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Taxonomy, Ecology, and Behavior of the Sooty Ant-Tanager (*Habia gutturalis*) and Other Ant-Tanagers (Aves)

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ABSTRACT

Morphological and behavioral differences among the allopatric Red-throated (*Habia fuscicauda*), Black-cheeked (*H. atrimaxillaris*), and Sooty (*H. gutturalis*) ant-tanagers suggest that they are separate species. Only the first species has strong sexual dimorphism; only the second has courtship feeding; and only the third has a rapid "chatter." All three forage diversely, capturing insects and fruit, but stay low in woodland undergrowth; all follow army ants.

Crested (*H. cristata*) and Red-crowned (*H. rubica*) ant-tanagers forage diversely but stay high in the undergrowth. Northern Red-crowns "chatter" and make thin nests; southern ones chirp and make leafy nests. Possibly they are separated genetically because those from Colombia south center breeding in the austral summer; those from Colombia north, in the boreal summer.

Sympatric ant-tanagers diverge and narrow their foraging niches little more than they do when separate. Possibly ecological counterparts or combinations of specialized species replace the missing ant-tanagers where only one or no ant-tanager is present, and thus restrict their geographical and ecological ranges. The ant-tanagers forage rather adaptably, but adaptation to certain strata of leafy undergrowth limits them on one side and failure to oust specialized species, such as antbirds over army ants, limits them on the other. For ant-tanagers, medium adaptation and adaptability go with medium-height forest habitats.

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INTRODUCTION

The taxonomic status of the Sooty Ant-Tanager (*Habia gutturalis*) of northern Colombia and its relatives in Colombia and Central America has been undecided for many years. Many authors have followed Hellmayr (1936), who called all northern forms subspecies of *Habia gutturalis*. Others, such as Eisenmann (1955), Slud (1964), and Parkes (1969a), separated the Black-cheeked Ant-Tanager (*Habia atrimaxillaris*) of southern Costa Rica and the "Dusky-tailed" or Red-throated Ant-Tanager (*Habia fuscicauda*) of northern Mexico to northern Colombia as distinct species. Ridgway (1902) also separated the Red-throated Ant-Tanager into the pale *Habia salvini* from Nicaragua north and the dark *Habia fuscicauda* from Nicaragua south.

There are moderate to striking differences in plumage among these forms. Males of the *salvini* group are dusky to brownish red, with bright rose or pinkish red throats and similarly bright but concealed crown-patches. Females are dusky yellowish brown, with bright yellow bibs but no crown-patches. Northern males of *fuscicauda* are much darker, with dark purplish red rather than dusky red tails. Females also average dark, and are almost brown except for their yellow throats and bibs. Southern birds of the *fuscicauda* group (*willisi* and *erythrolaema*) are much paler, more like members of the *salvini* group. Male and female Black-cheeked Ant-Tanagers are nearly alike, although females are somewhat duller than males. The head is almost all sooty or black, except for a partly concealed red patch on the crown and for a reddish throat and bib (fig. 1). The body and tail are dusky, with only a faint reddish stain on the underparts. Sooty Ant-Tanager females are only slightly duller plumaged than males, which have reddish throats and long, bushy scarlet crests that contrast with dark or sooty plumage.

In 1957 I studied the behavior of a subspecies of the *salvini* group in British Honduras (Willis, 1960a, 1960b, 1961), comparing it with the Red-crowned Ant-Tanager (*Habia rubica*), a species found from northern Mexico to southern Brazil. These two similarly plumaged species differ in behavior and ecology, so I wondered if Hellmayr could have been mistaken in assigning the rather differently plumaged *atrimaxillaris*, *fuscicauda*, and *gutturalis* to the same species as *salvini*. Since 1960 I have briefly studied the behavior of the first three forms in Costa Rica, Panama, and Colombia, respectively. The present report compares the behavior of these three forms with the behavior of *salvini* and *rubica*. In addition, I list observations of other subspecies of *rubica* in Trinidad, Colombia, Ecuador, Peru, and Brazil and compare all forms of the genus *Habia* (including *H. cristata*, discussed in Willis, 1966) as to behavior and ecology.

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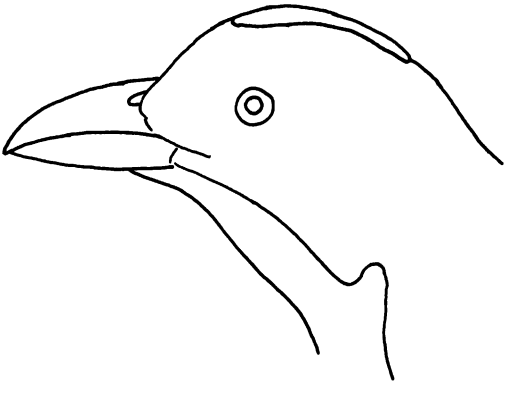

Fig. 1. Head of Black-cheeked Ant-Tanager, showing outlines of dark area on the cheeks and neck.

Study Areas

Areas in which I have observed ant-tanagers are listed below, giving only dates when ant-tanagers were observed and elevations only from 200 m. up. Black-cheeked Ant-Tanagers were briefly studied in patches of second growth and high forest on the steep ridge east of the south end of the town of Golfito. Red-throated Ant-Tanagers were studied occasionally between 1960 and 1970 in woodlands and second growth at Panamanian sites except El Volcán, where only Red-crowned Ant-Tanagers were studied; both species were in patchy forests at Cerro Campana and in the

Forest Reserve. Sooty Ant-Tanagers were at the first three localities in Colombia, and I searched similar patchy woodlands and second growth of nearby regions on the Cauca and Sinú and nearby rivers for the species in June, 1962 and March, 1965. Landslide-scarred woodland and undergrowth along rushing streams from 700 to 1800 m. up on the Western Andes at the central four Colombian localities held Crested Ant-Tanagers in 1962 and 1966. In forests with fairly dense lower mid-levels at the last three Colombian localities, and at the remaining localities, I encountered Red-crowned Ant-Tanagers in 1961, 1962, and 1965–1966. Red-crowns were at the Mexican locality and both Red-crowns and Red-throats in British Honduras.

Taxonomy

No recent authors have followed Ridgway (1902) in separating the Red-throated Ant-Tanagers into a northern species, *salvini*, and a southern species, *fuscicauda*. Although the darkest populations of *fuscicauda* live in southern Nicaragua and northeastern Costa Rica, near rather pale populations of *salvini* in northeastern Nicaragua, there are intermediate specimens from Greytown and Los Sabalos, Nicaragua, in the United States National Museum.

The sharp change from dark *fuscicauda* to pale *salvini* in Nicaragua suggests character displacement in the zone of contact between two related forms; away from the zone of contact, in Colombia and in Mexico, the birds are more alike. However, the dark color of populations from southeastern Nicaragua to western Panama may reflect Gloger's rule, that animals are darker in wetter climates. This is a region of very high rainfall, from 3 to 6 m. annually in most areas. Red-throated Ant-Tanagers generally are pale in color in dry regions, such as northern Yucatán and northern Colombia. Rainfall, perhaps by its effects on color and shadiness of vegetation, may be affecting the darkness of this plastic species rather strongly.

There are two theories about the origins of such sharp boundary zones between birds as the *fuscicauda-salvini* boundary. The usual suggestion is that isolated populations come together in a zone of secondary contact and there interbreed or fail to interbreed; for instance, Haffer (1967) explained a number of such boundary zones in northern Colombia by postulating that birds were isolated in forest refugia during dry climatic periods (chiefly interglacials) and came together again as forests rejoined during wet (mainly glacial) periods. Levins (1968), however, suggested that such boundary zones can evolve with or without geographical isolation if a polymorphic species uses two "patch types" (habitat or foraging

zones) and one morph of the species is better adapted for one patch type and another morph for the second patch type. If the frequency of patch types gradually changes geographically, there comes a point at which the dominant morph suddenly becomes quantitatively inferior to the other and is replaced by it. Levins suggested that the polymorphic boundaries in the Blue Goose-Snow Goose complex (Cooch, 1961) and in the Central American Brown Jays (Selander, 1959) may have arisen this way rather than by true geographic isolation. As any successful new genotype must arise in a single area and spread gradually, it is quite possible that at any one time a few species will be found that show polymorphic situations of this type. Temporarily stable zones of meeting, or gradually shifting meeting zones, may also occur. However, geographical isolation into forest refugia (perhaps in eastern Costa Rica and in southern British Honduras) seems more likely as an explanation for *fuscicauda-salvini* evolution, even if their present meeting place may be north or south of their original meeting place because of competitive ecological shifts of the type suggested by Levins. Both geographical isolation and polymorphic replacement because of changing environments may be involved, of course. Further study of the boundary zone and its relation to shifts in rainfall and other ecological factors is needed.

At any rate, the presence of hybrids and the probability that plumage color is related to rainfall make it doubtful that *fuscicauda* and *salvini* are separate species, despite their dissimilarity where they approach. I thus agree with Hellmayr (1936) that they should be joined, and suggest that all be called Red-throated Ant-Tanagers, *Habia fuscicauda*. The name "Dusky-tailed Ant-Tanager" (Eisenmann, 1955), although appropriate for the subspecies *fuscicauda* and *willisi*, is not appropriate for *erythrolaema* or for forms of the *salvini* group.

Both the Black-cheeked and Sooty ant-tanagers are allopatric to the various forms of the Red-throated Ant-Tanager (fig. 2). No hybrids are known. All three are clearly closely related, more or less dark variants on a common pattern. Hellmayr (1936) considered the Black-cheeked Ant-Tanager as a form intermediate between the other two. As it is not intermediate geographically, one must be careful of arguing that its intermediacy of plumage indicates that the three belong to one species. The relatively dark plumage of the Black-cheeked Ant-Tanager may be an independent adaptation to life in an area of very high rainfall, the Golfo Dulce region. The very dark plumage of the Sooty Ant-Tanager is probably not so closely tied to rainfall, although it is a bird of areas of moderate rainfall (about 2500 mm. annually) in the cool foothills of the Andes.

