

ON THE BEHAVIOR OF FIVE SPECIES OF
RHEGMATORHINA, ANT-FOLLOWING ANTBIRDS
OF THE AMAZON BASIN

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IN the rain forests of the Amazon, separated for the most part by giant rivers that forest-loving birds do not cross, live five little-known antbirds (family Formicariidae) of the genus *Rhegmatorhina*. All are plump, short-tailed birds somewhat larger than House Sparrows (*Passer domesticus*); all have large pale greenish or blue bare areas around the eyes and lengthened crown feathers that they can erect to form crests. They differ strikingly in the arrangement of black, brown, rufous, and white in their pied plumages (see frontispiece), but they are clearly closely related species.

J. Natterer (according to Pelzeln, 1868, p. 166) recorded that two Crested Antbirds (*Rhegmatorhina cristata*) he took in 1831 on the Uaupés River, Brasil, were following army ants. Riker (1891) noted that the pair of Bare-eyed Antbirds (*Rhegmatorhina gymnops*) he collected near Santarém, Brasil in 1877 were following a swarm of ants. On the specimen label of a Hair-crested Antbird (*Rhegmatorhina melanosticta*) from Avila, eastern Ecuador (Philadelphia Academy of Sciences no. 169629, collected by W. Clarke-Macintyre) is a note that the local name is "tamia añangu pishcu." At Limoncocha, nearby on the Rio Napo, the Quichua word for the army ant *Eciton burchelli* is "tamia añangu." Nothing else has been recorded about the behavior of birds of this genus. In the course of studies of birds that follow army ants, I visited the Amazon briefly in 1962 and for seven months in 1965 and 1966. These studies show that all five *Rhegmatorhina* are "professional" ant-followers, birds that forage most of the time over swarms of army ants and capture arthropods flushed by the ants.

DESCRIPTIONS AND DISTRIBUTIONS

The Crested Antbird (*R. cristata*) was the first species described (Pelzeln, 1868). There are three known specimens, Natterer's pair from São Jeronimo (Cachoeira Ipanoré, Rio Uaupés, northwestern Brasil) and a male from Mitú (Olivares, 1964), upstream on the

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FRONTISPIECE: Antbirds of the genus *Rhegmatorhina*, from a painting by Guy Tudor. Males in slight alarm poses at left, females loafing at right. Top pair, Bare-eyed Antbirds (*R. gymnops*). Second pair, Harlequin Antbirds (*R. berlepschi*). Central pair, White-breasted Antbirds (*R. hoffmannsi*). Fourth pair, Crested Antbirds (*R. cristata*). Lowest pair, Hair-crested Antbirds (*R. melanosticta*).



TUDOR

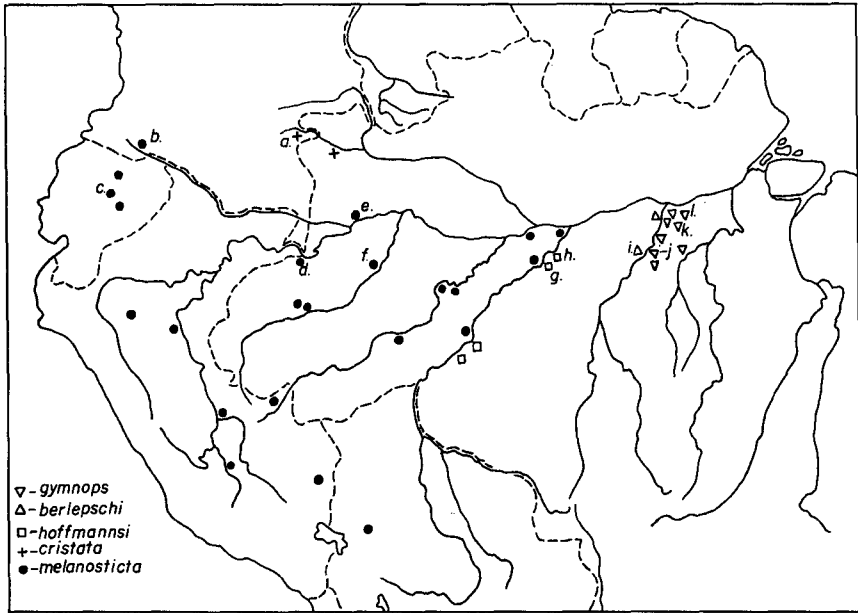


FIG. 1. Ranges of the five species of *Rhegmatorhina*. a, Mitú. b, Umbria. c, Zatzayacu. d, Benjamín Constant. e, Tonantins. f, Carauarí. g, Borba. h, Coatá. i, Maloquinha. j, Itapucurá. k, Palhão. l, Barreirinha.

same river in southeastern Colombia (Fig. 1). Males are black, rufous, and olive-brown (frontispiece); females have small dark marks on the back and perhaps on the wing coverts but are otherwise like males. Hellmayr, who examined the immature female taken by Natterer, says (1924, p. 306) it lacks the elongated crest and has a darker, blackish-chestnut crown as well as a more russet-brown back than does the male.

Natterer (fide Pelzeln, 1868, p. 167) states that the eye-ring of the adult male he took was "blaulich weiss," but that the eye-ring of the young female was "schwarzlich, nackte Haut, um die Augen sehr hellgrau, bloss gegen das Ohr in Violett ziehend." Young birds in this and related genera commonly have dusky and smaller bare faces than do adults. Young commonly have short crests and tend to be brown in areas where adults are brightly colored. Olivares (1964) suggested that the male from Mitú must have had a red face in life; however, among antbirds only three species of *Phlegopsis* have red faces, and it is nearly impossible to guess facial color in life from any antbird specimen once postmortem changes have set in. All Crested Antbirds I saw at Mitú had pale bluish-white faces.

The type species of the genus is the Bare-eyed Antbird (*R. gymnops*). It is known from many localities from the west bank of the Rio Xingú to the east bank of the Rio Tapajoz. Male Bare-eyed Antbirds are sooty black, with contrasting large pale bluish-green faces and brown mantles and tails. Females are dark brown, varying to blackish around the bill and bare eye-ring.

Harlequin Antbirds (*Rhegmatorhina berlepschi*) live on the west bank of the lower Tapajoz. Males are strangely pied birds (see frontispiece). Except for a chestnut breast-splotch, gray underparts, and blackish borders of the crest, the male Harlequin Antbird is rather like the male Crested Antbird. The females differ strongly, as female Harlequin Antbirds are barred black and buff on the underparts and barred black on the upperparts.

To the west of Harlequin Antbirds, on the east bank of the Rio Madeira, live Hoffmanns' or White-breasted Antbirds (*Rhegmatorhina hoffmannsi*). The female looks like a female Harlequin Antbird, but has wider bars underneath and a darker, dusky-rufous crown; the whole lower face and throat and bib below a pale greenish face are white. Male White-breasted Antbirds also are white from eye-ring to chest; the underparts are gray and the upperparts greenish-brown, much as in *berlepschi*. There is less rufous on the wings and much less in the crest of *hoffmannsi*, which is black-crested and black-naped.

The Hair-crested Antbird (*Rhegmatorhina melanosticta*) lives south of the Amazon from the west bank of the Rio Madeira west to the Andean foothills in Bolivia and Perú, thence north across the smaller branches of the upper Amazon into eastern Ecuador and southeastern Colombia. At Tonantins, on the north bank of the Amazon in western Brasil (Fig. 1, e), the Ecuadorean subspecies occurs (fide Kenneth C. Parkes). Presumably *R. m. melanosticta* occurs down the length of the Putumayo River, from Colombia into Brasil. Possibly it meets the Crested Antbird somewhere between the Vaupés and Putumayo Rivers, or is separated from it by the rather small Caquetá or Japurá.

