favored by White-bellied Antbirds (*Myrmeciza longipes*), but they sometimes move through such areas to forest areas. They may move occasionally over narrow open areas like pastures and water courses unless such small populations as those at Caucasia and on Orchid Island are self-sustaining. We have not seen them in the laboratory clearing on Barro Colorado Island, however. We found them uncommon in the Madden Forest Reserve (9° 06′ N, 79° 37′ W) in the Panama Canal Zone, where an immature forest has few treefalls and where rainfall is lower than on Barro Colorado Island.

The Chestnut-backed Antbird is usually in dense places in the forest undergrowth. It

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FIGURE 1. Foraging male Chestnut-backed Antbird (from Ektachrome slide, Barro Colorado Island, 1961).

favors tangled fallen trees and branches, especially rotting older treefalls where dense young saplings are beginning to crowd upward for light. After a windstorm felled many trees on Barro Colorado on 1 October 1961, Chestnut-backed Antbirds increased in abundance at swarms of army ants until 1966 and then declined almost to earlier levels by 1970 as saplings grew upward and opened around the rotting trees. Probably the total population increased to 1966 and then decreased, as a result of the habitat changes. However, they also frequent dense patches of wild pineapples (*Ananas magdalenae*), and wander widely in the open undergrowth near dense cover, especially where twisted lianas mark the sites of vanished fallen trees. Treefalls and wild pineapples are so frequent on Barro Colorado that there is suitable habitat even in areas of old forest. On Barro Colorado they seem to be absent in some flat areas of relatively young forest, such as the area west of the tower at the center of the island, and in some areas of very tall forest without treefalls, but otherwise they are fairly evenly distributed.

FORAGING

The large, dark eyes and dark plumage of this antbird seem well suited for its foraging, which usually occurs in dim light near the ground in heavy or dense cover. At times, a Chestnut-backed Antbird will follow a swarm of army ants into open woods, or will move with a bird flock into the dense tops of *Coussarea impetiolaris* saplings at 3 or 4 m above the ground, but more often it hops or bounds from one low perch to another in low, rather dense cover.

We observed foraging mainly on the infrequent occasions when a Chestnut-backed Antbird followed a swarm of army ants, but its foraging methods there seldom differed greatly from those of birds we and others (Skutch 1969; Slud 1964) have observed away from ants. From low perches, it peers carefully at overhanging vegetation or debris and at the ground. Occasionally it stretches the limber neck far up to peer over some obstruction. On long, low flights, it flutters between patches of vegetation, or hurriedly bounds and flutters from one low perch to another to reach new areas. Undisturbed birds carry the closed tail somewhat down, and rarely pound it.

TABLE 1. Characteristics of Chestnut-backed Antbird perches over swarms of ants.

Height		Angle		Diameter	
cm	*n*	°	*n*	cm	*n*
0[a]	52	20	15	1	40
1	66	40	7	2	34
2	76	60	2	3	22
3	48	80	3	4	15
4	37	100	17	5	5
5	25	120	1	6–25	4
6	11				
7	10				
8	6				
9	6				
10	4				
20	23				
30	2				
40	1				

[a] 0 = ground.

Chestnut-backed Antbirds ordinarily wander around a swarm rather than stay and forage over it. They also tend to work swarms near treefalls and wild pineapple thickets. Words we often used for their behavior at swarms of ants included "wanders" (172 records), "treefall" (148), "ahead" (116) or "left" (100) or "right" (102) of the ants, "*Ananas*" (71), "behind" the ants (73) or over the rear ("fan") of the swarm (61), "fallen lianas" (58), "thickets" (62) or "palmetto" (34). Records for "peripheral" to ants (28) outnumber records of swarm "center" (16). "Log" (18), "roots" (9), "palm clump" (12), and "ferns" (15), outnumber records of "open woods" (15) and "open near treefalls" (17), but the last two phrases indicate some use of uncluttered places. "Gully" or "ravine" (22) are other common words.

Foraging heights near ants are mostly low (table 1), and there is some hopping on the ground or on fallen twigs on the ground. Often the bird bounds from one root or fallen liana to another, avoiding stepping on the ground. The perches taken are horizontal, vertical, or inclined—thick, strong legs allow Chestnut-backed Antbirds to cling to vertical perches in

a way that the slender-legged White-bellied Antbirds (*Myrmeciza longipes*) seldom do. Many perches are slender, but Chestnut-backed Antbirds often use the ground, a perch of "large diameter."

At swarms of ants, much prey is captured on or near the ground. Of 71 records of height of capture, 49 were between the ground and 0.1 m up, 5 were between 1.0 and 2.0 m up, and 3, 4, 3, 2, 2, 0, 2, 1, 0 captures were recorded for each 10 cm interval from 0.1–0.2 to 0.9–1.0 m, respectively. Away from swarms they do not capture such a large proportion of their prey on the ground. Most prey-catching attempts (71 of 108) at swarms were made between 08:00 and 10:00, few (3) after 16:00. Of 37 attempts for which sex of bird was recorded, 31 were by males, perhaps because males hide from the observer less persistently than do females.

In contrast to other ant-following antbirds (Willis 1967, 1972), Chestnut-backed Antbirds peck most of their prey rather than sally or dart for it. We have 67 records of pecking or stretching the neck to snap at prey and only 34 records of aerial or semi-flying captures. Of the latter, 23 are "groundcatches" in which the bird darts at the ground, grabs prey, and leaps back up in one V-shaped movement. On 20 occasions the antbird merely pecked at the ground from a perch, and on four occasions one tossed leaves after seeing an arthropod run under them. Most captures above the ground were by pecking leaves (16), lianas (7), debris (2), or in the air (1). A few were clumsy, fluttering sallies to leaves (4), liana (1), or into the air (1), and none of the sallies was more than 0.7 m long.