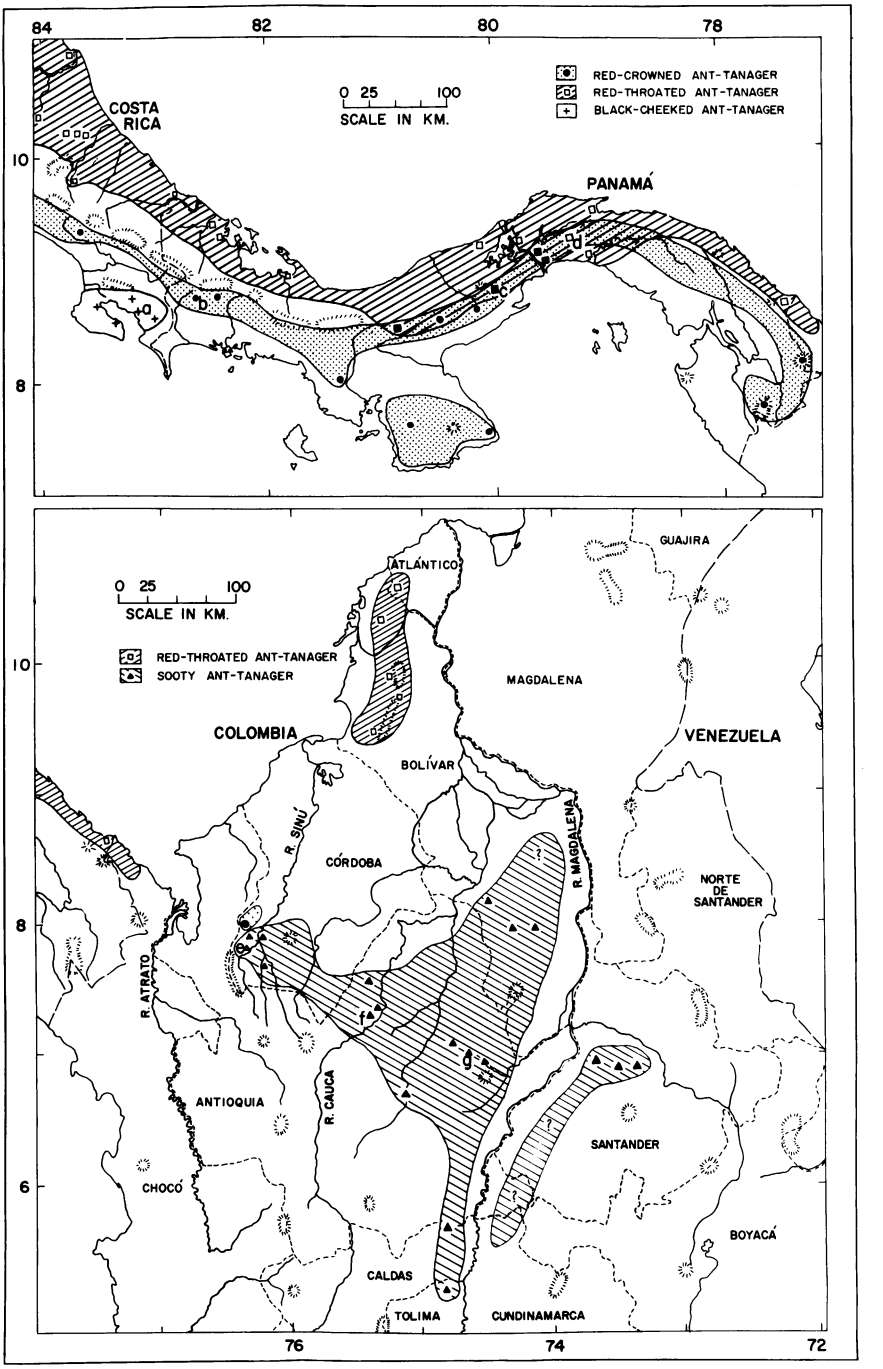

FIG. 2. Distribution of ant-tanagers from central Costa Rica to northern Colombia, excepting records for Red-crowned Ant-Tanagers east of the Rio Magdalena in Colombia. a, Golfito; b, El Volcán; c, Cerro Campana; d, Cerro Azul; e, Las Pulgas; f, Puerto Valdivia; g, Remedios. A recent specimen of the Sooty Ant-Tanager in the University of Michigan Museum of Zoology is from Pauna, 25 km. SE of the indicated range in Boyacá (courtesy of R. W. Storer).

The striking red-and-black color pattern, long crest, lack of sexual dimorphism, chattering alarm call, and other behavioral peculiarities (see below) of the Sooty Ant-Tanager clearly separate it from other ant-tanagers. I suggest that it be considered a separate species from Red-throated Ant-Tanagers, albeit closely related.

In behavior, Black-cheeked Ant-Tanagers are unlike Sooty Ant-Tanagers but rather like Red-throated Ant-Tanagers. Probably Black-cheeks arose from Red-throated stock that invaded the Golfo Dulce region and differentiated there. An alternative theory, that Red-throated stock competitively split apart an original monomorphic, dusky stock and left Black-cheeked and Sooty ant-tanagers as relict populations, seems unlikely in view of the morphological and behavioral differences between the last two forms. Although some may prefer to consider *atrimaxillaris* a subspecies of *H. fuscicauda*, I shall tentatively consider them separate species because the contrasting plumage, low sexual dimorphism, and courtship feeding of *atrimaxillaris* suggest reproductive isolating mechanisms that could serve to keep it from interbreeding with *fuscicauda* if they ever come into contact.

Red-Throated Ant-Tanagers

Comparison of Panamanian Red-throated Ant-Tanagers with those previously studied in British Honduras (Willis, 1960a, 1960b, 1961) may serve to indicate what ecological and behavioral similarities and differences one may expect from forms approaching, but not at, the specific level of differentiation in this group.

Habitats: Southern forms of the Red-throated Ant-Tanager are absent from large areas on the dry Pacific slope (fig. 2), just as northern forms are absent from dry Pacific forests northwest of the Isthmus of Tehuantepec. Here and there, as in northwestern Costa Rica and in central Panama, they spread in mesic woodlands over the continental divide onto the Pacific slope. They are unknown from eastern Panama east to the state of Bolivar in Colombia, and I was unable to find any at Chigorodó (latitude 7° 41′ N., longitude 76° 41′ W.) or San Pedro (latitude 8° 27′ N., longitude 76° 18′ W.) in the gap in 1965. Haffer (personal commun.) has worked other forested areas in the gap, so that it may be real rather than a product of lack of study. The population in Colombia (*H. f. erythrolaema*) seems isolated, its range separated from *H. f. willisi* in Panama probably by the extensive swamps of the lower Atrato and by the cultural savannas north of Monteria. However, the dry forests from Turbo past San Pedro to near Monteria seem suitable, and Sooty Ant-Tanagers reach just south of that region. The absence of Red-throated Ant-Tanagers from the wide

forests of Darién and of the Azuero Peninsula in western Panama is also puzzling.

As is true for northern populations (*salvini* and related subspecies), the southern subspecies are most common in the lowlands and foothills. Few have been recorded over 1000 m. elevation. Like the northern forms, the southern ones are commonest in patches of mesic low to moderately tall second growth or woodland and rare in extensive areas of old, tall, or very humid forests. On Barro Colorado Island the species was once fairly common (Chapman, 1929), but as the forest matured the species disappeared except for occasional pairs along the shores of Gatun Lake. Perhaps the absence of a thick leafy layer in the normal foraging zone, about 2 m. up, keeps the species out of mature tropical forests. Competing antbirds over army ants, particularly Ocellated Antbirds (*Phaenostictus mcleannani*), may also be a factor. Ant-tanagers are common in rather old forests on tiny Orchid Island, near Barro Colorado, where large antbirds are absent.

FORAGING: Red-throated Ant-Tanagers forage in Panama much as they do in British Honduras. Pairs or family groups, consisting usually of three or four birds and hence seldom as large as in British Honduras, drift rapidly from one area to another through moderately dense undergrowth. The birds generally look up, down, and around for as long as a minute at a time, their bodies angled about 35 degrees above the horizontal, from horizontal or diagonal (seldom vertical) perches a centimeter or two in diameter (fig. 3). They seldom alight on or hop along branches small enough to sway, so that they rarely flush food by their activity. Over army ants (swarm raids of *Eciton burchelli* or *Labidus praedator*) they use vertical perches more often and cling closely but fairly well. The perches are mostly between 2 and 5 m. up (624 of 1030 records) away from ants, below 1 m. over ants (211 of 298 records). Away from ants they seldom go to the ground, except to dissect prey, and are below 1 m. only a small part (132 of 1030 records) of the time. The perches are generally uncluttered, with a clear view of overhanging leaves, but at times a bird hops up or through vine tangles around tree trunks. Very tangled undergrowth or low dense second growth seldom occupies them for long, perhaps because visibility of prey or predators is hindered. Normally these birds seem somewhat phlegmatic and do little active flipping or reversing, but females that have been incubating are more active and use more vertical perches. After each careful search, a bird dashes rapidly to another perch, a meter or more at a time, horizontally or at a slight angle. These birds forage high for several perches in a row, then move to a series of low perches, but seldom show steep ascents or descents even to fly high

FIG. 3. Male Red-throated Ant-Tanager on Buenavista Point, Panama Canal Zone. Above, foraging. Below, swinging back and forth during scolding. From Ektachrome slides.

(10 m. up) into a berry bush. Often the traveling bird gives "week" or other notes that seem to draw other members of the family in its wake, so that the pair or family usually are 3 to 10 m. apart in irregular formation. In patches of tall forest they tend to travel rapidly or to forage high, in the leafy zones 8 to 10 m. up, rather than stay for long periods in the relatively leafless lower zones. As they forage, whether alone or with others, they give "chak" notes every few seconds.

Away from ants, they hop to peck prey or flutter short distances to overhead foliage for prey. Occasionally an ant-tanager goes to the ground, hawks prey in the air, pecks off berries (especially melastomes, *Miconia* spp.), or hangs and flutters to eat seeds of drooping open fruit of *Stemmadenia Donnell-Smithi*. The long ant-tanager tail may help in hovering under leaves and elsewhere. Insect prey noted included caterpillars, one fully three times the length of the bill of the bird, and long-horned grasshoppers. Most of the animal prey was too small and eaten too fast to be detected, but large prey was often taken to the ground for dissection.

When no competitors are present, ant-tanagers forage over ants much as they do in British Honduras, by repeatedly flying to the ground and up with prey. Competing antbirds, when present, relegate ant-tanagers to wandering about peripherally or overhead, where they sally to leaves and lianas or stems in the same manner as when away from ants. The birds sometimes move near the observer or to unoccupied spots and capture prey on the ground. They also wander away from the ants periodically if competing antbirds are present, even if the antbirds are subordinate to ant-tanagers. However, they sometimes search for ants with a leap-frogging band of Bicolored Antbirds (*Gymnopithys bicolor*) and Ocellated Antbirds (*Phaenostictus mcleannani*); and at times a Gray-headed Tanager (*Eucometis penicillata*) joins an ant-tanager group away from ants. Thus, they do associate with other ant followers despite competition.