Instead of the long, pointed, shiny crest feathers of adults of other species of *Rhegmatorhina*, Hair-crested Antbirds have whitish crown feathers that separate like aigrettes into hairlike filaments. In the Andean foothills west of the Rio Ucayali and south of the Rio Marañon, Hair-crested Antbirds have buff crown feathers. The range of the buff-crested subspecies (*R. m. brunneiceps*) separates the ranges of the white-crested subspecies (*melanosticta*) north of the Marañon and the similar subspecies (*badia* and *purusianus*) southeast of the Ucayali. All the subspecies have dark brown bodies and dark, velvety faces around large, pale blue eye-rings. Females are spotted above with small, black, reddish-tipped crescents.

THE STUDY AREAS

Table 1 lists places where I studied the five species of *Rhegmatorhina*. The forests of all these areas are very similar in general aspect, but differ in detail. They are tropical to upper tropical forests, moderately hot and very humid, with dense canopies and fairly uncluttered undergrowth. As in most mature forests, occasional treefalls break the canopy and grow up to dense thickets of saplings and sprouts around tangles of fallen limbs and lianas. The ground is covered with a thin layer of recently fallen leaves, which in wet weather are decomposed by invertebrates and reused by plants so fast that there is relatively little humus or evidence of decay except in treefalls.

The very wet forests at Mitú, Colombia, rest almost directly on the rocks of the pre-Cambrian Guianan Shield, in an area of creeks stained red by humic acids and of rivers of clear, blackish water. Rainfall is probably about 3500 mm a year, with slightly lower monthly totals in April and September. The extremely thin soil is seldom visible, for it is interlaced by a carpet of roots and rootlets over the rocks and under

TABLE 1
STUDY AREAS

Locality ^a	Elevation (Meters) ^a	Dates
COLOMBIA		
Mitú, Vaupés (1°5'N, 70°04'W)	150	29 Apr.-9 May 1966
Umbria, Putumayo (0°53'N, 76°34'W)	350	18 May-2 June 1962
ECUADOR		
Zatzayacu, Napo-Pastaza (1°6'S, 77°52'W)	550-950	20-23 Oct. 1965
BRASIL		
Benjamín Constant, Amazonas (4°22'S, 70°02'W)	75	16-18 Apr. 1966
Carauarí, Amazonas (4°52'S, 66°54'W)	75	15-20 Mar. 1966
Borba Road, Amazonas (4°28'S, 59°35'W)	75	28-29 Mar. 1966
Coatá Ridge, Amazonas (4°15'S, 59°18'W)	75	2-11 Apr. 1966
Coatá-Madeira Trail (4°12'S, 59°20'W)	75	12 Apr. 1966
Itaituba Road, Pará (4°14'S, 56°04'W)	75	3 Mar. 1966
Maloquinha, Pará (4°18'S, 56°05'W)	75	20 Feb.-1 Mar. 1966
Itapucurá, Pará (4°21'S, 56°04'W)	75	2 Mar. 1966
Palhão, Pará (2°47'S, 54°17'W) ^b	75	25 Jan.-9 Feb. 1966
Barreirinha, Pará (2°35'S, 54°01'W)	75	11 Feb. 1966

^a Latitudes, longitudes, elevations from available maps, are approximate.

^b Just above Cachoeira do Portão.

the fallen leaves. Trees with tangled stilt roots perch on the rocky soil. The lush and moss-covered undergrowth resembles that of a wet montane or cloud forest. However, it is obvious that the poor soil and rocky basement make living conditions difficult for trees, despite the high rainfall and moderate temperatures. From the air, one sees elevated mesas and ridges, covered with rocky to bushy savannahs or scrubby woodland, interlacing these forests of the Vaupés. The variety provided by the stilt-rooted trees and the lush undergrowth of these patchy forests may explain why Crested Antbirds can live along the Rio Vaupés. However, the interlacing forests and savannahs of the Guianan Shield extend from the Cordillera Macarena, a huge table mountain against the Colombian Andes, past great mesas like Roraima in the Gran Sabana of Venezuela, into the Guianas. If conditions like those at Mitú are found over much of this region, the narrow range of Crested Antbirds is puzzling.

I studied Hair-crested Antbirds in less peculiar but similarly lush forests. The annual rainfall varies from four or five meters in the Andean foothills at Zatzayacu, Ecuador, and four or so at Umbria, Colombia, to 2742 mm at Benjamín Constant and 2534 mm at Carauarí in Brasil. The rain is distributed over the year, with slight dry seasons about July and January.

Richards (1952) and others have emphasized that the undergrowth of mature tropical forests is relatively open and uncluttered, and that dense "jungle" is generally a sign of second growth after man or floods or other natural catastrophes have removed the natural canopy. However, such very wet forests as these of upper Amazonia have fleshy-leaved plants crowding the undergrowth, moss on trees and fallen logs, and large numbers of epiphytes. The trees are usually less tall and magnificent than in areas with two to three meters of rainfall per year and with strong dry seasons, as in central Amazonia.

The forests of upper Amazonia look somewhat like the lower montane rain forests (where low evaporation leads to similarly humid conditions, despite low rainfall) of Trinidad, Colombia, and Panamá. Perhaps, with very high rainfall, trees fall to fungus and insects and weather so frequently that rain forests are actually lower and thicker than "monsoon" forests, such as the magnificent forests of northern Colombia and of central Amazonia. However, Indians and others may have cut most of the forests of upper Amazonia; it is difficult to get away from human interference and second growth anywhere in Amazonia. I have seen occasional patches of fairly uncluttered and tall forest in eastern Ecuador, suggesting that really mature rain forest may be nearly as uncluttered as mature seasonal or monsoon forests.

Since Hair-crested Antbirds range eastward into relatively dry forests near the Madeira and to strongly seasonal forests in Bolivia, they may live in open forests with little undergrowth in some regions. However, I found them only where the undergrowth is lush. At Carauarí, near an oxbow lake of the meandering yellow Rio Juruá, there are swampy oxbows and cutoff channels dissecting the rather swampy lowland forests. At Benjamín Constant I found them in wetter but less swampy forests back from the Amazon, which is too large and fast to form oxbows. At Zatzayacu the steep lower montane forests east of the Baños-Napo highway are rain-drenched but not swampy. Umbria is in rolling foothills just out from the Andes, and the forests are swampy only along the nearby Rio Guineo.

I found the other three species of *Rhegmatorhina* in less cluttered and more typical lowland forests south of the Amazon in central Brasil. Rainfall is lower in central Amazonia than in upper or lower Amazonia, or two to three meters annually; there is a strong dry season from June to October or later. An unusually severe dry season had extended into January when I arrived on the Tapajoz Plateau near Santarém in 1966. The crackling dead leaves on the forest floor and the dry lower levels of the forest were protected by the evergreen canopy, except in areas where colonists had turned the region to a semi-desert, but it was evident why there were few epiphytes and little moss.