The few prey items recorded at ant swarms were all orthopterans, including crickets, grasshoppers, and a walking-stick. One cricket was dissected in the style of Bicolored Antbirds (Willis 1967), by chewing and by holding one leg at a time in the bill as the bird shook its head until the insect body fell off. Away from ants, one hopped upward and snapped a spider off a web, and another got a spider ⅔ the length of the visible part of the bill (1B or visible bill length = 17.5 mm). Most prey was under 2B in length.

We recorded Chestnut-backed Antbirds at 306 swarms of ants between 1960 and 1971, but they are not regular or frequent ant-followers. Quite often they wander past an active swarm and ant-following birds as if uninterested. They seldom work swarms if no regular ant-following birds are active, but large numbers of ant-following birds also discourage them from staying long. They often wander away from ants and return briefly later, working the swarm at irregular intervals.

Bicolored and Ocellated Antbirds (*Gymnopithys bicolor*, *Phaenostictus mcleannani*) supplant Chestnut-backed Antbirds, or chase them from their perches, when they come near the centers of active swarms of ants (22 and 7 times, respectively). They moved away as ocellateds moved nearby ("displacings") 8 times, and evaded bicolors 6 times. Twice Chestnut-backed Antbirds supplanted Bicolored Antbirds (once a young bicolor was involved, and once a bicolor came near a chestnut-back's nest).

Chestnut-backed Antbirds seem to have a special antagonism toward the small Spotted Antbird (*Hylophylax naevioides*), and flew as far as 5–10 m out of their way to supplant it vigorously (Willis 1972). We recorded 46 supplantings and 10 displacings at swarms of ants between 1960 and 1971, and many others away from ants. At times the Chestnut-backed Antbird is so excited it spreads and pounds its tail, fluffs out its body, and spreads its white wrists. If it can get close enough to snap at its small rival, it gives a brief *chiangh*! snarl.

WANDERING FLOCKS

Chestnut-backed Antbirds readily join and forage around wandering interspecific flocks of birds, but are not regular members of the flocks. Their tendencies to wander irregularly and to stay near dense undergrowth often interfere with any tendencies they have to follow these flocks, which on Barro Colorado center around White-flanked and other antwrens (Johnson, 1954). However, these antbirds readily join and move with the flocks when the latter stay in or near dense undergrowth. At times one or more antbirds move through open undergrowth with the flock, fleeing to dense cover when an observer appears but returning when the flock calms down. Perhaps these antbirds use the flock as an antipredatory substitute for dense cover, and can thus forage in places that would otherwise be unsafe. However, their protective coloration and rather inconspicuous foraging may make it safe for them to move away from flocks, especially when cover is nearby.

VOICE AND DISPLAYS

The song of Chestnut-backed Antbirds is a brief series of two or three full, mellow whistles (Slud 1964; Skutch 1969), the last note lower than the first one or two: "fee, few!"

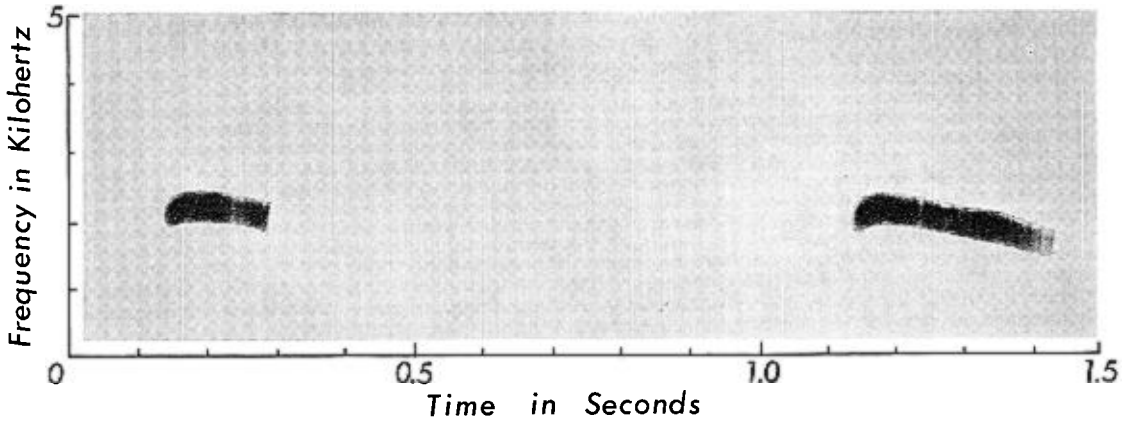

FIGURE 2. Sonogram of song of Chestnut-backed Antbird, recorded on Barro Colorado in 1961.

(fig. 2) or "fee, feh, few." Chapman (1929: 184) paraphrased the song as "come here" or "come-right-here." We have found it easy to attract the bird by whistling this song, as did Chapman. The song is given as many as 15 times a minute (average, 7.6 for regular singing) as the bird wanders and forages, and is one of the characteristic sounds of the forest at all hours of day. Songs are regular during and after disputes with distant neighbors, or when a pair are separated, but when members of the pair are foraging together they sing infrequently. Dark periods after rains and in the early morning are especially songful. Singing declines somewhat in September, perhaps for molt, and again from November to March in the nonbreeding season. Occasional rains in the dry season (January to April) bring out songs briefly, and the start of the rainy season in late April and May brings out regular songs. As Chapman notes, the song of the female is sometimes like that of the male, but is more often weaker or at a slightly higher pitch. Often there are faint introductory whistles before the main song, especially when the whole song is given faintly.

The singing bird often stands rather upright, with tail somewhat down (fig. 3a). Each note is emphasized by a slight upbeat of the tail, rarely by the downbeat or "pounding" noted in other situations. The tail may be slightly spread and the corners of the wing out, showing white patches that are normally concealed.