COMPETITION: When Red-throated Ant-Tanagers in Panama are away from ants, they forage at much the same levels and in the same ways as they do in British Honduras, even though there, Red-crowned Ant-Tanagers (birds that tend to live in forests and forage high) compete with the Red-throated Ant-Tanager. Red-throats in Panama forage high (5 to 10 m. up) more often than those in British Honduras, but they do not really occupy this stratum or spread into forested areas left vacant by Red-crowns. Probably other species occupy such zones where Red-crowns are absent in Panama, and one obvious candidate is the very common Slaty Antshrike (*Thamnophilus punctatus*). According to recent studies by Yoshika Oniki (personal commun.), this species forages by looking carefully at foliage in the forest mid-levels and undergrowth and

by capturing large insects similar to those taken by ant-tanagers. The Slaty Antshrike perhaps replaces the Red-crowned Ant-Tanager more than it does the Red-throated Ant-Tanager, but on two occasions I saw Red-throated Ant-Tanagers on Buenavista Point supplant snarling fluff-backed antshrikes and steal away the latter's prey. In the medium height second-growth woodland on the Point, Red-throats are very common, antshrikes uncommon.

Once I saw a Red-throat on Buenavista Point supplant a pair of Green Honeycreepers (*Chlorophanes spiza*) and another time I saw one supplant a Red-capped Manakin (*Pipra mentalis*). The former probably take some berries that would otherwise be eaten by the ant-tanager, and the latter sally for small prey on foliage at levels sometimes occupied by ant-tanagers, but probably the honeycreepers are usually in the treetops and the Red-capped Manakin in tall forest. Thus, neither competes much with ant-tanagers.

There is much more competition over ants. Ocellated Antbirds supplant Red-throats, which usually stay well away from the former. Even though Red-throats regularly supplant Bicolored Antbirds, the antbirds are so quick at catching prey and so good at clinging to vertical saplings near the ground that the ant-tanagers often give up and move away. However, on the Bohio Peninsula and in the Madden Forest Reserve all three species are together regularly over swarms of ants. Red-throats regularly supplant Gray-headed Tanagers and Spotted Antbirds (*Hylophylax naevioides*), and these smaller species keep well out of the way of ant-tanagers over ants. At one swarm of *Labidus praedator* on the Bohio Peninsula, January 21, 1962, a Blue-crowned Motmot (*Momotus momota*) pair repeatedly flushed ant-tanagers, but the ant-tanagers stayed because the motmots were aggressive only when fighting over prey. As ant-tanagers can forage away from ants readily in all areas having enough leafy undergrowth, they probably are not seriously affected by the attacks of other ant-following species, except in areas of tall forest and little undergrowth. In Panama the highest densities of ant-tanagers encountered are on Buenavista Point, where no Bicolored or Ocellated Antbirds are present and perhaps no *Eciton burchelli*; there, however, are *Labidus praedator*, Spotted Antbirds, and Gray-headed Tanagers.

FLOCKING: Away from ants, Red-throats occasionally join wandering flocks or are joined by them. However, the fast-moving ant-tanagers tend to run rosettes around the forest flocks and to desert them periodically, just as they do in British Honduras. Often they are away from flocks for long periods. On Buenavista Point, Red-throats associated with small groups of White-flanked Antwrens (*Myrmotherula axillaris*), Checker-

throated Antwrens (*Myrmotherula fulviventris*), Dot-winged Antwrens (*Microrhopias quixensis*), Buff-throated Woodcreepers (*Xiphorhynchus guttatus*), Plain Xenops (*Xenops minutus*); occasional members of flocks were Thrush-like Manakins (*Schiffornis turdinus*), Dusky Antbirds (*Cercomacra tyrannina*), Rose-breasted Thrush-Tanagers (*Rhodinocichla rosea*), Gray-headed Tanagers (*Eucometis penicillata*), Southern Bentbills (*Oncostoma olivaceum*), Slaty Antshrikes (*Thamnophilus punctatus*), Long-billed Gnatwrens (*Ramphocaenus melanurus*), Spotted Antbirds (*Hylophylax naevioides*), Song Wrens (*Cyphorhinus phaeocephalus*), Yellow-backed Orioles (*Icterus chrysater*), Yellow-rumped Caciques (*Cacicus cela*), and Fasciated Antshrikes (*Cymbilaimus lineatus*). In the Forest Reserve flocks with Red-throats sometimes included Red-crowned Ant-Tanagers, and on the Agua Salud in the Navy Pipeline Reservation Dusky-faced Tanagers (*Mitrospingus cassini*) were sometimes with Red-throats.

ALARM BEHAVIOR: Red-throats in Panama react to humans much as they do in British Honduras—the family gathers around the intruder for a minute or two, scolds him actively with a series of rough "waaj" notes at two or three per second. Each bird flips one way and then the other, its partly spread tail dipping at the center of an exaggerated flourish to the other side at each flip; there is little flitting of the wings. Often the body is somewhat spread and the legs splayed. There are occasional "static" notes (see next paragraph) among the scolds, especially when the birds flee through the undergrowth ahead of the observer. "Static" notes were given once when a Red-throat jumped as a Gray-chested Dove (*Leptotila cassini*) flew down nearby. At another time the ant-tanagers scolded instead of fleeing when a White Hawk (*Leucopternis albicollis*) flew over an ant raid. Quite often there is a series of scolds and static notes when a bird flees.

VOICE: The scolds and "chatters"—I now prefer to call them "static" notes because they do not really correspond to the chatter of Red-crowns—are much like those heard in British Honduras. Scolds perhaps express irritation, for they were often used after supplantings by *Momotus momota* and also when territorial trespassers approached, as well as in their reactions to me. A short, faint scoldlike sound was used in supplanting Bicolored Antbirds. The usual note given when foraging is a faint "chak" rather than a high "wik" as given by the birds in British Honduras. Such grunts may keep the family together, but are used when a bird is alone or captures prey, and hence may also be notes that keep some distance between individuals of the same or other species. A bird flying off ahead of its mate or a young bird often gives a series of "week" notes mixed with

other faint notes, much as they do in British Honduras; these calls seem very attractive and often induce following.

One call not noted in British Honduras was a distinct rapid "cha-a-a-a-a-a-a!" between mates, uttered by either bird but especially by the male as one flew near the other. This "rattle" was often preceded by or ran into faint notes of the "chak" type, and often preceded or followed a sexual chase. One male held his spread tail down and his open bill up after rattling near his mate. One female puffed her throat out, perhaps threatening, when the male rattled on his approach.

Perhaps the rattling and sexual chasing partly replace the interactions between day-singing males and noisy females in British Honduras. In Panama, the day songs are very irregular in form and rate of repetition and only occasionally follow or precede an excited scold or scold-week series from the female. Usually day songs in Panama sound like garbled forms of the dawn song: soft, whistled "wheh-cherk-wuh, wher-cherk-weh, wherk chee" in a triplet sequence with two lower notes between successively higher third notes (A, CBB, DCC, E) instead of an alternating sequence with one low note between successively higher second notes (BA, CB, DC, ED, EDE) as in British Honduras. Chapman (1929) was impressed by the contrast between one form of this musical series and the rough scolding one normally hears, but the irregularity and variability of this song suggest it is more a subsong than a song. I have heard it during a territorial dispute in December and in excited scolding at me in February, but most records were made while female and male were apart in the breeding months of April to July. The bird forages and looks about during singing, unless it is busy in a dispute or sexual chase.

The dawn song is more regular, a series of 12 to 15 mellow but repetitive whistles like a music box, such as "wheek, perk, cher" over and over, at six or seven songs per minute (undergrowth along shore of Fairchild Point, Barro Colorado, 05:54 to 06:30 on April 9, 1961 and 05:41 to 05:50 or later on April 30). By 06:30 or 07:00 most were giving irregular songs, scolds, rattles, and static as they traveled about with their mates. At Fort Davis similar songs were given at 17:00 to 18:00, May 22, 1961. A caged male at the Barro Colorado Laboratory regularly sang "ch'erk werk hoo" two or three times per song from about 05:45 to 07:00 each morning in May, 1961; his crest was not raised. Most such songs were given in the April to June period, but one was noted at 10:40 on November 6, 1961 in the Forest Reserve. In all these respects the dawn songs seem similar to those heard in British Honduras; dawn songs do not differ much in the genus *Habia*. The evidence that the captive unmated male dawn-sang

very late adds to the evidence that dawn songs are primarily used when the mate is not present, but they may have the usual oscinine dual function of attracting a mate and advertising the territory.

REPRODUCTION: I have not seen precopulatory or copulatory activity in Red-throated Ant-Tanagers in Panama, except for rattling and sexual chasing and irregular day singing, even when I watched a pair at Buenavista Point weekly during 1961. The male of this pair occasionally held strands of material in his bill April 23. On May 14, he carried an insect near the incubating female, but drifted off and ate the insect himself after a few "chak" notes between day songs. May 21 he gave excited "chak" notes and rattles when she joined him after incubating, foraged phlegmatically as she chased prey actively, and accompanied her back to the nest. He never helped with incubating. On May 28, I finally found the nest, which at 5 m. up was much higher than any nest I had seen in British Honduras. It was a loose, leafy cup much like one pictured in Willis, 1961, and was set on a sloping limb against small twigs. The pair carried food to young from anywhere in the territory with streams of excited "static" and "week" notes; quite often the mate quickly captured an insect and followed the noise of the nestward-bound bird. The female brooded after feedings, but not the male.

June 4 from 07:30 to 08:30, the female made about six visits with material to a new nest, a few epiphyte rootlets and leaves and palm strips 3 m. up on the twigs of a sapling 50 m. southeast of the earlier nest. She arrived with a stream of "week" and "static" notes that the male followed to about 10 m. from the nest, where he foraged as she worked. Once he pulled at an epiphyte rootlet she had tried to pull off, but otherwise he did not take part in getting material. From 09:00 to 10:45 they foraged away from the nest without any precopulatory activity. On June 11, 18, and 25, the female was incubating or brooding; July 2 the nest was deserted, and there was no further evidence of nesting on my weekly visits until early September.