The Tapajoz Plateau or "planalto," home of the Bare-eyed Antbird, is an undulating forested plateau, generally less than 100 meters above the sandy plains along the rivers. Bounded to the north by the immense yellow Amazon, to east and west by the great blue Xingú and Tapajoz Rivers, it rises gradually to savannahs on the low Serra do Cachimbo to the south. It is a northern extension of the pre-Cambrian Brazilian Shield. I was unable to find Bare-eyed Antbirds at the type locality of Diamantino, about eleven kilometers out the Palhão road from Santarém. The forests there have been cut into patches by refugees from northeastern Brasil, and the diversity of forest-inhabiting birds has decreased since the time of Riker (1891). Beyond Diamantino, the wave of cutting and burning has reached about fifty kilometers from Santarém, but from there to the end of the road at Palhão, about eighty kilometers from Santarém, the forest is little disturbed. Palhão, the future site of a hydroelectric plant for Santarém on the falls or Cachoeiras of Palhão and Portão, was an airstrip scrape and a few shacks by the clear little Rio Curuá-Una when I visited it. The tall forest was quite open underneath. Stilt roots, buttressed trees, and epiphytes were uncommon. I was reminded of the open and magnificent older forests in Panamá and northern Colombia, in areas that also have a strong dry season. Similarly well-drained and tall forests covered the planalto inland from Barreirinha, the forestry and research center of the United Nations (FAO) down the Curuá River below Palhão. There were similar forests at Itapucurá, behind a pasture and a few houses on the Tapajoz River. Despite the tall forests and the deep

soil of the Tapajoz Plateau, Indians seldom used it for crops; Americans and Brazilians, from Civil War slave-owning refugees at Diamantino to Henry Ford and his rubber plantations and Brazilians who are trying to resettle refugees, have spent fortunes finding that modern man is no more successful than the Indians in using this poor-soil region.

At Maloquinha, a few kilometers across the blue Tapajoz from Itapucurá, one steps into the different world of *Rhegmatorhina berlepschi*. "Maloquinha" means "little maloca" or "little Indian site," and there are evidences of Indian and later use everywhere in the forest. The huge brasilnut trees (*Bertholletia excelsa*), each cleared out underneath by castanheiros who gather and open fallen pods each January and February, are probably the only remaining trees of the original forest. Otherwise trees are small to medium in size, often densely capped with vines. The undergrowth is fairly dense in many areas, as is usual in secondary forest. It is difficult to tell how different this forest would be from the relatively undisturbed forests across the river had man not interfered.

There is no plateau on the west side of the Tapajoz, so the river in flood does most of its work on this side. Swampy watercourses and sloughs break the forest. Behind Maloquinha Cupituã Creek, which flows south to meet the Tapajoz going north, had magnificent floodplain forest or "varzea." The varzea, at the time I visited, was not yet flooded; dead leaves littered the very open undergrowth among huge buttressed trees and swampy or incised channels of the Cupituã. Since leaves began on the saplings at about head height, I suspect annual flooding normally reaches a meter or so. Between the Cupituã and Maloquinha there are low, rolling hills with very irregular forest, cut by swampy little creeks with an undergrowth of palms.

The road west and south from Itaituba cuts behind Cupituã Creek, crossing at least one of its upper branches. After passing through several kilometers of cutover and burnt-over poor farmland, the road passes a ridge where the forest seemed little disturbed. The forest was open underneath, with numerous large trees. The presence of ropy-trunked and other unusual trees suggested that the natural forests of this area may differ from those across the river in some tree species as well as in dozens of bird species.

In general, forests along the east bank of the Madeira in the range of *Rhegmatorhina hoffmannsi* seem much like forests at Itaituba. There is a greater difference in birds and plants across the Tapajoz, three to fifteen kilometers wide, than in the 440 kilometers from Itaituba to Borba or Coatá.

Near Borba I found no White-breasted Antbirds, for the forests have been cut to shreds by colonists. There is an area of sandy soil, a "campo" with savannah vegetation; it must be an outlier of savannahs that break the Madeiran forests in two to the south. A new road south from Borba skirts the campo and passes into open forests very like those on the ridge south of Itaituba; near the road, at about 10 kilometers south of town, I saw some White-breasted Antbirds. Later I briefly visited similar but more swampy forests behind Nova Olinda do Norte on the island of Tupinambaranas, but found none of these antbirds. Tupinambaranas is cut off by a channel or "paraná" from the wide, muddy Madeira to the wide blue Rio Canumã, and from there the mixed waters of both flow east past the Rios Abacaxis and Maués to the Amazon.

Between the lower Canumã and the muddy Madeira, I studied White-breasted Antbirds near Coatá, a village of the Mundurucú Indians. The blue Canumã floods wide bays and creek valleys around Coatá, so that scrubby varzea woodland nearly surrounds the town. Low ridges of "terra firme" to the south and west are covered with fairly old forest. These forests, extending past many flat, swampy areas and small creeks, are characterized by large palms as well as brasilnuts and other giant trees. There are

few epiphytes and moss-covered trees, so the dry season must be severe. Near the Madeira to the west the forest drops to flooded swampy creeks, full of water plants and shrubs dripping with epiphytes. Yellow soil washed off the Bolivian highlands nourishes a rich aquatic and swamp vegetation on the Madeira, while the dark waters of such "rivers of hunger" as the Canumã and Tapajoz support little life.

THE ARMY ANTS

Rettenmeyer (1963) discusses the activities of army ants. *Eciton burchelli*, the most important species of ant for birds, has been studied by Schneirla (1957). In tropical lowland forests from México to Argentina, these ants send out huge raiding parties that flush large numbers of roaches, spiders, and other arthropods from the leaf litter and from tangles of vegetation on or above the ground. Numerous species of parasitic flies lay eggs on the leaping insects, while many species of birds chase the fleeing arthropods. Birds less often follow a smaller swarming ant, *Labidus praedator*, in forests and scrub from México to Argentina. In the upper Amazon, *Eciton rapax* forms straggling swarms that sometimes attract birds.

Most *Rhegmatorhina* followed swarms of *Eciton burchelli*. I also saw *melanosticta* at a swarm of *Labidus praedator* at Carauari, *cristata* at two swarms of *praedator* at Mitú, and *gymnops* at a swarm of *praedator* at Itapucurá. I encountered no swarms of *praedator* at all within the ranges of *berlepschi* and *hoffmannsi*.

CALLS

Antbirds of the genus *Rhegmatorhina* are so like Bicolored Antbirds (*Gymnopithys bicolor*) in calls and movements that the terminology used for the latter (Willis, 1967) can be applied to the species of *Rhegmatorhina*. Many calls are so similar to those of related species of *Gymnopithys* or *Phlegopsis* at the same swarms that one can tell which species is calling only after long practice.

Chirring.—All five species utter a deep buzz or *chirrrrrrr* when disturbed by the observer or others, including insect-eating hawks. The chirr of Hair-crested Antbirds is slightly deeper than the chirring of the White-cheeked Antbirds (*Gymnopithys leucaspis*) and White-throated Antbirds (*Gymnopithys salvini*) that forage with it in different regions, but I was often unable to tell the chirrs of *melanosticta* from those of *salvini* or *leucaspis*. Crested Antbirds have chirrs intermediate between the hissing chirrs of White-fronted Antbirds (*Pithys albifrons*) and the deeper chirrs of White-cheeked Antbirds, both of which forage with it at Mitú. Black-spotted Bare-eyes (*Phlegopsis nigromaculata*), which forage at swarms of ants with the other three species of *Rhegmatorhina*, have a similar but more nasal chirr; Pale-faced Antbirds

(*Skutchia borbae*), which I found with *Rhegmatorhina hoffmannsi* at Coatá, have chirrs almost exactly like those of the five species of *Rhegmatorhina*.

Chipping.—Alarmed or excited *Rhegmatorhina* of all five species call *chip* sharply and loudly. The chip is doubled or tripled to a *chip-ip* or *chip-ip-ip* only rarely; in this respect these species are unlike the double-chipping *Gymnopathys leucaspis* and its relatives. However, Crested Antbirds, which forage with *G. leucaspis*, double-chip more frequently than do other species of *Rhegmatorhina*.

Keening.—Keening, a thin *teeeeeee* whistle when a bird freezes in alarm, was noted only for *gymnops*, *berlepschi*, and *hoffmannsi*. This sound is faint and difficult to hear, and is widespread among related genera; *melanosticta* and *cristata* may well have it.