The usual note at a passing human is what Skutch (1969:237) has described as "a harsh, grating, nasal *waaa* or *aaaa*." As he notes, a mated pair may give this note ("Rasping") back and forth, and a bird going to the nest often gives it from every perch along the way. Rasping, when regular, is given about every 3 sec, or 20 notes per minute, but there are often longer intervals.

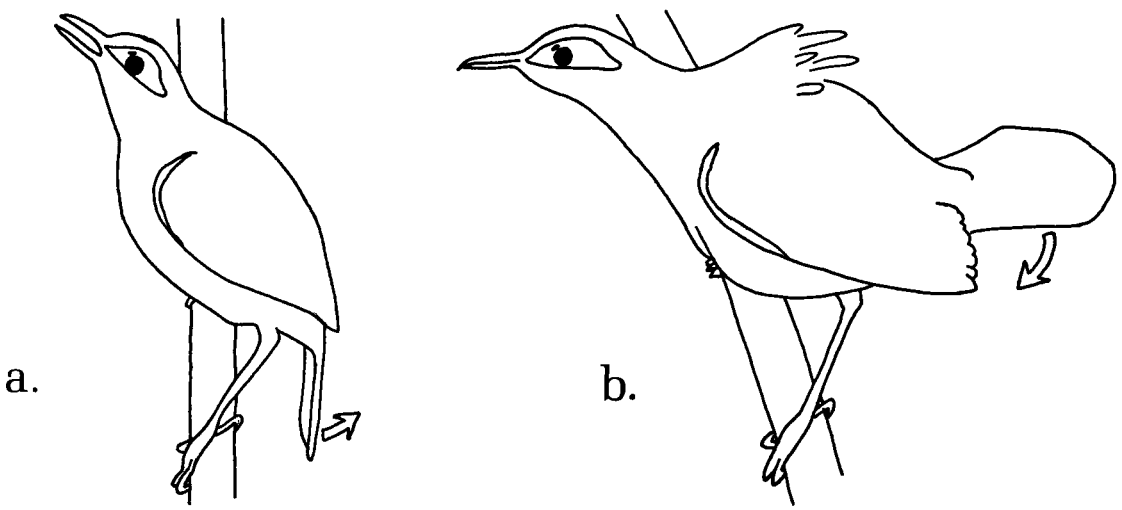

FIGURE 3. Male Chestnut-backed Antbird singing (a) and displaying aggressively (b); from field sketches.

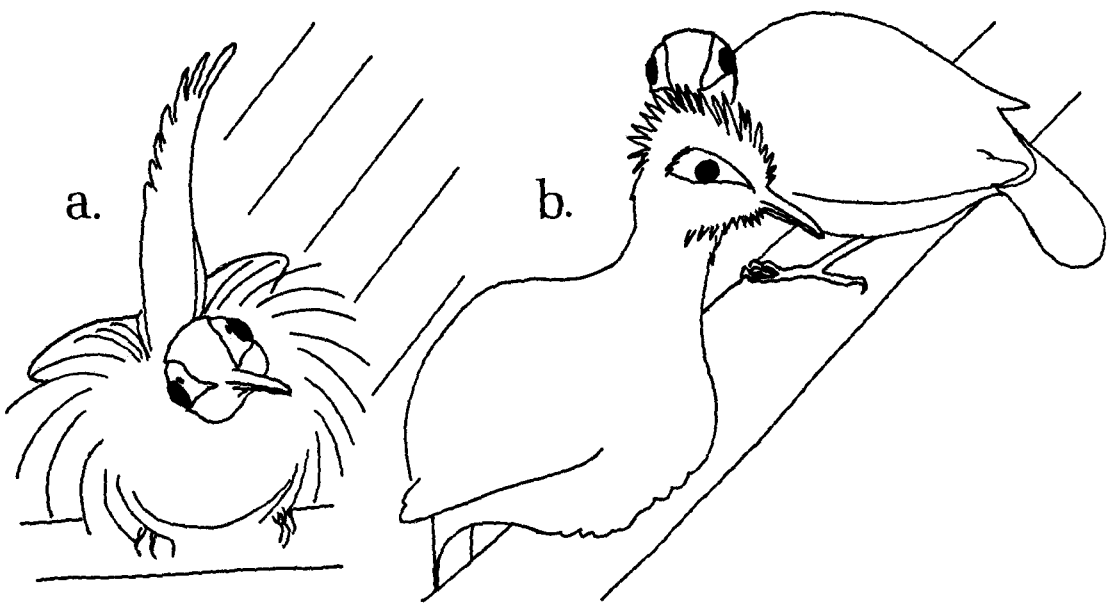

FIGURE 4. Sunning (a) and mutual grooming (b) of Chestnut-backed Antbirds; from field sketches.

A note of stronger alarm is a rapid Rattle, *di'i'i'i'i'i'i*, as given when a bird is flushed out of a patch of dense cover. When a bird is flushed off a nest, is supplanted unexpectedly by a large bird over ants, is fleeing to cover, or is similarly alarmed, the rattle may be given, or Chipping, a sharp *quit-it*. The latter is sometimes repeated rapidly, and then grades into a *wittit wittit wittit wittit*, such as Skutch (1969:237) recorded at nests.

Mates foraging near each other often give faint, musical Chirps, *cheup*, and faint glissando Warbles, *ch'woh-i-yo*. Chirps and Warbles often alternate as a Serpentine-song when one has food for a mate or young. *Chwear* and and other faint notes perhaps deserve naming, but here will be called Chirps. A series of *chaah* (rough, faint) Growls occurred when a mated pair came together.

A Chestnut-backed Antbird supplanting a Spotted Antbird or another of its own species gives a Grunt, a snarling and nasal *chiangh* noise, at the moment it chases the small or subordinate rival off its perch. Snapping the bill was a nonvocal sound at such times.