June 30, 1961 a pair in the Forest Reserve had a brown fledgling with tail one-quarter length. On July 30, 1961 one grown young was with a male at a Buenavista Point ant raid, as on July 28, 1963. Even on December 9, 1960 the immatures in a family flock there still had swollen gape angles, suggesting that these may persist several months.

Stone (1918) reported a nest with eggs 8 feet up in a clump of orchids May 14 in the Canal Zone. Harrower (1935) reported a nest with two white eggs (24.5 × 16.5 mm.) 2.5 feet up in a bush by a trail through second growth at Pedro Miguel in the Canal Zone, July 17. The nest was a leafy cup, 7 inches across by 4.5 inches deep, with a lining of fern stalks

and brown and black "rootlets" (perhaps rhizomorphs) in a cup 3.5 inches across by 2 inches deep. The nesting season is probably late April to July, in the first few months of the rainy season.

Young apparently stay with adults for at least a year, for a male that was molting to the red adult plumage was with a pair on Buenavista Point, August 15, 1964; and on a few occasions two or more adult males were in a family group. Carriker's (1910) observations that in Costa Rica these birds are not in groups as often as are Red-crowned Ant-Tanagers are the opposite of my observations.

TERRITORIES AND AGONISTIC BEHAVIOR: One pair, sometimes with one or two others that are probably their one or two young of the previous breeding season, hold each territory. Groups on Buenavista Point had very small territories, under 200 m. across, and crisscrossed them repeatedly during foraging but did not trespass often. Territories in more mature woodland on the Bohio Peninsula and in the Forest Reserve seemed larger. During the nonbreeding months a large swarm of ants sometimes attracts two or three families, but even then there is much feuding between the families and different families tend to alternate at the swarm or to take separate forks of it. In the breeding season there is seldom trespassing or disputing, even over ants.

The usual pattern of a boundary encounter, as in British Honduras, is that of a melee of birds flying about and scolding, giving static, and uttering faint notes mixed with a few song phrases. At times the adult males face each other with bodies and tails spread but heads and crowns sleeked; sometimes one wigwags back and forth with the body upright, and once (December 9, 1960) such a male had the bill pointed to the chest. At a swarm of ants, February 6, 1962, one sleek-headed male supplanted the other and wigwagged from a tail-spread upright (fig. 4A) as the other wigwagged from a tail-closed upright (fig. 4B) and raised its crest at times. It soon subsided (fig 4C) and departed. Occasionally in other disputes one of the two facing males raised its crest. Perhaps crest-raising indicates a somewhat submissive tendency, or that the bird is unlikely to attack; pure threat always involves closing the crest, as it does in British Honduras. After such brief encounters the pairs or families usually separate, foraging toward the centers of their respective territories with loud static and scolding.

PREENING: Red-throats in Panama scratch over the wing. Occasionally as one preens it raises the crest, the only other situation in which I have seen crest-raising. Once a female-plumaged bird of a family came up and nibbled at the wing of another as if eating a parasite. At times a bird bathes in a forest pool.

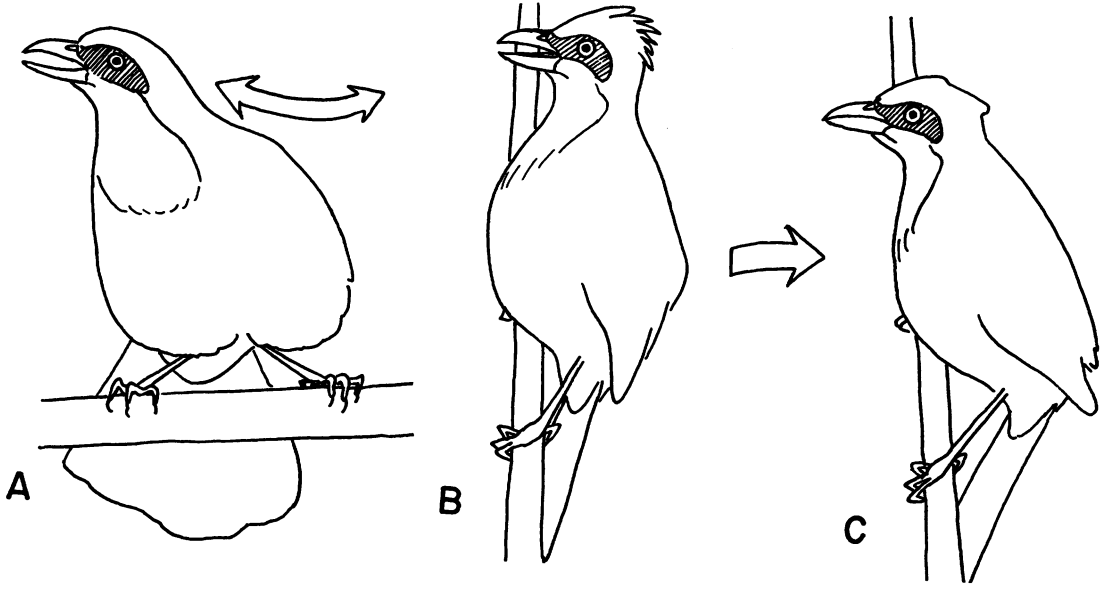

FIG. 4. Postures in territorial dispute of Red-throated Ant-Tanagers. A. Dominant male. B. Subordinate male challenging. C. Same subordinate male, just before fleeing.

Black-Cheeked Ant-Tanagers

Habitats: Black-cheeked Ant-Tanagers (*Habia atrimaxillaris*) occupy a zone of very wet forests around the Golfo Dulce in Costa Rica, but as Slud (1964) noted, they generally live more in broken forests and tall second growth than in the interior of unbroken forests. However, they were sometimes inside patches of fairly tall forests above the town of Golfito, and may use them to some extent to fill out territories in second growth or streamside woodlands. Perhaps the absence of the domineering Ocellated Antbird in this region makes it possible for them to follow army ants in tall forests there.

Foraging: They forage much as do Red-throats, except that they wander through very tall forests regularly. They are sedate to moderately active antshrike-like searchers, using open twigs (mostly horizontal and 1–2 cm. in diameter), but wander in pairs or small groups through the undergrowth rather than slowly, alone or in pairs, as does an antshrike. They check dense leafy tangles, rotten limbs, and vine tangles 1 to 6 m. up more often than do Red-throated Ant-Tanagers; sometimes they seem to overlap in foraging with the Buff-throated Foliage-Gleaners (*Automolus ochrolaemus*) that accompany them. I saw none eating fruit, but perhaps fruit is rare in March at Golfito. Slud (1964) reported they ate fruit.

Over swarms of *Eciton burchelli*, they usually wandered widely, probably because they were subordinate to Bicolored Antbirds. When the ants crossed a landslide area, the ant-tanagers took the front and center positions as Bicolored Antbirds hesitated in nearby cover. In areas of second growth the ant-tanagers were very active above the antbirds, but whenever the ants passed through tall forests the ant-tanagers left the swarms to Tawny-winged Woodcreepers (*Dendrocincla anabatina*) and Bicolored Antbirds. Spiders, roaches, and long-horned grasshoppers of up to 1.5 times the exposed bill length of the bird were the items of prey noted; commonly the bird carried prey to the ground beyond the ants for dismembering and chewing.

Competition: Away from ants Black-hooded Antshrikes (*Thamnophilus bridgesi*) replace the Slaty Antshrikes of other regions as the efficient mid-level peerers for large insects; perhaps these antshrikes keep the ant-tanagers from expanding into tall forest or using levels above 6 m. in the undergrowth. Over ants, the blue-faced Bicolored Antbirds of this region supplant the ant-tanagers rather than the reverse as in Panama. Perhaps the blue faces, as "eyespot" designs, are more frightening than dark faces (Willis, 1969). A Tawny-winged Woodcreeper and a Barred Woodcreeper supplanted ant-tanagers once each. The ant-tanagers often

wander peripherally when these species are active.

FLOCKING: Away from ants, and even when a flock passes birds at army ants, these ant-tanagers sometimes follow the small insectivorous birds of forest flocks. At Golfito Dot-winged Antwrens (*Microrhopias quixensis*), Tawny-crowned Greenlets (*Hylophilus ochraceiceps*) and Buff-throated Foliage-Gleaners were with ant-tanagers several times; other associates included Tawny-winged Woodcreepers, Black-hooded Antshrikes, Russet Antshrikes (*Thamnistes anabatinus*), Chestnut-backed Antbirds (*Myrmeciza exsul*), Riverside Wrens (*Thryothorus semibadius*), Plain Xenops (*Xenops minutus*), Philadelphia Vireos (*Vireos philadelphicus*), Blue-black Grosbeaks (*Cyanocompsa cyanoides*), and Shining Honeycreepers (*Cyanerpes lucidus*).

ALARM BEHAVIOR: At Golfito, the ant-tanagers seemed rather tame and incurious; they scolded little at me. Static notes came once as a toucan flew over an ant swarm, and on several occasions static caused other ant-tanagers and other species to flee for cover.

VOICE: The scolds, "chak" grunts, static, and "wik" or "week" notes are much as in Red-throated Ant-Tanagers from Panama. The male often gives a rattle similar to the Panamanian kind when approaching the female. The occasional faint and fragmented day songs seem much like dawn songs and like the dawn songs of Red-throats in Panama and British Honduras: a musical series of mellow whistles, "tonk, myerr" or "chong, cherk, m'lerk" or "chong, chuk, cherk, hoo" or "chock, per, chew" on a rising or descending scale, repeated for six to 11 notes (in most cases seven) per song. Two singing down in a ravine and in second growth at 05:28 to 05:45 on March 27, 1961 gave seven or eight songs per minute; the next morning both were singing at 05:20 but one ended at 05:29 with static, scolds, rattles, chaks, and song fragments as he chased his mate; the other sang to 05:40. Later in the day, singing was usually irregular and occurred mainly when the female was briefly distant from the male. One seen at 12:14 had his tail down at −60 degrees, his throat pulsing, but his crest folded. Females often scolded and moved to a singing bird, ending their songs.