Songs.—It is convenient to divide the wide spectrum of songs into “loud-songs, why-songs, faint-songs, and serpentine-songs” as I did for Bicolored Antbirds. The basic pattern of the “loud-song” in *Rhegmatorhina* is a loud, pure *heeeeeee* followed by several shorter whistles at a lower pitch or descending in pitch. The loud-song is most commonly used when mates are distant from each other, when birds search for a swarm of ants, and when birds dispute with each other. In the last case, the song often descends to rough, snarling noises like the word “why” as a “why-song.” These species seem to use the loud-songs and why-songs more frequently in disputes than do Bicolored Antbirds, which use snarling.

At Benjamin Constant, a typical why-song of *melanosticta* was a loud “*Wheeeeer, whee-whee-whee-ee-ai-aihh!*” At Zatzayacu, one why-sang “*Wheeeh, wheep, eep, why!*” A typical loud-song of *cristata* was “*Eeeee, HEEER, you-you-you-you!*”, the last notes successively lower in pitch, length, and volume; the second note is sharply inflected in both pitch and volume. Why-songs add one to several snarling “*hraah*” noises to the loud-song in *cristata*.

A loud-song of *gymnops* at Palhão was “*Heeeeeee, hew-hew-hew-hew!*” The last notes are on the same low pitch or fade into snarling “*whaihh*” noises if the song becomes a why-song. The bird raises and extends the neck and opens the beak for a loud-song, but there is otherwise little change from standard postures. The loud-song of *berlepschi* at Maloquinha was like that of *gymnops*, but the “*hew*” notes were repeated more rapidly. Harlequin Antbirds also used long songs, with five to ten or more “*hew*” notes, more often than did *gymnops*. The posture for a song is much the same as in *gymnops*; in *berlepschi*, I noted that the crest is raised during the snarls at the end of a why-song.

The loud-song of *hoffmannsi* is much like that of *gymnops* or *berlepschi*, but the “*hew*” note is rarely repeated more than twice. However, *hoffmannsi*

often adds as many as 15 snarls to the end of a song. One day when it was raining, I noted that the song of *hoffmannsi* sounded like that of *berlepschi*. Apparently the "white noise" of the rain drowned out the rough overtones of the snarls, leaving only their pure tones and making them sound like "hew" notes. All these species vary their loud-songs and why-songs widely in length and volume, and they occasionally drop out introductory notes or other distinctive characteristics, so that their songs sometimes resemble those of the allopatric species of *Rhegmatorhina* or even the songs of species of *Phlegopsis* and *Gymnopathys* that occur at the same swarms with them.

When several rhegmatorhine antbirds of a species are at a swarm, they keep up a cross-talk of chirping little "faint-songs," which usually are faint versions of loud- or why-songs. At Zatzayacu, Carauarí, and Benjamín Constant the faint-songs of *melanosticta* were a hissing whistle followed by one to five or so hissing notes: "wheeeee, whihh whihh!" or the like. These songs were very like the faint-songs of *Gymnopathys salvini* at Carauarí and Benjamín Constant, although unlike the less sibilant faint-songs of *Gymnopathys leucaspis* at Zatzayacu and Umbria. The faint-songs of *cristata* were a "whreeeeeer, wheer-whihh!" or the like, the second note generally emphasized. The faint-songs of *gymnops* were faint versions of the loud-songs or why-songs, often shortened to one or two notes. The faint-songs of *berlepschi* were similar to those of *gymnops*, although often longer and faster. Faint-songs of *hoffmannsi* were like those of *gymnops*, except that the "hew" note was seldom repeated before it graded into one or more snarls or the song ended. The faint-songs of these three species thus differ in about the same ways as do their loud-songs.

Serpentine-songs are faint ditties when a bird is leading its mate or young. Usually the serpentine-songs are repeated faint-songs, often with inflected notes and punctuated with faint "chup" or "chup-up-up" grunts. A male *melanosticta*, leading his mate past me to a swarm at Zatzayacu, whispered "whreer, whee'eeep wheer chup chup chup" over and over. A lone male *cristata* muttered to himself "wh'yurr, wh'yeer-whree chuf-uh-uh-uh-uh-uh-uh" as he wandered around a swarm near me. Another chirped "chip-ip-whseep-whseep" over and over when he arrived at a swarm. At Palhão, male *gymnops* occasionally warbled "hew, hew, hew chip-ip-ip" over and over as they led their mates in to swarms. A male *berlepschi* showing a nest-site to a female at Maloquinha muttered "chuc-chuc-chuc-uc-u-u-u" over and over. A male *hoffmannsi* arriving at a swarm warbled "cherieriew chup, chup-up-up" over and over. Otherwise I noted no serpentine-songs for these three species, which usually alternate "chup" and faint-songs at rather long intervals as they lead their mates more often than they warble serpentine-songs.

Snarling.—Loud, snarling hisses like those at the ends of why-songs are

often given separately, one to fifteen times in a row, when birds are feuding with others of their own species: "whahh, whahh, whahh" or the like. In *hoffmannsi*, I noted that snarls seemed different when given separately rather than with loud-songs or faint-songs; however, there is so much variation in snarls in such species as Bicolored Antbirds that this could occasionally be true for any species. Hoffmanns' Antbirds snarl more times in a sequence and more frequently, on the average, than do other species of *Rhegmatorhina*; they are like the similarly white-bibbed *Gymnopithys bicolor* in this respect.

Bugling.—The battle cry, uttered before or as a bird chases its rival, is a rapid and musical "Chrrrrrrrt!" in all species, with about the speed and tone of the word "chert" if the "r" is rolled as a Scotsman would. The bugling of *melanosticta*, at Benjamin Constant, descended in pitch and was somewhat slow compared to the bugling of other species. I recorded the bugling of *gymnops*, at Palhão, as "chew'ew'ew'ew'ew'ew!" or "r'r'r'r'rew!", but I remember it as very similar to the bugling of other species; it may be slightly slow. All five species have a bugling call that is much faster than bugling in any species of *Gymnopithys* or *Phlegopsis*. Although rhegmatorhine bugling can be written like chirring, bugling has much slower and more musical notes than the rapid clicks that make up a chirr; chirring and bugling are easily told apart even if one has not had experience with related species, in which bugling and chirring are extremely different.

Peeping.—A fledgling *hoffmannsi*, just out of the nest April 3 at Coatá, called "Pee pee pee!", two to five notes, loudly in the hand. A well-grown young *melanosticta*, following its parents at a raid at Zatzayacu 20 October, had a "Whee, pee pee peep!" that was intermediate between the peeping of young and the loud-singing of adults. I was not able to discover if young antbirds in this genus have squeaking notes when they are fed, as do young Bicolored Antbirds (Willis, 1967). In the latter species, squeaking and peeping are different notes, and peeping eventually becomes the loud-song as young grow up.

Chirping.—Antbirds of the genus *Rhegmatorhina* commonly chirp "cheup" or "chup" when the mate is nearby. A similar "chup" is used by tame antbirds when the observer is nearby. However, I have not established whether this note is like the "grunting" of Bicolored Antbirds, which repeatedly use the notes whenever supplantable competitors are nearby and crowding their foraging zones. I rather think that rhegmatorhine antbirds lack the "grunt" or use it rarely, for I have been close to them when competitors of other species moved nearby and have failed to detect grunting.

Snapping and Hissing.—When rhegmatorhine antbirds supplant others of their own or other species, they generally give a single "snap!" of the bill. Double or multiple snaps are less common than among birds of related genera.