Young out of the nest beg with nasal, grating *chraihh chaihh chaihh* series of Squeaking. Young in the nest give Peeping notes. "Screaming" is a series of rough noises given by a bird in the hand.

PREENING AND MAINTENANCE BEHAVIOR

Chestnut-backed Antbirds usually preen and rest in dense tangles or near cover. The head is scratched over the wing. Mutual grooming is frequent (see "reproductive behavior" below). Chestnut-backed Antbirds "sun" in rather extreme ways by fluffing up the whole body and extending the under side of the wing up while staying frozen a minute or so in a bright beam of sunlight (fig. 4a). Perhaps they dry their plumage or kill mites and feather-lice by sunning.

ALARM BEHAVIOR

Slightly alarmed Chestnut-backed Antbirds, as ones in open woods, flit the wings and pound the tail as they look about nervously. Coatimundis (*Nasua narica*) caused one female to flee silently, tail-pounding. Alarmed birds quickly flee for palm clumps, into treefalls, or behind other dense cover. Sharp Chipping notes may accompany the flight; once in cover, Chipping becomes Rattling and finally Rasping. The bird pounds its spread tail as if fanning the ground, raises the sleeked head, hops about or swings like a gate around perches as if displaying the bright blue and exposed face as an eyespot design (Willis 1969). Minor alarm, as from our passing a bird safe in cover or a distant bird with young, results in tail-pounding and Rasping. Slightly greater alarm, as from a parent near young or when one is flushed through dense cover, brings out Rattling and pounding the spread tail. Once an agouti (*Dasyprocta punctata*) running past a bird caused Rattling. The white forward edge of the wing sometimes shows when a bird with young is approached, but this may ex-

press agonism rather than alarm. Strong distraction displays at the nest and near young out of the nest are described below.

In the hand, a Chestnut-backed Antbird sometimes ruffs up the crown until it is almost like fur; the blue bare area around the eyes is rendered doubly conspicuous. The blue skin of the crown and throat can be seen when feathers of those regions are ruffled. It is interesting that both sleeking and ruffling the head feathers expose the blue facial areas (sleeking by pulling the tips of feathers toward the center of the crown, and ruffling by exposing the areas around the feather bases). Kicking and rough Screaming also occur in the hand.

AGONISTIC BEHAVIOR AND TERRITORIALITY

Whistling imitations of Songs brings a singing male Chestnut-backed Antbird up rapidly. He hops up to a low perch with tail spread so that it is arched, and pounds both it and the rear end of the body vigorously from 40–60° above the horizontal to 40° below the horizontal. His wrists flash in and out, exposing the white forward edges of both wings. The body is rather expanded, and the back conspicuously fluffed. The head, by contrast, is rather sleeked and the bright blue areas around the eyes more exposed than usual (fig. 3b). He sings loudly and gives chipping notes as he circles the imitator, keeping near or in cover. The female may also appear, sing and display more weakly; she usually stays even deeper in cover.

Pairs hold territories all year and sing back and forth to other pairs at a distance from territorial boundaries for long periods each day, especially in the nesting season. However, boundary encounters involving both singing and displays seem to be uncommon, for we have seen very few disputes. More often birds moved separately through dense vegetation singing, Chirping, and Chipping for several minutes. They seldom approached each other closely.

Behavior seen at boundary encounters or in chases of wandering immature birds was like responses to whistled imitations, and included pounding the spread tail, wrist-flashing, and spreading the back feathers (fig. 3b). At swarms of ants there were occasional supplantings with Snapping and Grunting, perhaps of wandering first-year birds. Recorded supplanting of Spotted Antbirds alone far outnumber recorded intraspecific supplantings.

Supplantings by large species of antbirds caused sharp Chips and flight to cover, or, in some cases, pounding the tail vigorously with Chirps. The pounding and Chirping may be submission or insubordination, but the flight and Chipping was probably alarm.

Banded birds held territories year after year. Two adult males, banded with their offspring in 1966, were still on their respective territories in 1970 (fig. 5 shows the territory of one of these males). A female and a male, banded in adjacent territories in 1965, were still on those territories in 1966. The territory of Male "OO" was about 225 × 150 m, and at least 2.5 ha (6.4 acres) in extent. Other birds seemed to have similarly sized territories. We estimate that, allowing for unoccupied areas, there are 30 pairs per square kilometer, or 450 pairs on Barro Colorado Island. Granted a few wandering immature birds as late as April, before the first young leave, there should be some 65 birds per square kilometer, or 18 g/ha, at this low point of the annual cycle. The biomass is thus higher than for ant-following antbirds, such as for Spotted Antbirds at 8 g/ha (Willis 1972) and Bicolored Antbirds at under 3 g/ha (Willis 1967).

REPRODUCTIVE BEHAVIOR

Pairs wander together in or near their territories all year. They sing back and forth in every month of the year, especially when separated from each other. At times a singing bird calls its mate to a swarm of ants from as far away as 100 m. When Male OO lost his mate in 1969 he sang repeatedly throughout his territory. When mated birds forage near each other there are often Chirps, Warbles, and other faint notes, including once (when Willis brought up a pair of aggressive birds by imitating songs) a series of rough, faint Growls.