COURTSHIP: One pair observed for several days were in full precopulatory behavior, which was of the usual ant-tanager type except for repeated courtship feeding. This pair were with another old bird plus a grown juvenile that often fluttered its wings at the female and gave faint "myurr" or "chiuiut" notes. The female ignored the juvenile and foraged, but when the male approached she often fluttered the outspread wings upward, lifted the closed tail upward, and uttered a series of slow, wheezy "chwie" notes as she looked back and forth with head retracted and bill up in a standard precopulatory display. At times her crest was ruffed, showing its

reddish center. Often the male then came up with a rattle and alighted briefly beside her up to three or four times in a row. On several occasions between March 25 and 27 he fed her a large insect and then flew off or wiped his bill. At 10:10 on March 27 he fluttered to atop her, then away; she fluttered after him with tail and wings up and legs dangling, then was fed. At 10:37 he rattled and copulated with her, then fed her a katydid abdomen. As she carried it off downhill, chacking rapidly, he looked around, tail spread somewhat, and wiped his bill. In a third copulation there was apparently no feeding. At 12:47 he hopped near her, pecked an insect from the landslide, then tilted up his bill and puffed out his body as he gave a rattle. She immediately fluttered her wings and raised her tail, but subsided abruptly when he ate the food. Possibly this pair may have been aberrant, or the male may have transferred feeding from the juvenile to her, but even so the courtship feeding suggests that monomorphism may have led to a different courtship behavior in a form that is otherwise like the Red-throated Ant-Tanager. The feeding procedure is not as well developed as in antbirds, among which the pair normally copulates after the female receives food rather than beforehand.

Reproduction: The grown juvenile, if hatched that year, must have come from a January or February nest. It was dull-throated and the head feathers were irregular, but it was not otherwise in juvenal plumage. Once it stuck the head into a clump of dead leaves, suggesting that its foraging was not yet adult. Dawn singing and courtship indicate that all the birds I saw at Golfito were breeding in late March. This suggests nesting in the dry season, perhaps as an adaptation to the very wet climate of Golfo Dulce.

Territoriality: Two to four birds occupied separate, moderately large areas (about 4–6 hectares, as do other ant-tanagers in areas of moderate density) on the slope at Golfito; even at large swarms of ants there was no trespassing. I saw no agonistic behavior besides faint "wik" notes from a nonbreeding adult that twice caused the immature bird of the family to back off 0.2 m. and give a bill-down pose briefly.

Preening: These ant-tanagers scratch over the wing. A resting male sat looking about for more than 10 minutes with wing tips a little down, tail notched, body at 45 degrees but head horizontal, at 2 m. up on a horizontal 1 cm. twig in dense saplings. The crest showed as a bright red line.

Sooty Ant-Tanagers

Habitats: Unlike others of this group, Sooty Ant-Tanagers are apparently restricted to foothill localities, mostly at 100 to 1000 m. above sea level from the northeastern end of the Western Andes in Córdoba (Rio

Naín, Haffer, 1959) southeast across the Cauca gorge near Puerto Valdivia into the northern end of the central Andes, from near Honda in Tolima almost to the swamps of the Cauca-Magdalena junction, and onto the western slope of the Eastern Andes in Santander and thence southward (fig. 2). These are or were forests with 2000–3000 mm. rainfall per year; perhaps before human occupation the ant-tanagers lived mainly along streams and in landslide areas, because I found them mainly in human-created second growth and patchy woodland. Expanding human populations in this region are eliminating all forests as they go, so that the ant-tanagers are helped in the short run but may disappear in the long run unless water conservation measures are enforced and patchy woodlands remain.

FORAGING: Foraging is much as in Red-throated and Black-cheeked ant-tanagers, including the "chak" calls. When Sooty Ant-Tanagers at Remedios foraged in patches of tall forest they tended to work high, 4 to 10 m. above the ground rather than the usual 1 to 5 m. up. Usually open, horizontal, steady perches with good views of foliage lead to horizontal flights to other perches or sudden hawking flights to foliage to capture insects. I did not note them eating fruit, but T. K. Salmon (Sclater and Salvin, 1879) did record fruit as food.

Even over ants the birds repeatedly flew for prey to foliage above the ground, but they also flew to the ground in the usual way. They tended to wander over or around the swarms, especially if Bicolored Antbirds were present.

COMPETITION: Occasionally a Sooty Ant-Tanager displaced or supplanted a Bicolored Antbird at a swarm, but the faster and more numerous antbirds tended to oust the ant-tanagers by infiltration in the forested areas. Once an ant-tanager supplanted a Wedge-billed Woodcreeper (*Glyphorhynchus spirurus*) near ants. Slaty Antshrikes occur over most of the range of Sooty Ant-Tanagers, but competition is not obvious.

FLOCKING: Away from or near ants, these ant-tanagers often associated with wandering flocks by foraging slowly or in a rosette pattern or back and forth. When not with flocks, the ant-tanagers were often wary, fast-moving, and difficult to approach or follow. At Remedios, White-flanked and Checker-throated Antwrens (*Myrmotherula axillaris* and *M. fulviventris*), Plain Xenops (*Xenops minutus*), Buff-throated Foliage-Gleaners (*Automolus ochrolaemus*), Rufous-rumped Foliage-Gleaners (*Philydor erythrocercus*), Black-tailed Flycatchers (*Myiobius atricaudus*), and Half-collared Gnatwrens (*Microbates cinereiventris*) were frequent members of the flocks; occasionally there were Red-billed Scythebills (*Campylorhamphus trochilirostris*), Slaty Antshrikes, Dusky Antbirds, Striped Manakins (*Machaerop-*

terus regulus), Thrushlike Manakins, Southern Bentbills, White-breasted Wood-Wrens, Song Wrens, and Stripe-breasted Wrens (*Thryothorus leucopogon*). Above Puerto Valdivia there were some of these species plus Spotted Woodcreepers (*Xiphorhynchus erythropygius*) and Red-bellied Grackles (*Hypopyrrhus pyrohypogaster*). At Las Pulgas there were some of the same species plus Dot-winged Antwrens, a Plain-brown Woodcreeper (*Dendrocincla fuliginosa*), and a Buff-throated Woodcreeper (*Xiphorhynchus guttatus*). At Remedios, Bicolored Antbirds came up and followed ant-tanagers about on several occasions, as if looking for ants.

ALARM BEHAVIOR: The reaction to an observer includes chattering, staring with one eye, and sudden flitting of the wings as the tail flicks from -70 to -40 degrees; but there is little flipping from one side to the other as in related species. A Spectacled Owl (*Pulsatrix perspicillata*) I flushed elicited a chattering chase from a pair. Once a big bird (possibly a pigeon) whirred past and started both of a pair into an outburst of static. Chatters and static often mark the movements of a pair or family as they come to investigate the observer and then flee ahead of him.

CALLS AND SONGS: The fast chatter, "chak-cha-cha-cha-cha-cha," some five to 15 notes at five notes per second, resembles the chatter of Red-crowned Ant-Tanagers rather than the scolds of Red-throated and Black-cheeked ant-tanagers. Chatters often end in static, one or more "chagat" notes like static on a radio; the call is rather like the static of Red-throats and Black-cheeks. "Chak" notes during foraging and "wik" and rattles and other notes as birds follow each other or come together are like those of the last two species.

Distinct day songs apparently are lacking, for the occasional faint and broken songs during the day are rather like dawn songs. These are the most musical of the ant-tanagers, with some phrases approaching those of thrushes in beauty even if not in complexity: "cheh, wher, whereyeh, whoa, whereyeh, whoa," the crest folded, the throat pulsing as whitish bases appear on the pink feathers, and the tail closed, the male looks around casually. Commonly, series of two or three rich whistles are repeated over and over at two per second, six to 11 notes per song, but new series are in most cases interspersed: "pong, peh, whee" at the simplest; "wheh, hee, whereeheh, wher'erer" at the most complex. Such songs come near the nest or when the female is out of sight. She often gives a chatter and static as an answer.

At dawn and dusk the songs are given loudly and regularly, six to nine times per minute, as the male moves from place to place low in the dense second growth or along the forest edge. "Per, aver, p'reek" three to four times was one male's song; another sang, "wheh, per, whoa, h'heh, per,

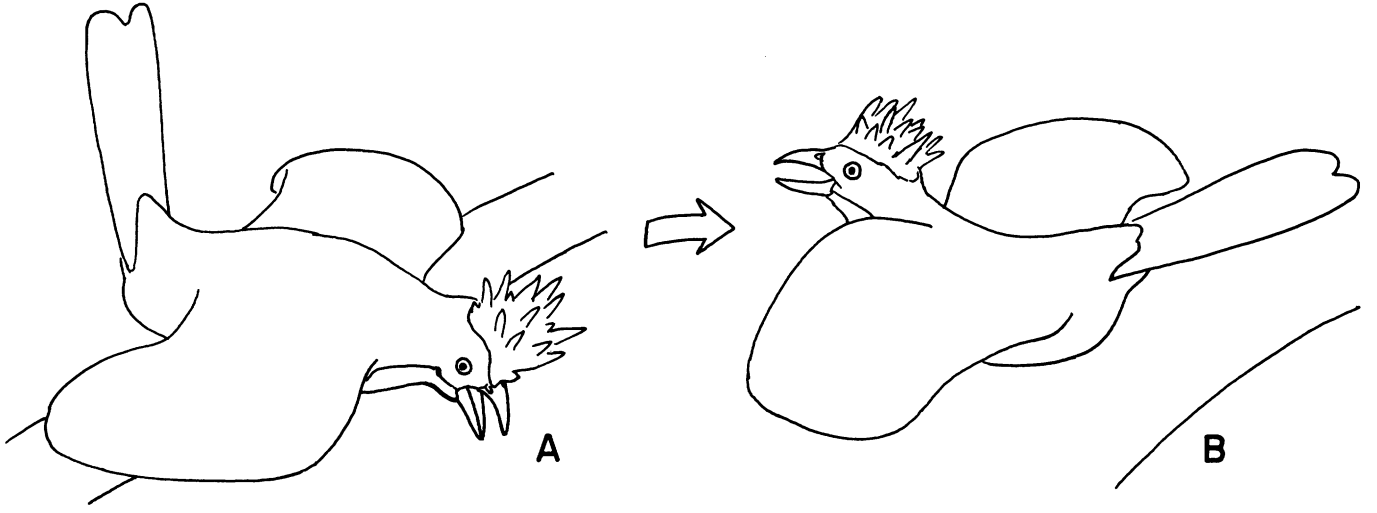

FIG. 5. Display given by male Sooty Ant-Tanager to female after he stopped dawn singing (A); he then flew away from her in the same display (B).

whoa, h'heh, per, whih, hrih, per, wheriyeh, heh, wheriyou" but often dropped the last five to nine notes. "Per, aver, p'reek" and "weh, peroo, work, tea" were other motifs.