Often a rhegmatorhine antbird hisses "whiahh" as, before, or after it snaps and sends the competitor flying. I recorded hissing for all species except *cristata*, a bird for which I had few records of supplantings.

Growling.—A female *berlepschi* gave growling "chauhh" series, three to five notes, very faintly on three occasions when her mate fed her. Once he had to call "chee" faintly several times before she accepted his gift. Courtship feedings in *melanosticta* and *gymnops* seemed to be silent, but I was too far away to be certain the birds were not growling faintly. In Bicolored Antbirds, growling is used by the female mainly when the male holds back with the food; he may chirp or growl if she refuses his gift; feedings are often silent.

BASIC POSTURES AND MOVEMENTS

The standard posture for all five species of *Rhegmatorhina* is like that for Bicolored Antbirds (Willis, 1967). However, all species except *melanosticta* are heavier than Bicolored Antbirds and stand closer to the perch (Fig. 2) than do the latter. The various *Rhegmatorhina* are adept at clinging to vertical saplings, common near the ground in tropical forests. These antbirds are similar to Bicolored Antbirds in the clinging posture: the upper leg of the bird is flexed, the lower leg extended, and toe II on the lower foot angles 20 to 40 deg above the closely appressed toes III and IV.

The various simple movements are about the same as in Bicolored Antbirds. The tail is "flicked," or lowered to as much as 80 deg below the angle of the body and jerked back suddenly to as much as 30 deg above body level, when a rhegmatorhine antbird is excited. Compound movements like yawing and pitching on or around a perch, pivoting and reversing on or along a perch, and hopping from perch to perch or on the ground, are performed easily in much the same ways as in Bicolored Antbirds. Generally rhegmatorhine antbirds fly rather than hop progressively. Flight is usually slow and fluttery, and it is often started by a powerful jump with the big legs and feet. Most *Rhegmatorhina* seem heavy and slow compared to Bicolored Antbirds, but all can be quick and agile when chasing prey or excited by predators or competitors.

WANDERING

I never saw antbirds of the genus *Rhegmatorhina* foraging away from army ants. One group of *berlepschi* at Maloquinha were disputing busily at 17:20, but they may have been near an inactive ant colony. One pair of *hoffmannsi* at Coatá were with a poorly-flying fledgling. All others seen away from ants were wandering through the forest undergrowth as if looking for ants.

A wandering antbird generally travels between one and two meters above the ground, higher than it forages at swarms. It leaps and flutters from one

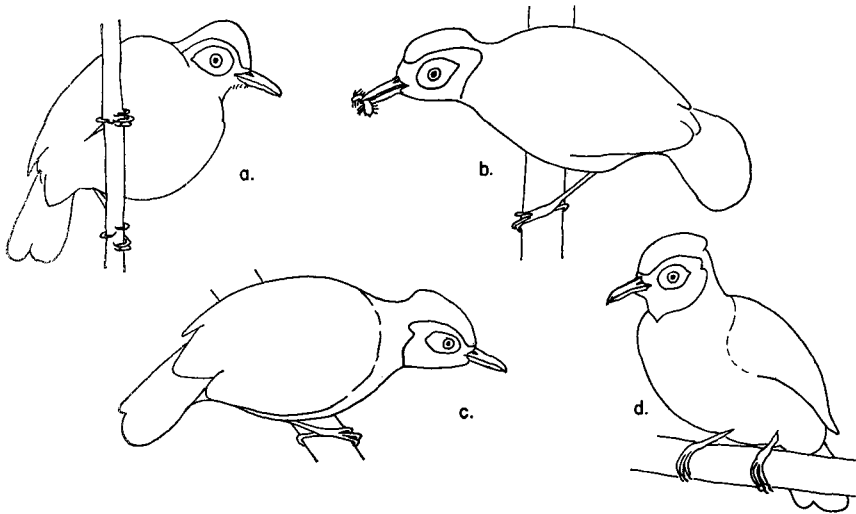


FIG. 2. Typical foraging postures for *Rhegmatrhina*: a, loafing-foraging *melanosticta*; b, *melanosticta* head down chewing prey; c, d, *cristata*. From field sketches.

vertical sapling to another, one to fifteen meters at a time, and alights precisely and easily. It looks around at each perch, but it seldom cocks the head as if looking at the ground for food.

Often an antbird loud-sings periodically as it wanders. Ones that encountered me chirred, reversed a few times, flew up higher, and circled around me before continuing in the general direction they had been traveling. When a wandering antbird encounters a trail of army ants or nears a swarm, it often chips excitably between faint-songs. Males with females commonly serpentine-sing as they precede their mates to the raid along the trail of ants.

Birds wander and loud-sing or wait and preen near a swarm that has been stopped by rain, at least until they find spots where the ants are active.

FORAGING

Birds of the genus *Rhegmatrhina* forage over the ants in much the same way as does *Gymnophithys bicolor*. All spend most of their time between 0.1 and 0.5 meters above the swarming ants, generally on the slender vertical saplings or more or less horizontal fallen branches so common in the lowermost layers of a tropical forest. They pitch and yaw, pivot and look about, or cock their heads at the ants below them. They hop or flutter to new perches if no prey appears in a minute or two, thus keeping above the active parts of the advancing swarm. They seldom hop on the ground, but they readily hop over logs and fallen twigs. At times one flies up to one or two meters

above the ground, looks about, flies to another part of the swarm, and drops to near the ground again.

Most of the prey is captured by sallying to or near the ground. The bird leaps or leap-flutters after a fleeing arthropod and bounces back up to a perch with it so rapidly that army ants seldom have a chance to attack either the arthropod or the bird. At times the antbird yaws or pitches from a low perch and pecks the prey out of the air or off the ground. At other times one tosses leaves by grasping them between the mandibles and flicking one away at a time until the hiding prey is uncovered and pecked. Occasionally a bird flutters up rather clumsily and catches prey on a tree trunk or other low vegetation. I never saw them hopping through tangles of fallen limbs or lianas one to five meters above the ground as subordinate Bicolored Antbirds sometimes do. However, there were seldom enough rhegmatorhine or larger antbirds at swarms I watched to force subordinate birds to forage above the ground.

Both *melanosticta* and *cristata*, which forage in the lush and cluttered undergrowth of the wet forests of upper Amazonia, spent much time hopping about the stilts of stilt-rooted trees or the buttresses of mossy or vine-covered trees, through rotten tangles of fallen limbs, and from perch to perch in low sprouts. They searched more actively than did the smaller *Gymnopithys leucaspis* at the same swarms. However, *melanosticta* and *cristata* also spent much time waiting for prey to jump, and they promptly supplanted nearby *G. leucaspis* as if to eliminate competition. Differences between *Rhegmatorhina* and *Gymnopithys* in foraging are as slight as differences in calls and morphology.

The other three species of *Rhegmatorhina* live in less moist and cluttered forests, in regions where there are no competing species of *Gymnopithys*. As one might expect, they forage almost exactly like the species of *Gymnopithys* that live in similarly uncluttered forests across the equator, such as *G. bicolor* in Panamá. These three *Rhegmatorhina* did seem a bit slow and prone to take horizontal perches compared to *bicolor*, but one might expect this from the slightly larger size of the three. The sudden sallies of *Rhegmatorhina* were as quick or quicker than the sallies of *bicolor* when the former did move.

The prey of *Rhegmatorhina* were almost always insects, spiders, and other arthropods. Roaches, crickets, and orthopterans in general were favored prey. I never saw a bird eat army ants. In upper Amazonia there are black ants that, when the army ants invade, grab their white larvae and stream up nearby vegetation in a frantic race to escape. One such stream of ants at Benjamín Constant attracted a male *melanosticta*, who pecked 10 larvae and tossed away the adult ants from a nearby petiole as fast as he could, as if

working on an assembly line; he ignored a similar stream of ants with larvae up another petiole near him, then relinquished the job to a pair of *Gym-nopithys salvini*.