As in several other kinds of antbirds, courtship feeding is the main courtship behavior pattern. The male with food for the female gives a series of Chirps and Warbles, a series we have called "Serpentine-songs" in other antbirds. The Chirps run into faint songs, each song with repeated first notes on a rising scale—*fer, fer, fer, fer, FEW*!—if the female does not answer. Loud songs are sometimes needed if she is distant. Finally she sings or Chirps and the male resumes Chirps and Warbles as he moves her way or she flies to him. One female Chirped as she watched her mate dissect a cricket, but he left with it. Chirping notes come from both birds as a male hops up and feeds his mate. One male, 25 June 1967, watched his mate a second or two and hopped onto her back, but she fluttered away with the

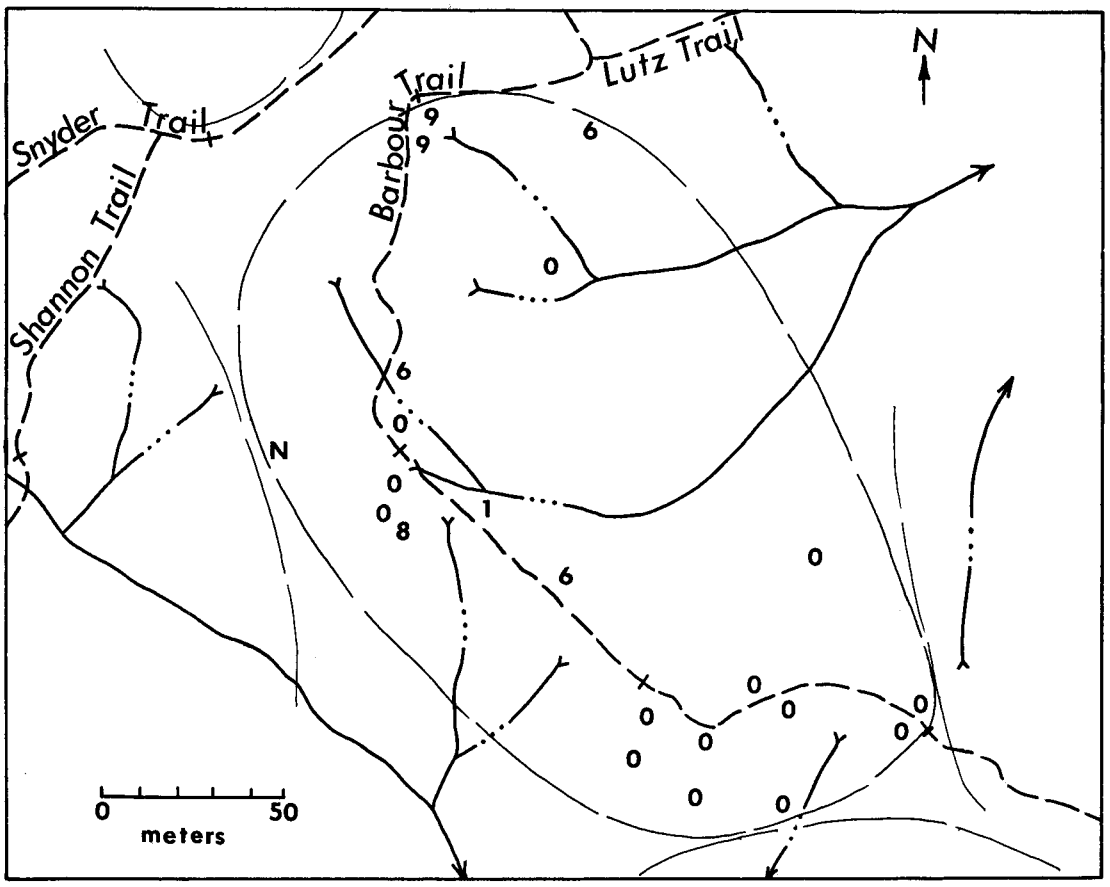

FIGURE 5. Territory of banded male "OO" and his mates, 1966–1971 (6 = 1966, 8 = 1968, 9 = 1969, 0 = 1970, 1 = 1971). Marks on trails represent signposts 100 m apart. The edges of territories of neighboring pairs in 1970 are marked approximately. "N" marks the location of the Barbour nest in 1969.

food. This pair had a grown young female with them. Probably, as is the case in Bicolored and Spotted and Ocellated Antbirds, copulation occurs after a few of the many courtship feedings during the few days before eggs are laid. Presumably the pair bond is cemented originally by courtship feeding, as in those other antbirds.

Mutual grooming is also regular between mated Chestnut-backed Antbirds. Our observations agree with those of Skutch (1969:236): the groomed bird stays immobile as if frozen, neck extended but the head pointing downward as the feathers are fluffed. As Skutch notes, the blue skin of neck and head shows through and gives the small bird a vulturine appearance. The grooming bird hops up and peers at the head, then pecks at the base of the beak and elsewhere on the head (fig. 4b). At times the two groom back and forth, alternately taking different poses. On other occasions the groomer merely examines the neck and head of its mate carefully without pecking. After grooming, there is often more preening, or the pair separate.

Grooming occurred not only during periods of resting near ant swarms, but near one nest we noted it between incubation periods. There was always the same sequence: the incubating bird left the nest and groomed the arriving mate; then the latter groomed the other. The grooming periods grew longer (from 15 to 30, 50, 90, and 150 sec) as incubation progressed. The female pecked the male 29 times during the last period.

NESTS AND EGGS

Carriker (1910:616–617), A. O. Gross (in Eisenmann 1952:35), and Skutch (1969:238–243) report on nine nests of Chestnut-backed Antbirds. We found 12 nests on Barro Colorado Island between 1961 and 1969, and Oniki watched incubation at one (the "Barbour nest") on the Barbour Trail there in 1969.

The bulky and cup-shaped nest sits loosely on short plants, dead palm leaves, or debris

FIGURE 6. The Barbour nest, on a spiny fallen frond of a black palm (*Astrocaryum standleyanum*).

near the ground. One nest, on a dead palm leaf, was knocked over once by Willis and once by unknown causes. Heights of eight nests varied from about 0.1 to 0.4 m and averaged 0.24 m. Most nests discovered have been in somewhat open but dark undergrowth near logs, treefalls, or other dense cover; none has been in dense cover. One, a neat cup of strands rather than the usual mass of leaves, was in ferns on a rock in a gully.