At 05:30 on May 9, 1962, as potoos (*Nyctibeus griseus*) stopped singing, a male started songs from a small clearing just off the trail; his crest was fully expanded as he stood upright, the closed tail down and 10 degrees ahead of vertical, on a horizontal limb 3 m. up on a fallen tree. His throat pulsated with the notes, but he looked around between songs. As static from the female approached through the nearby woods, the male gradually came down to a horizontal pose, tilted his spread crest in her direction, his throat to his left, and then seemed to struggle back to a normal head position. He quivered his wing tips as he extended them slowly until he was fluttering them like a female in precopulatory display. As she flew to a branch below him and looked up, he raised his closed tail to vertical (fig. 5A), fluttered his outspread wings, and with crest raised gave a few faint songs before reversing and fluttering off (fig. 5B) into the forest. She remained as he sang faintly there, then gave a little static and flew after him. This pair had lost young in the nest two days before. May 14 the male sang from 05:30 to 05:50, and came up when I whistled an imitation: his closed tail was brought forward from -50 to -100 degrees for each song, and his crest was up. Crest-raising during dawn singing occurs in *Habia rubica*, but has not been recorded for *H. fuscicauda*. Male "soliciting" has not been recorded for any other ant-tanager.

COURTSHIP: Quite often there are rattles and faint songs or "wik" series as males and females come together, especially the above pair at 06:00 to 08:00 on May 9. Precopulatory and copulatory behavior were not observed.

REPRODUCTION: The above pair were feeding two young in a nest 0.5 m. above a little pool in a creek in a patch of tall forest at Remedios, May 2 to 6. The nest was like that of *H. fuscicauda*, a rather leafy cup set in the crown of a fishtail palm. The yellowish-gaped young were downy on May 2, and were open-eyed and had long pinfeathers on May 5 (about five days old). On May 2 the pair dashed around with food and gave chatters and static whenever I approached the nest; when I retreated the male began faint songs and "wik" and "chak" notes, then silently flew to the nest and fed one nestling; as I followed him away he foraged silently, and the female was brooding on the nest when I returned.

May 6 a full-tailed juvenile was calling "chiaj!" loudly and repeatedly after the male of another pair. Often the juvenile fluttered the tips of the wings as it stood at 10 to 20 cm. from the searching male. The dusky, disheveled small juvenile had a very pale and restricted orange throat-

patch and an off-orange perpetually ruffed crown. It followed the male whenever he rattled and flew, but ignored his occasional songs. The other bird, probably a female, gave chatters and static as it foraged separately. Two different foursomes on May 8 each had a juvenile with pale gape angles and a dull brownish black body, paling to orange on the throat and ragged crest; several times there were "wik ik eek chak" series as an adult led a juvenile off. June 8 at Puerto Valdivia the young bird in a foursome was in rather adult plumage except for a reddish suffusion down the chest. There was little singing that afternoon or the next dawn, suggesting that June may be at the end of the breeding season; probably nesting comes in the last months of the dry season (February and March) and the first months of the rainy season (April and May).

Salmon (Sclater and Salvin, 1879) reported that the nest is "cup-shaped, rather deep, and loosely made of coarse roots and fibers, lined with fine stalks etc. of ferns, and placed in low bushes by the side of mountain-streams." The eggs are "pale greyish white, mottled, especially at the larger end, with red-brown and lilac spots; axis 1.1, diam. .71." Plate XLII, figure 4 shows that the egg is indeed heavily mottled, and thus quite unlike the white eggs of Red-throated Ant-Tanagers.

TERRITORIALITY: Two to four birds were in separate family groups, and there was no trespassing even at swarms of ants. When I whistled imitations of songs, males (fig. 6) at Remedios and Puerto Valdivia approached and flew back and forth with crests raggedly spread like spiky red tufts of cotton, bodies compressed and upright, tails closed and down, and sang or were silent. The male at Puerto Valdivia leaped sidewise a few centimeters now and then to take the upright pose again; he jerked the tail from -80 to -10 degrees and dropped it suddenly as he alighted, as if to emphasize the jumping display. This display is almost the reverse of the agonistic display in Red-throated Ant-Tanagers, in which the head is compressed and the body and tail spread. On their leaving, these males came down to more normal +45-degree poses and closed the crests, then chattered. One boundary encounter at Remedios involved distant chattering and loud static back and forth and a few faint songs from the other pair. These chatters were short and metallic, and ended in static: "chang-chaing-chaing-chat."

PREENING: The crest is raised occasionally during preening, although it is usually closed during foraging.

RED-CROWNED ANT-TANAGERS

Red-crowned Ant-Tanagers (*Habia rubica*), studied intensively in British Honduras, have now been encountered in many other parts of

FIG. 6. Display of male Sooty Ant-Tanager when I imitated his songs.

their wide range: Mexico, Panama, Trinidad, Colombia, Ecuador, Peru, and Brazil. Their behavior shows some intraspecific variation, in some cases approaching the levels I have interpreted as variation between species in Sooty Ant-Tanagers and related forms.

HABITATS: In contrast to the species previously discussed, Red-crowned Ant-Tanagers do well in the interior of extensive forests, but they extend into woodland and scrub in many regions. Their habitats overlap those of Red-throated Ant-Tanagers in central Panama, but there the Red-crowns stay in the mesic woodlands in the foothills (to 1300 m. at El Hato del Volcán, Chiriquí, in western Panama) along the Pacific slope rather than centering in Caribbean-slope lowland second growth. In Trinidad and Amazonia, Red-crowns regularly live in extensive foothill or lowland forests, but seem to be most common where streams or human activities provide some disturbance, so that there is moderately dense foliage at the usual foraging levels.

FORAGING: Red-crowns forage in all regions much as they do in British Honduras, fluttering and peering for fruit and insects as would overgrown vireos or small jays, in undergrowth from 1 to 10 m. up. Red-crowns tend to center at 4 to 5 m. above the ground, even in regions where the low-foraging Red-throats are absent, but often move closer to the ground in all

areas. As in British Honduras, they tend to drop in flight and then hop up in a sapling or leap with reversing along sprays of foliage rather than looking from solid perches and then flying to a distant one horizontally in the fashion of Red-throats. Prey is often pecked off foliage or captured by short, tumbling flights. Red-crowns, however, use a wide variety of other searching and chasing maneuvers in the typically variable fashion of ant-tanagers.

In Trinidad, they occasionally follow army ants, but do not do so regularly or persistently. Probably the local lack of low-foraging ant-following antbirds allows them and such other nonprofessional ant-followers as White-lined Tanagers (*Tachyphonus rufus*) to move in over the ants.

I am impressed that Red-crowns forage much the same in all regions despite different competitive and climatic regimes; but it may be that new competitors in most cases replace the old.

FLOCKING: The association of pairs or small families of Red-crowns with wandering flocks of other species is as regular a feature of their lives elsewhere as it is in British Honduras (Willis, 1960c) although in all regions they wander in and out of flocks. The other ant-tanagers also regularly join forest flocks, except that Red-throated Ant-Tanagers do not do so frequently in British Honduras or in the Forest Reserve (Panama), where Red-crowned Ant-Tanagers seem to usurp this role. Since the lesser flock attendance in British Honduras seemed a result of fast and horizontal Red-throat foraging there, it may be that Red-throats forage rapidly and horizontally more and join flocks less wherever Red-crowns take those roles. In Amazonia, one hardly ever sees Red-crowns away from the wandering flocks of antbirds (*Thamnomanes caesius*, *T. ardesiacus*, *Myrmotherula longipennis*, *M. menetriesii*, etc.) and other birds. In Trinidad, however, Red-crowns are much more common and many are away from bird flocks.

ALARM BEHAVIOR: Chattering at the intruder and flipping from side to side with flitting of the wings are regular alarm reactions, as they are in British Honduras. After the first chatters, the pair tend to flee rapidly with the forest flock.

VOICE: In Panama and Trinidad the "chatter," at five notes per second, is much the same as the scolding chatter of Sooty Ant-Tanagers and like the chatter of Red-crowns in British Honduras. In Amazonia the usual chatter is only a single or double rough "chij," sometimes trailing off into "cheu cheu cheu" softer notes. Notes of the latter type, "cheup" or variants, come from foraging members of a family and extend into short series as a bird flies and another follows. In Panama, the "cheup" was

harsher than in British Honduras and more like the "chak" of local *H. fuscicauda* or like a single note of the chatter. In Amazonia, the foraging note is "choork," much as in British Honduras. "Peir peir peir peir" series as the male flew and the female followed also seemed more sibilant and harsher than in British Honduras. Distinctive day songs seem more characteristic of ant-tanagers in British Honduras than elsewhere,

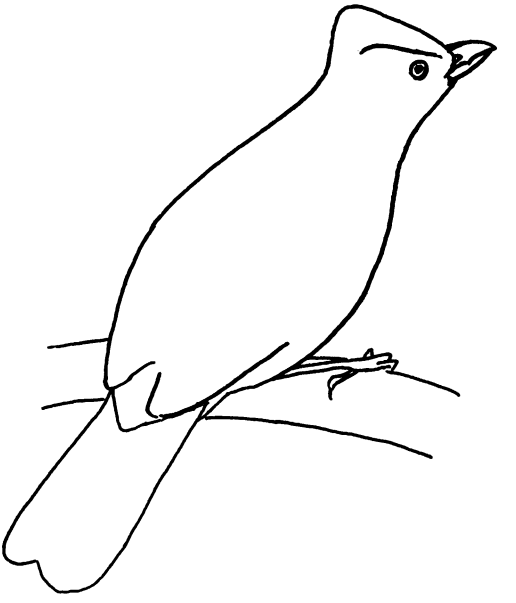

FIG. 7. Posture of dawn-singing male Red-crowned Ant-Tanager at Cerro Campana.

although some of the "peir" series seem songlike. At times Amazonian birds sing short indistinct phrases, "heer, wheriyer, wher-ker, whoo-ker" (San Alejandro, Peru) or "ser he-her, he-her veer" (Maloquinha, Pará, Brazil; near female building nest), but these may be dawn song fragments.