Most of the prey seems to be one-third to one and a half times the length of the exposed bill (one bill length = about 16 mm). The largest prey seen was a centipede three times the length of the bill of the young male *hoffmannsi* that captured it.

Large prey may be taken to the ground or to a broad, horizontal perch for dismembering. The bird shakes and chews the prey, drops it to the ground and looks at it, then takes it up again. The bird usually flies off a few meters if other birds or the ants are nearby. The prey is never held by the foot or hammered against the perch.

One female *hoffmannsi* performed anting. She flew up to two meters over the ground with prey half as long as her beak, chewed it and repeatedly poked it into the under sides of her remiges and rectrices. She finally ate the prey and wiped her beak energetically. She did not raise the crest, although such noncrested relatives as the Bicolored Antbird commonly do so after bill-wiping or billing a distasteful prey.

OTHER MAINTENANCE ACTIVITIES

Periodically antbirds of the genus *Rhegmatorhina* preen over the ants, even if they have just arrived and are foraging busily. At times one loafs and preens in a sheltered spot near the swarm.

Loafing and preening resemble the same activities in Bicolored Antbirds. All pick horizontal perches, sit or half-sit, and fluff the feathers of the body. The preening bird looks about every second or two. One preening female Hair-crested Antbird gave a head-shaking nibble at the base of each feather preened, then a sweep of her head as she ran the rest of the feather between the tips of her mandibles. When one *berlepschi* turned the head to preen the upper breast, the scanty feathers of the neck parted from those of the body in the same way as do the neck feathers of Bicolored Antbirds.

"Underwing-looking" was noted for *hoffmannsi* and *cristata*. The latter displayed a cinnamon wing-lining as he stretched one wing laterally and peered under it as if mesmerized; this behavior is so frequent among birds with plain wing linings that the birds are probably looking for parasites rather than displaying.

In all *Rhegmatorhina*, the head is scratched over the wing. However, one young female *gymnops* scratched repeatedly under the wing at a spider web plastered on her bill. Related antbirds usually scratch over the wing, but nearly all scratch under the wing at times.

Stretching movements are much the same in *Rhegmatorhina* as in Bicolored

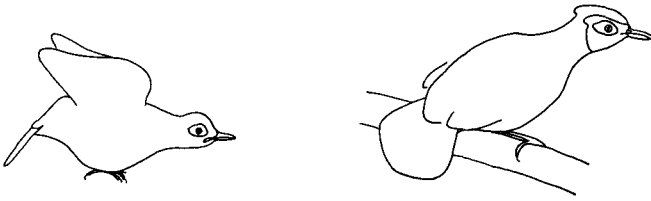


FIG. 3. Two-wing stretch, juvenile Bare-eyed Antbird. From field sketch, Palhão.

FIG. 4. Panicking Crested Antbird. From field sketch, Mitú.

Antbirds and other birds. Full side-stretches (wing, leg, and tail on one side of the body) were noted for *melanosticta*, *gymnops*, and *hoffmannsi*. Two-wing stretches over the back, as in a stretching human, were noted for *melanosticta* and *gymnops* (Fig. 3). Toe-standing was recorded for *melanosticta* and *berlepschi*. All these stretching movements, and yawning as well, are so widespread in birds that they probably occur in all species of *Rhegmatorhina*.

Frequently these antbirds twitch the rear end of the body or shake the head from side to side. Often the twitching includes a sudden flit of the wings. One Hair-crested Antbird jabbed down at her ventral apterium after a flitting twitch. Since isolated antbirds as well as ones close to other antbirds or to me perform such motions, I suspect the persistent mosquitoes rather than the presence of observers incite these movements. On a few occasions when sunlight outlined the hovering parasites, I saw that alighting mosquitoes provoked similar twitches and head-shakes in related antbirds, *Pithys albifrons* and *Gymnopithys bicolor*. To the birds, I must have seemed similarly twitchy.

REACTIONS TO DANGER

I observed freezing only for *berlepschi*, although it is to be expected in all species of *Rhegmatorhina*. The bird crouches, sleeks the body, and stays immobile for a few seconds. Keening, the sound that characteristically accompanies freezing in Bicolored Antbirds, was noted for *gymnops*, *berlepschi*, and *hoffmannsi*.

Chipping, panicking, and hyperactivity were noted for alarmed birds of all five species. The panicking antbird sleeks the body, flexes the femora as it extends the next two joints of each leg, and extends the neck and head (Fig. 4). It often angles the front of its body downward. It flicks the spread tail rapidly. It darts from perch to perch or into cover with sharp "chip!" notes. Panicking and hyperactivity were difficult to see clearly in other respects, but seem to resemble the same activities in Bicolored Antbirds.

One male Hair-crested Antbird at Benjamín Constant was very sleeked and flicked his tail rapidly as he wandered in the exposed branches atop a treefall. An arriving male Crested Antbird at Mitú sleeked his head and body and flicked his tail when he saw me. His throat was ruffed, his crest folded (Fig. 4). Throat-ruffing is often a sign of mobbing in this group of birds, but the other movements suggest panic.

Bare-eyed Antbirds chipped and panicked when hawks arrived: *Leucopternis kuhli* once; *Leucopternis albicollis* once; *Micrastur gilvicollis* twice. One Bare-eyed Antbird chipped and fled when a Scale-backed Antbird (*Hylophylax poecilonota*) gave its alarm call, and two other *gymnops* chipped and became hyperactive when a squirrel started chattering above the ants. On three occasions, Harlequin Antbirds chipped and fled when *Micrastur gilvicollis* arrived at swarms. One White-breasted Antbird double-chipped and fled when a big Hoffmann's Woodcreeper (*Dendrocolaptes hoffmannsi*) glided down from above. Several other *R. hoffmannsi* started a chipping panic when a White-chinned Woodcreeper (*Dendrocincla merula*) started chattering. Another *R. hoffmannsi* chipped at the distant alarm call of a nunbird (*Monasa morphoeus*). An arriving hawk (*Micrastur gilvicollis*) caused another chipping panic among White-breasted Antbirds.

One Bare-eyed Antbird chipped once, then chirred twice when a tayra (*Eira barbara*) wandered past. Antbirds of the genus *Rhegmatorhina* generally performed mobbing and chirring when I appeared at the swarms. After chirring from behind cover for a time, they converged on the swarm again. Finally one or more flew up to two meters or so above the ground or to some other place where they were in plain sight. Still chirring, they flicked the partly spread tails and stared at me with one eye and then the other.

The large, seemingly glowing greenish-blue bare area around the dark eye, set as it is in a black face against the dark undergrowth, resembles at such times the eye of a large cat. Perhaps this bare area is used as the "iris" in an "eyespot" design, frightening potential predators or competitors of the same or other species. The bare area is very prominent when the bird is mobbing and when it is displaying to an opponent of its own species, hence may serve both purposes.

Mobbing antbirds commonly extend the head and neck as they flex the femora, thus presenting the bare facial area to the object of mobbing. One occasionally swings round and around a vertical perch, 30 to 100 deg at a pitch, displaying the face before darting behind cover again. Perhaps the bird is uncertain whether to approach or flee. Bare-eyed Antbirds, which have unusually large bare areas in otherwise rather unmarked bodies, were very prone to swing around perches and stare at the observer (Fig. 5). The related Harlequin and White-breasted Antbirds were less prone to do this. I did not note such behavior for Hair-crested or Crested Antbirds, and it is rare in related species unless they have bright blue facial areas.