Most nests are made of dead leaves and strands, with a thin lining of rhizomorphs. The Barbour nest (fig. 6) measured 12.5 cm in external diameter, 6.8 × 6.0 cm in internal diameter, 10 cm in external height, and was 5.3 cm deep. Nests for the western subspecies measured by Skutch (1969:238–9) were similar in size, but internal diameters were somewhat greater. The Barbour nest had a thin lining of 43 rhizomorphs, 16 yellowish rootlets with green bark, 8 long and dark-brown rootlets, and 4 fragments of palmleaf rachises. Outside this, a soft interwoven layer of 25 to 30 fragments of dead leaves, 45 to 50 dead fragments of palm leaflets, and a few small twigs gave the nest a bulky, irregular appearance. The outer, binding part of the nest included 9 small twigs interwoven with 22 rhizomorphs (5 were thick and branching and 5 were branching with hook-like projections) and 16 moss fragments (7 *Meteriopsis patula*, 9 *Orthostichopsis tetragona*).

Two of Skutch's nests and one of ours had one egg each; one of our nests had a large young bird. Eggs in Skutch's nests (in the same area a year apart) were about to hatch; probably they were complete clutches. Our records may have been of an incomplete clutch and of a nest in which one egg did not hatch and was removed. Two of Skutch's nests, both of Carriker's nests, and 10 of our nests had two eggs or young; this is the normal clutch in antbirds. Eggs are light pinkish-white, heavily scrawled and splotched all over with reddish-brown or rufous-purple, concentrated at the large end. The small end of the egg has only a few reddish lines and small spots. Eggs in the Barbour nest weighed 3.2 g on July 19 but decreased to 2.7 g just before hatching on August 1. These eggs measured 22 × 16.5 and 22 × 16.0 mm; eggs in another nest were 24 × 18 and 24 × 17.5 mm. Carriker (1910) reported measurements of 22 × 17.5 and 22.5 × 17 mm for eggs in Costa Rica. Skutch (1969:239) reports similar measurements and colors for eggs in western Costa Rica.

INCUBATION

Oniki watched incubation at the Barbour nest from 20 July to 1 August. Both male and female have incubation patches and incubate. As Skutch (1969:239–40) noted for a pair in Costa Rica, the approaching bird usually gave Rasping notes. Usually it stopped calling about 10 m away and moved quietly to the ground under the nest, where it pounded the tail and looked about. Then it hopped up to the nest edge, pounding the closed or half-open tail, turned the eggs with its bill, looked about the nest and its surroundings, and settled on the eggs. The mate, when on the nest, often hopped off when the other came under the nest. Occasionally one or both birds gave a few notes or there was mutual grooming before the new bird went to the nest edge.

When incubating, the bird stayed low in the nest. Infrequently it raised the head to look about or to peck at the inner wall of the nest. Before leaving, it usually raised its head, yawned, and champed the beak several times. The crown feathers were often slightly fluffed. Gradually it turned the head to look about carefully, then perched on the nest rim for several seconds before leaving. Often the departing bird gave Rasping, then sang loudly, at a distance from the nest.

When there was heavy rain, the partner off the nest returned as the rain slowed down. At such times the two changed places rapidly, without looking about carefully or even poking at the eggs.

The incubation routine at the Barbour nest is shown in figure 7. The female usually came on the nest very late in the evening and presumably left early the next morning, as Skutch (1969:240) noted in Costa Rica. Sessions during the day were often long, up to 217 min for the female and to over 236 min for the male,

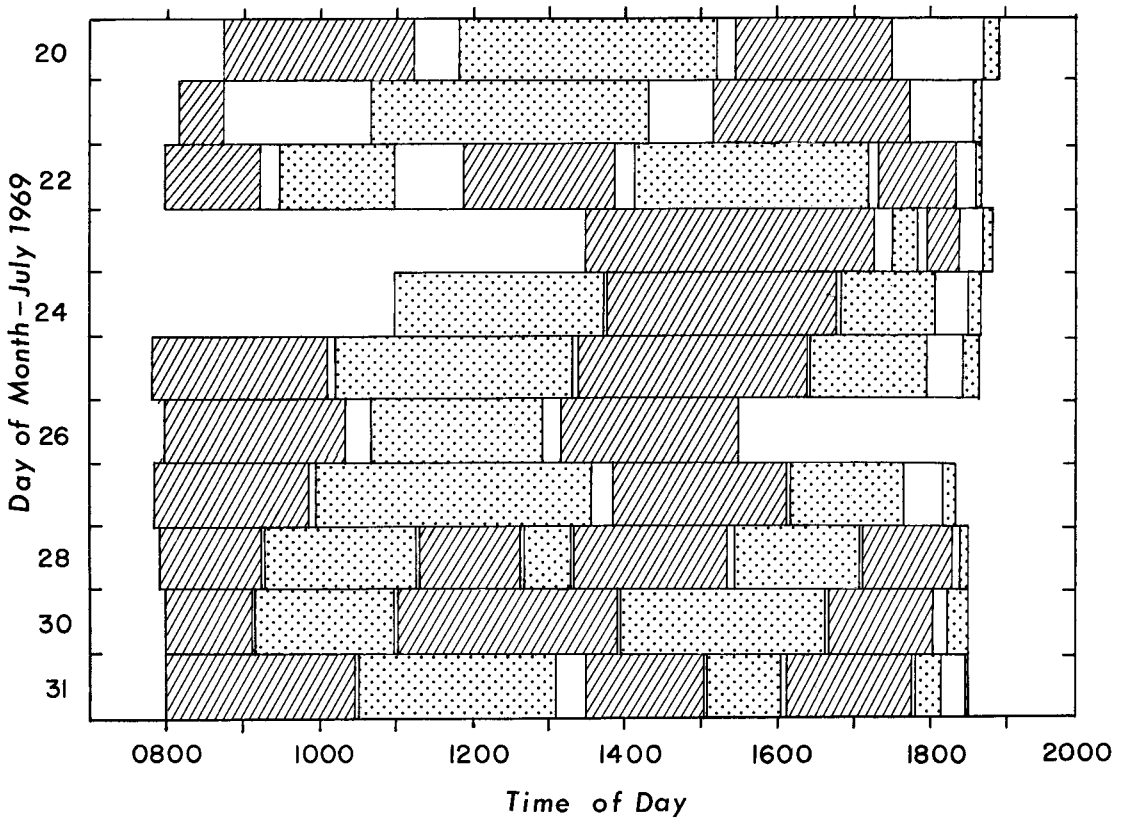

FIGURE 7. Incubation at the Barbour nest. Incubation by male, lined; incubation by female, dotted; blank areas in enclosed area, recesses.