Dawn singing was still fairly regular at Cerro Campana, August 28–29, 1961; the male sang low in dense second growth and wandered among low perches like *H. fuscicauda* rather than staying atop one high perch as does the male *H. rubica* in British Honduras. Each perch change was marked with a "chut-ack pee pee pee" as if he started a chatter but ended with leading notes. His crest was slightly raised (fig. 7) for each song, a rather monotonous and sibilant "eit-er'pyer" or "pshe'ik der-er" repeated three to five times, much like the "intervene" song Skutch (1954) reported from Costa Rica and musically decidedly inferior to the clear songs of northern Red-crowns. There were as many as seven or eight songs per

minute, from 05:50 or before to 06:30 the first day, and to 06:25 the next day, before the male and female joined to forage in the gathering interspecific flocks.

REPRODUCTION: Snow and Snow (1964) reported nesting in Trinidad from February to November, but mainly May to August. February 26, 1966 at Maloquinha, Pará, Brazil, a female was sitting and pressing the body down and wings out as she tried to place a long strand on four leaflets from a 70-degree palm frond; she gave up and tried the next higher frond the same way. April 3, 1966 I twice flushed a female from a nest and two cinnamon-splotched white eggs on the Coatá-Madeira Trail (about latitude 4° 12′ S., longitude 59° 20′ W.). The nest was a rhizomorph-lined leafy cup 1.3 m. up on a petiole in the crown of a spiny palm 2.5 m. tall, more like the nest of a Red-throat in British Honduras than like the nest of a Red-crown there (Willis, 1961). Snow (*in litt.*) found nests in Trinidad were of the northern type, except that they often had pendent dead twigs whitened by fungus.

TERRITORIALITY: Two, less often three or four birds, travel together over each territory. On May 20, 1962 a boundary dispute at Umbria, Colombia was rather like disputes in British Honduras: chattering "chij" notes mixed with songs from "cree-chree" to "chee-cher, chur-chee, chereeher" were hurled back and forth as the families approached, flew about, then retreated. One male kept flying back and forth between the boundary and his flock as it moved away, giving a variety of songs.

CRESTED ANT-TANAGERS

Since I have recently discussed the behavior of this Colombian species (Willis, 1966), I shall only tabulate its behavior for comparison (table 1). I found it in second growth and landslide woodlands along the plunging Río Cali at 1750 m. elevation, La Margarita, on April 26, 1966, and must withdraw my earlier suggestion that the species occurs only on the Pacific slope of the Andes.

DISCUSSION

Decisions on conspecificity or lack of it must be tentative when similar birds are allopatric, as is often the case for ant-tanagers. The moderate differences between the chatters and nests of Amazonian and northern (Trinidad to Mexico) Red-crowned Ant-Tanagers suggest that these may prove different species on closer study. If so, the boundary may be between *rhodinolaema* of southern Colombia (north to the Cordillera de la Macarena, Meta) and *coccinea* of northern Colombia (Boyacá) to western Venezuela. Parkes (1969b) noted that these two forms show no approach

TABLE 1

BEHAVIOR OF ANT-TANAGERS

	Crested	Red-crowned			Red-throated		Black-cheeked	Sooty
	Colombia	British Honduras	Panama	Amazonia	British Honduras	Panama	Costa Rica	Colombia
Habitats								
Median elevation (m. in 100s)	13	1	7	2	1	1	2	7
Median rainfall (mm. in 100s)	45	15	25	25	15	30	45	25
Second growth used	S	S	S	S	F	F	F	F
Landslide woodland	F	N	N	N	N	N	S	N
Creekside woodland	F	S	S	F	S	S	S	F
Continuous woodland	S	F	S	F	S	S	S	S
Foraging								
Median height (m.)	4	5	5	5	2	2	3	2
Horizontal travel	S	S	S	S	F	F	F	F
Open twigs used	S	S	S	S	F	F	F	F
Hop upward	F	F	F	F	S	S	S	S
Hop on foliage	S	F	F	F	S	S	S	S
Dissect large prey	S	F	•	•	S	F	S	S
Fruit used	S	S	•	•	S	S	S	S
Follow army ants	N	R	N	N	F	F	F	F
Voice								
Chatter (notes/second)	2	5	5	2	2	2	2	5
Static used	N	N	N	N	F	F	F	F
Foraging grunts	S	F	F	F	F	F	F	F

TABLE 1—(*Continued*)

	Crested	Red-crowned			Red-throated		Black-cheeked	Sooty
	Colombia	British Honduras	Panama	Amazonia	British Honduras	Panama	Costa Rica	Colombia
Leading notes	F	F	F	F	F	F	F	F
Rattles	N	N	N	N	N?	F	F	F
Distinct day songs	S	F	N	N	F	N	N	N
Dawn songs	F	F	F	•	F	F	F	F
Crest Raising								
For dawn songs	N	F	F	•	N	N	N	F
In disputes	F	N	•	•	N	N	•	F
Female precopulatory	F	F	•	•	S	•	S	•
Submissive	•	•	•	•	•	S	•	•
Alarm Behavior								
Much flipping	F	F	F	F	F	F	S	R
Flits wings	F	F	F	F	R	R	R	F
Chatter or scold	F	F	F	F	F	F	F	F
Special fleeing notes	S	F	F	F	F	F	F	F
Preening								
Scratch over wing	•	F	•	•	F	F	F	F
Courtship								
Songs to female	N	F	N	N	F	N	N	N
Short sexual chases	S	S	S	•	F	F	F	F
Courtship feeding	N	N	•	•	N	N	S	•
Female call rapid	N	F	•	•	N	•	N	•
Strong male display	N	S	•	•	N	N	N	S

TABLE 1—(*Continued*)

	Crested	Red-crowned			Red-throated		Black-cheeked	Sooty
	Colombia	British Honduras	Panama	Amazonia	British Honduras	Panama	Costa Rica	Colombia
Reproduction								
Median nest height (m.)	•	3	•	2	2	3	•	1
Leafy nest	•	N	•	F	F	F	•	F
Male helps build	•	R	•	N	R	R	•	•
Male accompanies building female	•	F	•	F	F	F	•	•
Clutch size	•	3	•	2	3	2	•	2
Eggs unmarked white	•	N	•	N	F	F	•	N
Male incubates	•	N	•	N	N	N	•	•
Male feeds incubating female	•	N	•	N	N	N	•	•
Male feeds nestlings	•	F	•	•	S	S	•	S
Female feeds nestlings	•	F	•	•	F	F	•	F
Male broods nestlings	•	N	•	•	N	N	•	N
Female broods nestlings	•	F	•	•	F	F	•	•
Both parents feed fledglings	•	F	•	•	F	•	•	•
Family groups persist	F	F	F	F	F	F	F	F
Families 5 or more	S	S	R	R	F	S	R	R
Territoriality and Disputes								
Present	F	F	F	F	F	F	F	F
Much song in disputes	R	F	•	F	R	R	•	R
Dashing about	F	S	•	S	F	F	•	S
Strong displays	F	R	•	R	R	R	•	F
Prolonged disputes	F	F	•	F	R	R	•	•

Symbols: F, frequently; N, not recorded; R, rarely; S, sometimes; •, not possible to check.

to each other in plumage. The division may have been promoted because of difficulty in gene interchange between birds breeding in the austral summer (September to April) and those breeding in the boreal summer period (March to October). Some striking morphological and behavioral differences between Sooty, Red-throated, and Black-cheeked ant-tanagers are here interpreted as indicating they are separate species, but the differences between the undoubtedly conspecific *salvini* and *fuscicauda* groups of Red-throated Ant-Tanagers approach the level of differences here interpreted as between species.

All ant-tanagers are clearly closely related. If it were not that Red-crowned Ant-Tanagers overlap Red-throated Ant-Tanagers in geographic range, there would be ornithologists who would consider them allopatric members of a single species. In general, however, I estimate that the strongest behavioral differences are between Crested, Red-crowned, and the other ant-tanagers; among the others, the Sooty Ant-Tanager is most distinct; the Black-cheeked and Red-throated are less distinct. All of these forms are more distinct, however, than are groups I tentatively consider subspecies (the various forms of *H. rubica* and *H. fuscicauda.*)

Ant-tanagers are rather similar in their behavior patterns. All are adapted to moderately fast searching for small fruits and large insects through moderately dense undergrowth in secondary or riverine woodlands. The Crested Ant-Tanager finds these woodlands on mountain slopes, the others in a variety of lowland habitats. The Sooty, Black-cheeked, and Red-throated ant-tanagers regularly follow army ants and tend toward the second growth type of woodland, the Red-crowned Ant-Tanagers to taller woodland. All behave, in a sense, like large vireos or small jays that must travel rapidly because of working narrow foraging zones and because their size requires considerable quantities of rather small and scattered prey.

In other parts of Central and South America, various species seem to replace ant-tanagers and forage in similar ways. On the lower montane slopes at Cariblanco, Costa Rica, I found Azure-hooded Jays (*Cyanolyca cucullata*) behaving like ant-tanagers. Several kinds of tanagers seem ecological replacements for ant-tanagers in other regions: Lemon-browed Tanagers (*Chlorothraupis olivacea*) of the lowland forests of western Colombia and nearby, Carmiol's Tanagers (*Chlorothraupis carmioli*) of Central America and the lower eastern slopes of the Andes from Colombia to Peru, and Ochre-breasted Tanagers (*Chlorothraupis stolzmanni*) of the lower western Andean slopes all remind one of ant-tanagers; Tawny-crested Tanagers (*Tachyphonus delattrii*) are in large flocks like small ant-tanagers in the lower levels of humid woodlands from Nicaragua to

Ecuador; Dusky-faced Tanagers (*Mitrospingus cassinii*) occupy dense streamside thickets from Costa Rica to Ecuador. Tricolored Brush-Finches (*Atlapetes tricolor*) seem to replace ant-tanagers in mossy second growth from 1500 to 2000 m. elevation from Colombia to Peru. In drier forests at these elevations Lineated Foliage-Gleaners (*Syndactyla subalaris*) and Montane Foliage-Gleaners (*Anabacerthia striaticollis*) replace ant-tanagers to some extent.

Although ant-tanagers are rather flexible or adaptable in their foraging techniques, being almost as generalized as jays, they are limited on one side by their tendencies to keep to certain levels in the forest undergrowth and to travel either horizontally or vertically. On the other side, they are apparently limited by specialists or groups of specialists, such as the ant-birds over army ants. Habitats and geographical ranges probably are limited toward the borders of the tropical forest by unsuitable habitats, toward the centers of the forest by bird species that can better utilize the scanty low foliage. The medium degrees of adaptation and of adaptability in the foraging of ant-tanagers seem to lead to use of forest habitats of "medium" height.