Foraging but nervous antbirds of the genus *Rhegmatorhina* flick their closed tails, dart behind cover periodically, or chirr. Slightly tamer birds stay but have their throats ruffed, at least in *cristata*, *gymnops*, and *hoff-*

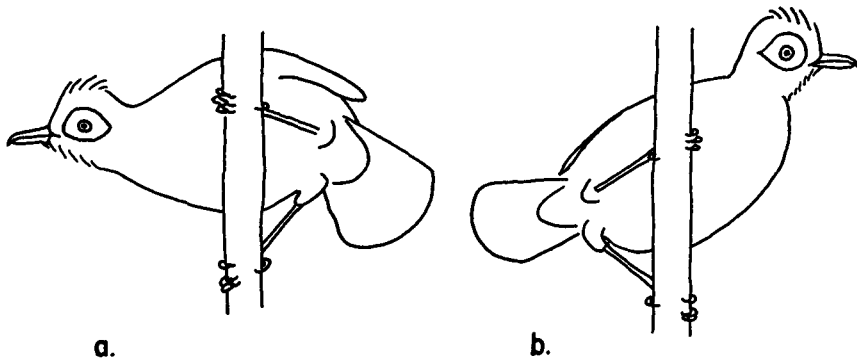


FIG. 5. Mobbing Bare-eyed Antbirds, probably showing signs of panicking. From field sketches, Palhão. See also males on frontispiece.

mannsi. Throat-ruffing is common in semi-tame Bicolored Antbirds and other species of *Gymnopathys*, but in addition the half-tame *Rhegmatorhina* of all species raise their crests now and then. Occasionally when I was near them, the tame antbirds popped up to two meters or so above the ground, stared and crest-raised, and dropped down again even though they did not chirr or show other signs of mobbing. One *berlepschi* flew up in this fashion when a brocket (*Mazama* sp.) wandered through the swarm. Semi-tame *Rhegmatorhina* often call "chup" or faint-sing, as do semi-tame Bicolored Antbirds. I recorded some body fluffing from one semi-tame *melanosticta*.

Semi-tame *Rhegmatorhina* often perform displacement activities when they forage near me. They crest-raise, wipe their beaks, toe-look, flit the wings, flick the closed tail, reverse repeatedly, hop up and down perches. One moderately tame *hoffmannsi* was sleeked and high on his legs, his femora flexed so his body angled down, and his head extended and up, when he came near me. Perhaps he was performing a mixture of foraging and panicking.

Rhegmatorhine antbirds watched for long periods mobbed, panicked, or froze less and less strongly when I came near. However, none became very tame. Some young birds, changing from the juvenal to the adult plumage, approached and investigated me. Presumably, if I had been able to stay with the birds more than a week or two, they would become as tame as do the related Bicolored Antbirds when I watch them repeatedly. The *Rhegmatorhina* species became tame less rapidly than do Bicolored Antbirds, or about as rapidly as does the Amazonian *Gymnopathys leucaspis*.

At Palhão and later at Curuá, *R. gymnops* chipped as they readily but rapidly darted across dirt roads 10 to 15 meters wide. Crested Antbirds

readily used low second growth, two years old or so, when following swarms in a largely forested area. Otherwise these species seem as restricted to forest as are members of related genera. Since the army ants also avoid open areas, it is probably very unlikely that rhegmatorhine antbirds cross large rivers like the Tapajoz and Madeira even if they can fly well enough to do so.

Occasionally a rhegmatorhine antbird forages in rather open situations, although it shows signs of panicking. One male *berlepschi* at Maloquinha followed ants for several days in the very open undergrowth of the varzea along Cupituã Creek. He stayed by fallen logs and near tree trunks or groups of saplings whenever they were available. Other males there flew down and worked in a tractor trail through second growth when ants swarmed along the trail. They hopped or stood on the road briefly, feet splayed and tails up slightly, and pecked here and there before fleeing to the roadside thickets for a time. One male hop-fluttered over the grass in the center of the tractor trail and resumed hopping in the other rut. When these antbirds crossed the road, they generally flew out from 1.2 to 1.5 m up. The *Phlegopsis nigromaculata* foraging with them crossed at various levels, suggesting that they were not moving to special heights before crossing. The Black-spotted Bare-eye is more of a bird of second growth than is *berlepschi*, and the Tapajoz and Madeira Rivers only separate the Bare-eye into subspecies.

When swarms passed over the open mounds of leaf-cutter ants at Coatá, most *hoffmannsi* waited at the periphery; however, an occasional bird worked over the ants. At Mitú, Crested Antbirds worked the edges but not the centers of clearings in the undergrowth below a species of sapling that either kills the other vegetation or has ants that do this for it.

AGONISTIC BEHAVIOR

As in an earlier paper (Willis, 1967), I shall use "agonistic behavior" to mean such competitive behavior as fighting, supplanting, aggressive display, and submissive display.

I saw fighting only once, when two White-breasted Antbirds fluttered up and had a brief aerial peck and scrabble duel. Fighting is so rare in the related Bicolored Antbirds that I could easily miss it in such short-term studies as these. I saw no submissive displays in *Rhegmatorhina*, perhaps because I did not watch them long enough to get them really tame. These displays are best observed when birds are very tame, since wary dominant birds tend to flee rather than persecute subordinate ones persistently enough to start submissive displays in the latter.

Supplantings and Displacings.—One male Hair-crested Antbird ducked his head and raised his crest as a woodcreeper dove past. A juvenile *gymnops* jumped and ruffed its crest and throat strongly when a Rufous-capped Ant-

thrush (*Formicarius colma*) ran past and snapped up an insect. A male *hoffmannsi* jerked up when a woodcreeper (*Dendrocincla merula*) sallied to the ground for an insect in front of him. A female *hoffmannsi* raised her crest when a smaller female antbird (*Myrmoborus myotherinus*) hopped nearby. Crest-raising at a competitor of another species was seen on several other occasions.

When several birds of various species work over the swarms of army ants, a rhegmatorhine antbird keeps away from competitors by moving away or by supplanting any birds that come closer than a meter or two. The antbird supplants a competitor by flying at it and taking its perch with a snap of the beak. Once I saw that a *hoffmannsi* supplanting another had its beak open until the terminal snap. A *melanosticta* supplanting a *Gymnopithys leucaspis* at Zatzayacu had the tail and wings partly spread and somewhat tented as it alighted. One female *hoffmannsi* snapped as she alighted above a larger woodcreeper (*Dendrocincla merula*), then pitched around the perch pecking repeatedly at the dodging woodcreeper. It flew but returned; she flushed but supplanted it successfully on her next try. Generally larger birds supplant smaller ones at ant swarms, so that *D. merula* is about the largest bird a rhegmatorhine antbird can supplant.

Hair-crested Antbirds twice supplanted White-plumed Antbirds (*Pithys albifrons*) and five times supplanted White-cheeked Antbirds (*Gymnopithys leucaspis*) at Zatzayacu. White-throated Antbirds (*Gymnopithys salvini*) lost to *melanosticta* seven times at Carraurí and seven times at Benjamín Constant. The large Rufous-winged Bare-eye (*Phlegopsis erythroptera*) supplanted *melanosticta* once at Zatzayacu and once at Benjamín Constant. By contrast, I saw *melanosticta* supplant *melanosticta* twelve times, all at Benjamín Constant.

Crested Antbirds at Mitú supplanted White-cheeked Antbirds thirteen times, White-plumed Antbirds three times, a Scale-backed Antbird (*Hylophylax poecilonota*) once, and a White-chinned Woodcreeper (*Dendrocincla merula*) once. Rufous-winged Bare-eyes supplanted *cristata* three times.