and averaged 119 min for her ($n = 19$) and 113 min for him ($n = 15$). Recesses, or periods off the nest, ranged from 1 to 117 min and averaged 16.5 min ($n = 45$). The female incubated for 40 per cent of the daylight hours and the male, 48 per cent of the daylight hours. They were off the nest 12 per cent of the time. During the last eight days before hatching they were off the nest only 7 per cent of the time. Late in incubation, one bird relieved the other more often than the latter left the nest by itself.

Incubating birds sit still when an observer approaches, and only hop off the nest silently when one is about to touch the nest. They often flutter away over the ground with loud Rattling, giving weak distraction displays.

The incubation period is unknown, but was at least 14 days (19 July-August 2) at the Barbour nest.

CARE OF THE NESTLINGS

On 1 August 1969, the first egg in the Barbour nest was pipped at 08:12 and hatched by 09:03. Egg no. 2 was pipped in the middle of the large end at 09:03, but did not hatch until the next night, or by 07:50 on 2 August. The male (banded "OO") left silently at 08:12 on 1 August, returned at 08:21 with a small piece of insect, and tried to feed the unhatched egg. After a few trials, he ate the food, turned the eggs, and sat again until 09:02. At 09:03 the female came, examined the nest, and flew with an eggshell in the beak. She returned at 09:11 and sat after she examined the nest and its contents.

The male first fed the young at 09:48, a dark insect abdomen about 1 cm long. The female first fed the young at 13:44. She fed it two or three other times, and the male fed it four times during the afternoon. One or the other parent brooded 84 per cent of the time after the young hatched. The next day the female called Rasping notes near the nest much of the day, but did not go to it. The male brooded 08:18–10:59, fed the young five times from 11:03 to 11:51, brooded until 14:18, fed young five times from 14:25 to 15:19, then fed them only three more times the rest of the afternoon. Probably he was foraging for himself after the demanding first part of the day.

The female went on the nest at 18:34. The

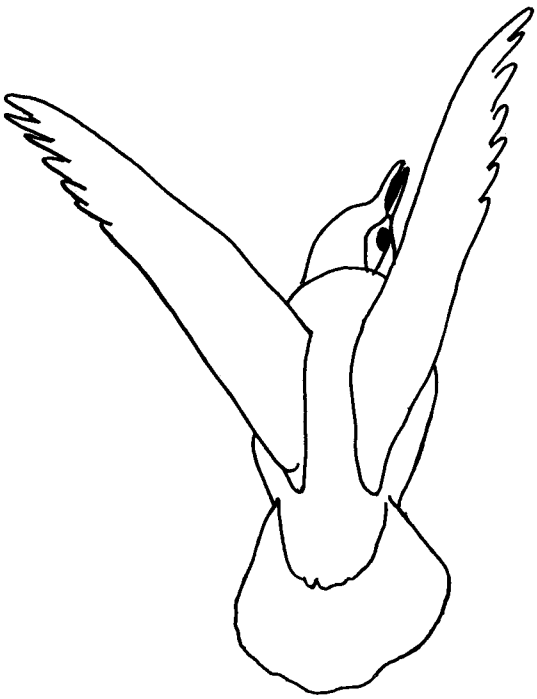

FIGURE 8. V-winged distraction display as female Chestnut-backed Antbird hopped away from a nest and young; from field sketches.

next morning at 08:10 the nest was torn out and on the ground, the young gone. Many body feathers of the female around the nest suggested that she had been killed. The male sang repeatedly in the nest area and to the east. Five days later he had a new female with him, a bird with faint calls that perhaps was a young female hatched that year.

Skutch (1969:240–243), in describing his observations at nests in Costa Rica, reports that the male fed and brooded the young at these nests more than did the female. Brooding decreased by the sixth day and there was none on the eighth day at one nest. Young were fed moths, orthopterans, and other invertebrates, as well as one small green lizard. Fecal sacs were usually carried away, occasionally eaten. A young bird left one of the four nests when 9 or perhaps 10 days old; the other nests were torn out and emptied by predators. He describes strong distraction displays toward agoutis, which probably robbed one nest.

Distraction displays we observed were quite like ones Skutch observed: the parent flushed off young hop-flutters away over the ground, often with tail spread and dragging and spread wings upraised (fig. 8), and starts loud Rattling or Chipping as it flees or as soon as it reaches cover. Skutch noted that, when such a hop-flutter failed to distract two agoutis, the male returned several times and fluttered away as if injured in front of the agoutis. Calls of that male included loud Rattling and a few Rasping notes.

Nests are rarely successful, despite the vigor of parental displays. One of six of our checked nests apparently produced fledged young, but since many of these nests were found with young, the true mortality rate must be even higher. Usually the nest is not damaged, suggesting that snakes or other careful predators may be the robbers rather than mammals.

At one of our nests, a male attacked nearby Bicolored and Spotted Antibrds at an army ant raid. He then hopped around pounding his spread tail, his head sleeked, body fluffed, and wrists out (fig. 2b). He Chipped loudly, then Rasped at the observer.