It is not otherwise evident why other species replace ant-tanagers in many regions, or why ant-tanagers are absent from many seemingly suitable areas outside their present ranges. Possibly historical factors and geographical barriers are also involved: the spread of ant-tanagers is blocked peripherally by swamps, dry regions, montane barriers, etc. Perhaps populations that do manage to start beyond such barriers are wiped out by periodic bad years or by series of bad years, or perhaps by disease organisms. The habitats that seem suitable may actually be unsuitable or have a competitor or a complex of competitors that make them unsuitable. Questions like these are among those basic to ecology, but even with the extensive work done on the genus *Habia* are still difficult to answer.

I suspect that tropical birds, which often have heavy nest predation and low reproductive rates, may be rather slow at extending their ranges or at replacing locally extirpated populations. The local extermination of birds by cutting forests for agricultural and other purposes may be a more serious matter than it has been for birds of the United States and Europe. The ant-tanagers could benefit from a low level of cutting activity, provided forest edges and second growth 10 to 60 years old are available, but ant-tanagers will disappear with the intensive deforestation that is turning most of northern Colombia and other neotropical regions into cultural savannas. The activities of river conservation groups of the TVA type, like the CVM (Corporación Autónoma Regional de los Valles del

Magdalena y del Sinú) in northern Colombia, may yet save riverine and other forests for birds like ant-tanagers.

SUMMARY

The Red-throated Ant-Tanager (*Habia fuscicauda*) of Colombia to Mexico and the Black-cheeked Ant-Tanager (*H. atrimaxillaris*) of the humid forests of Golfo Dulce in Costa Rica have been considered allopatric forms of the Sooty Ant-Tanager (*H. gutturalis*) of the northern foothills of the Andes in Colombia. Morphological and behavioral studies suggest that they are best regarded as different species, although they are closely related.

Sooty Ant-Tanagers have red throats, long red crests, and sooty bodies both in males and females. Black-cheeked Ant-Tanagers are blackish, with red bibs and slight red crowns in both males and females. Red-throated Ant-Tanagers are sexually dimorphic, the males being reddish and having red throats and crowns, the brownish females having yellow throats.

All forage in pairs or small family groups by crisscrossing rapidly over territories of a few hectares in patchy forest to low second growth, especially along streams. They fly horizontally low through the undergrowth, perch to look carefully from open but steady twigs and limbs, and sally or hop over to peck insects from the foliage. All eat small fruit at times. Sooty and Black-cheeked ant-tanagers, which seem to enter tall forest more readily, forage somewhat higher than Red-throats, but all keep below 10 m. up most of the time. All these species follow swarms of army ants readily.

All give faint grunts as they forage, static notes when alarmed, and rasping noises when mobbing the observer. The noises of Sooty Ant-Tanagers are very fast chatters, more like those of the related Red-crowned Ant-Tanager (*Habia rubica*) than like the slow scolds of Red-throated and Black-cheeked ant-tanagers. All sing musically at dawn, and scatter phrases of song later in the day; the Sooty Ant-Tanager raises its bushy crest to sing at dawn, in the fashion of Red-crowned Ant-Tanagers.

The Sooty Ant-Tanager also regularly raises its crest in boundary disputes, a habit shared in the genus only by the Crested Ant-Tanager (*Habia cristata*) of western Colombia. In Red-throated Ant-Tanagers, the losing bird in a boundary dispute sometimes raised the crest briefly.

A male Sooty Ant-Tanager showed his mate a strong display after dawn singing.

In reproductive behavior, the three all show rapid "rattles" during sexual chases. A Black-cheeked Ant-Tanager male performed courtship feeding. Since there is no other record of courtship feeding in the genus,

more observations are needed to determine whether others occasionally feed or if the behavior pattern is regular in Black-cheeks. Nests of Red-throated and Sooty ant-tanagers are leafy cups, set fairly low in the undergrowth. The eggs of Red-throats are unmarked white, those of Sooties are heavily speckled.

In mobbing behavior, Sooty Ant-Tanagers tend to stare and flit the wings, whereas Red-throats and Black-cheeks swing one way and then the other with flourishes of the spread tail.

The monomorphism, speckled eggs, chattering voice, and use of a crest display in dawn singing, boundary encounters, and to the mate are the most striking differences between Sooty Ant-Tanagers and the species formerly lumped with it. Black-cheeked Ant-Tanagers differ from Red-throats mainly in the females having plumages like the males and in courtship feeding. Possibly these differences would serve as reproductive isolating mechanisms, although the taxonomic status of forms as similar as the last two will probably remain uncertain unless they spread to meet each other.

Red-crowned Ant-Tanagers in the Amazon differ from those previously studied in British Honduras in a few aspects, such as in having indistinct day songs and short chatters (often one note) in the Amazon. The Red-throated Ant-Tanager of Panama also has an indistinct day song, suggesting that songs degenerate at low latitudes in both species. However, Sooty Ant-Tanagers have unusually good dawn songs, contrary to the general trend. Red-crowns in the Amazon have leafy nests, unlike the thin-strand cups of birds from Trinidad into Central America. Possibly southern races of the Red-crown constitute a different species from that of the northern ones. Foraging and other behavior throughout the Amazon is of the usual type, involving small groups wandering over territories in forests, keeping in the upper undergrowth. Only in Trinidad, where ant-following birds are nearly absent, do Red-crowned Ant-Tanagers follow army ants; even there they do so rarely. It is remarkable that such a widely distributed species varies so little in its foraging behavior, even in regions where competing other species of ant-tanagers are absent.

The species of the genus form a homogeneous group behaviorally and ecologically, adapted to moderately fast searching for small fruits and large insects through moderately dense undergrowth in secondary or riverine woodlands. Some other tanagers, jays, and perhaps antshrikes have similar foraging beats and replace them to a certain extent in other Neotropical woodlands, but the reasons why ant-tanagers are absent from many seemingly suitable tropical woodlands are not yet evident. Historical factors and geographical barriers may play a large role, and human

activities are sure to affect these birds in the next few years.

List of Study Areas

(Coordinates and elevations from various maps, are approximate)

Mexico: San Blas and Singayta (21° 34′ N., 105° 14′ W., Dec. 28, 1959, Jan. 2–5, 1968).

British Honduras: Gallon Jug (17° 33′ N., 89° 01′ W., Feb. 13–Aug. 2, 1957).

Costa Rica: Golfito (8° 38′ N., 83° 10′ W., Mar. 25–28, 1961).

Panama: El Volcán (8° 46′ N., 82° 40′ W., 1300 m., July 26, 1962); Cerro Campana (8° 41′ N., 79° 56′ W., 800 m., Aug. 27–29, 1961, June 24–27, 1968); Fort Sherman Road (9° 17′ N., 79° 57′ W., May 23, 1961); Rio Medio (9° 14′ N., 79° 58′ W., Sept. 2–3, 1963); Fort Davis (9° 17′ N., 79° 54′ W., May 22, 1961); Bohio Peninsula (9° 12′ N., 79° 51′ W., 16 dates); Rio Agua Salud (9° 12′ N., 79° 48′ W., 13 dates); Buenavista Point (9° 11′ N., 79° 50′ W., 33 dates); Frijoles (9° 11′ N., 79° 48′ W., 6 dates); Barro Colorado (9° 10′ N., 79° 51′ W., 14 dates); Pipeline Road (9° 10′ N., 79° 45′ W., 3 dates); Summit Gardens (9° 04′ N., 79° 39′ W., 3 dates); Forest Reserve (9° 06′ N., 79° 37′ W., 11 dates); Fort Clayton (9° 00′ N., 79° 35′ W., Aug. 3, 1966); Cerro Azul (9° 10′ N., 79° 25′ W., 800 m., June 23, 1964).

Colombia: Las Pulgas (7° 48′ N., 76° 20′ W., 200 m., Mar. 27, 1965); Puerto Valdivia (7° 14′ N., 75° 26′ W., 900 m., June 8–9, 1962); Remedios (7° 02′ N., 74° 41′ W., 800 m., May 2–14, 1962), Quibdo Road (*ca.* 5° 48′ N., 76° 15′ W., 1400 m., Feb. 21, 1962); Las Cascadas (3° 39′ N., 76° 47′ W., 700 m., Mar. 28, 1962, Apr. 26, 1966); Queremal (3° 32′ N., 76° 43′ W., 1500 m., Mar. 16–29, 1962); La Margarita (3° 30′ N., 76° 32′ W., 1700 m., Apr. 25, 1966); Tres Esquinas (0° 44′ N., 75° 15′ W., 200 m., Apr. 13–20, 1962); Umbria (0° 34′ N., 76° 34′ W., 350 m., May 20, 1962); Mitú (1° 05′ N., 70° 04′ W., Apr. 30–May 9, 1966).

Ecuador: Limoncocha (0° 25′ S., 76° 38′ W., 250 m., Oct. 28–Nov. 8, 1965); Putuimi (2° 39′ S., 77° 28′ W., 250 m., Nov. 25–Dec. 3, 1965); Yaapi (2° 51′ S., 77° 56′ W., 350 m., Nov. 10–24, 1965).

Peru: San Alejandro (8° 50′ S., 75° 14′ W., 250 m., Dec. 15–16, 1965).

Brasil: Benjamín Constant (4° 22′ S., 70° 02′ W., Apr. 17–18, 1966); Carauarí (4° 52′ S., 66° 54′ W., Mar. 14–21, 1966); Borba (4° 24′ S., 59° 36′ W., Mar. 28, 1966); Coatá (4° 14′ S., 59° 17′ W., Apr. 1–12, 1966); Nova Olinda do Norte (3° 43′ S., 59° 0′ W., Mar. 30–31, 1966); Itaituba (4° 14′ S., 56° 04′ W., Mar. 3–4, 1966); Maloquinha (4° 18′ S., 56° 05′ W., Feb. 18–Mar. 1, 1966); Itapucurá (4° 21′ S., 56° 04′ W., Mar. 2, 1966); Diamantino (2° 38′ S., 54° 43′ W., Jan. 17–19, 1966); Palhão (2° 45′ S., 54° 19′ W., Jan. 26–Feb. 9, 1966); Barreirinha (2° 35′ S., 54° 01′ W., Feb. 10, 1966).

Trinidad: Simla (10° 42′ N., 61° 17′ W., 300 m., Nov. 26–Dec. 16, 1961, Aug. 19, 1967).

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