The newly hatched young are naked and blind; the viscera are visible through blackish-pink skin. They move awkwardly and seem unable to hold their heads up. Just after hatching at the Barbour nest, one young weighed 2.35 g and gave a short, weak *tchiou* when handled. At another nest, where the eggs had weighed more (3.8 and 3.6 g) than at the Barbour nest, two young weighed 4.3 and 4.5 g at 15:55 on their second day, and had tiny wing quills up to 0.5 mm long. The next afternoon they were 7.1 and 6.7 g, with 2.5 mm quills and opening eyes; on their fifth day they were in the fallen nest (which Willis righted); weights were 11.7 and 11.1 g, wing quills to 9 mm. On their sixth afternoon they weighed 15.4 and 14.3 g and had 14-mm quills. The seventh morning (the day Willis left, 27 August), they were up to 15.5 and 14.9 g, with 17-mm wing quills. They gaped and gave peeping notes when handled, at least until five days old. Young ready to leave are fairly well covered by dark brown feathers.

Young out of the nest are dark brown, with blackish bare faces rather than the blue faces of adults. Their gape angles are pale, but they lack the white wing corners of adults for the first month or so. Short-tailed fledglings hide in low tangles, so that one scarcely ever sees them until they are nearly grown and are getting whitish or blue faces. Each parent takes one young if there are two, as in Bicolored and other antbirds. Much as in courtship, the parent gives Chirps and Warbles, plus faint Songs, to bring a young one up or find it for feeding. The begging young Squeaks loudly, especially after a feeding when it is starting to peck at twigs and leaves as if looking for food. It Chirps faintly as it follows its parent about. One such young, a female captured in

a mist net 8 June 1966, had new primaries at the tip of one wing. The young male of this brood had plumage like the adult male, and the young female had plumage like the adult female. One specimen (no. 456726 in the U. S. National Museum, from Alajuela in the Panamá Canal Zone) is a young male with a few brown feathers of the juvenal plumage on its black underparts and with new primaries at the tip of one wing. Probably the brown-plumaged juveniles molt into adult plumages while being cared for by their parents. Eventually the young obtains most of its own food, and its parents start mutual grooming again for the next nesting.

The nesting season on Barro Colorado includes much of the rainy season, April-November. A pair could have two, perhaps three, broods each year if not prevented by nest predation. Nearly independent young in June 1966 must have come from a nest started in early April, and begging large young of 1 November 1961 probably came from a nest started in September. The earliest nest recorded had two eggs on 7 June 1961; the latest nest had young about four days old on 12 October 1961. Skutch (1969:238) found a nest in Costa Rica in April during a year of early rains (1958), and Carriker (1910:616–617) found a nest on 10 May 1902, but other nests were found in July and August, the months in which we found most of our nests. Austin Smith collected a small fledgling (American Museum no. 390312) at Carrillo, Costa Rica, 28 April 1924; it must have come from a nest started in late March.

MOLT

Judging from 127 adult Panamanian specimens in museums we visited, Chestnut-backed Antbirds in Panamá molt mainly late in the rainy season or at the end of the breeding season, from August to November. The monthly molting ratios (birds in wing molt/birds seemingly not in wing molt) are, from January to December, respectively: 2/9, 1/22, 0/21, 1/16, 0/15, 0/4, 2/4, 8/8, 6/1, 1/0, 3/2, 0/1. There is definitely a season of molt just as there is a breeding season.

DISCUSSION

One of the surprises of this study was that Chestnut-backed Antbirds are commoner and have smaller territories than Spotted Antbirds, which are smaller birds. Usually, the larger the bird, the larger is its territory. Partial dependence on irregularly available army ants may restrict densities of Spotted Antbirds. The use of dense cover by Chestnut-backed Antbirds probably adds to their food supply, since dense cover should mean more food for insects and hence more insects. Perhaps the aggressive behavior toward Spotted Antbirds keeps the latter from encroaching on Chestnut-backed Antbirds significantly. If the Chestnut-backed Antbird or similar species were absent, Spotted Antbirds might be able to move into such dense cover as well as occupy areas around dense cover as they now do (Willis 1972). In such a case they might be able to evolve larger body size because of increased prey abundance, and/or become more abundant.

Spotted and Chestnut-backed Antbirds are similar in nesting seasons, roles of males and females at nests, and many other aspects of reproduction. The similarity is another line of evidence that their niches are similar. However, antbirds in general do not vary much from a pattern of monogamy; males help in all aspects of nesting, etc. (Skutch 1969). This pattern is one that is often successful in insectivorous birds of regular environments (Lack 1968:29; Willis 1972). It is probably much more efficient if the male helps rear young, for each parent has more time to forage. The male Chestnut-backed Antbird at the Barbour nest could scarcely brood the young, feed them, and feed himself as well on the day when his alarmed mate would not come to the nest.

SUMMARY

On Barro Colorado Island and nearby areas, the Chestnut-backed Antbird (*Myrmeciza exsul*) lives low in the undergrowth of moderately wet lowland tropical forests, especially near and in treefalls and dense thickets. It hops actively through low vegetation, peering and pecking rather than sallying actively for prey. On the infrequent occasions when it follows army ants, it forages in much the same way as when away from ants. It is dominated by Bicolored and Ocellated Antbirds over ants, but chases the small Spotted Antbird persistently, both at and away from ants. Perhaps, by being aggressive, it keeps the smaller bird from moving into its foraging niche.

Pairs of Chestnut-backed Antbirds live all year in rather small territories, singing and occasionally displaying at neighbors across territorial boundaries. They nest low on debris or small bushes from April to October, in the rainy season. Males feed their mates, and mutual grooming is another courtship activity. Both sexes incubate and care for young, which

molt into adult plumage and leave their parents. There is a definite molting season, mainly August to November.

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