At Palhão, Black-spotted Bare-eyes (*Phlegopsis nigromaculata*) supplanted Bare-eyed Antbirds twice, a Concolor Woodcreeper (*Dendrocolaptes concolor*) supplanted one once, and a Buff-throated Woodcreeper (*Xiphorhynchus guttatus*) displaced one once.

At Maloquinha, Harlequin Antbirds once supplanted a Spot-backed Antbird (*Hylophylax naevia*). On twenty occasions, Black-spotted Bare-eyes supplanted *berlepschi*. By contrast, I noted 46 supplantings of *berlepschi* by *berlepschi*.

At Coatá, White-breasted Antbirds supplanted a Scale-backed Antbird once, a Saturnine Antshrike (*Thamnomanes saturninus*) once, and White-

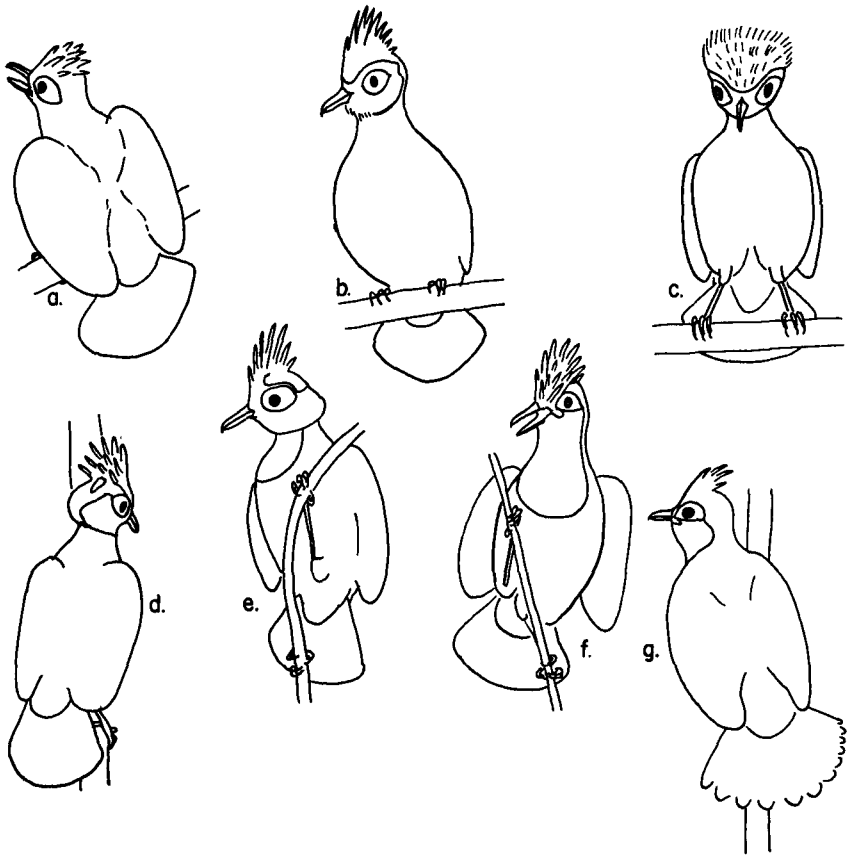


FIG. 6. Challenging in *Rhegmatorhina*, from field sketches; a, *gymnops* at Palhão; b, *cristata* at Mitú; c, *melanosticta* at Benjamín Constant (note the "giant-eyed" appearance caused by bare facial areas, also the "hair-crested" look); d, e, *berlepschi* at Maloquinha (note the "Bucephala-like" head and the exposed skin on the hind crown); f, g, *hoffmannsi* at Coatá.

chinned Woodcreepers fifteen times. The woodcreeper returned the favor three times. Black-spotted Bare-eyes supplanted *hoffmannsi* thirteen times, and Pale-faced Antbirds (*Skutchia borbae*) supplanted *hoffmannsi* twelve times. By contrast, *hoffmannsi* supplanted *hoffmannsi* 112 times.

Aggressive Display.—The aggressive display of rhegmatorhine antbirds is very like the "challenging" display of Bicolored Antbirds, except that all rhegmatorhine antbirds raise and spread their crests very strongly. The challenging display (Fig. 6) is graded: postures passed through on the way

to the maximum display are often the full display at other times. All species of *Rhegmatorhina* extend their legs so that their bodies rise as far as the vertical, whether the birds are on vertical or horizontal perches. The tail is spread more or less strongly, and flicking stops. The wings are often partly spread, and form with the spread tail a "tented" appearance. I have not seen the wings completely spread, but I may have missed the maximum form of challenging. Unlike Bicolored Antbirds, the rhegmatorhine antbirds do not part or fluff the interscapular feathers noticeably. I noted expansion of body feathers, due to fluffing or to inflation, only for female *hoffmannsi*. Her expansion displays barred feathers rather strongly. However, inflation and body fluffing are hard to detect, so I may have missed the movements in other species.

The neck is extended in challenging, but not strongly so. In *berlepschi* the neck-extending causes the feathers to part so that the rufous nape shows on a head shaped somewhat like that of a male American Goldeneye (*Bucephala clangula*). In *berlepschi*, *hoffmannsi*, and *cristata* and probably others the bill is pointed down at the chest during the strongest displays—that is, the head is strongly flexed. The bare eye areas become large and conspicuous as the crest is raised, and the bill-down posture displays both bare areas conspicuously against the black face. One female *hoffmannsi* turned her head so as to keep the bill and both facial areas toward a male flying past.

In *cristata* the throat of one challenging bird was fluffed (Fig. 6b). In that species and in all but *melanosticta* the raised crest is pointed. In Hair-crested Antbirds, the whole whitish crown seems to expand evenly, like a large hairy petal pushed up by a bee. In *cristata* the center of the crest is full and jaylike, but in *berlepschi* and *hoffmannsi* the long front feathers rise high over the few short feathers of the rear of the crown. In one male *berlepschi* the frontal crest was raised so strongly it left a bare blue spot at the center of the crown (Fig. 6d).

Even when they are no longer rising in indignant challenging poses at trespassers, the rhegmatorhine antbirds continue to raise their crests at competitors. Even a male *hoffmannsi* that was defeated and retreated from an encounter crest-raised before he wiped his bill. The crest, which is the best distinguishing characteristic for this genus of antbirds, is used far more in agonistic encounters than it is during bill wiping or as a reaction to competitors of other species or to the observer.

Once a male *hoffmannsi*, separated from another by a large Pale-faced Antbird, was utterly silent as he jerked into several upright challenges. Normally a challenging antbird snarls or bugles vigorously at the opponent, or why-sings loudly or faintly at the very least.

A snarling or bugling challenge is likely to start an outburst of supplantings,

challenging displays, snarls, more bugling, loud why-singing, chipping and even chirring. Challenge-flying, when one bird flutters with spread wings and tail after another, is often associated with bugling and with a series of supplantings. Eventually the defeated bird leaves, loud-singing, or wanders on the periphery of the ant-swarm, faint-singing. Songs seem more frequent than in the otherwise similar outbursts of Bicolored Antbirds; however, in the similarly white-bibbed *hoffmannsi* snarling is frequent, as it is for Bicolored Antbirds.

I saw only a few such outbursts for *melanosticta*, *cristata*, and *gymnops*. At the seasons I visited them there were rarely more than one pair at each swarm of ants. I saw many outbursts from *berlepschi* at Maloquinha in February and from *hoffmannsi* at Borba and Coatá in late March and early April. There were many young of the year out of the nest and two or even three pairs at some swarms, so there were many disputes. At times, however, birds foraged near each other with little sign of agonistic behavior. I suspect that they had determined the peck order and had habituated to each other, as is generally the case when Bicolored Antbirds tolerate each other.

The frequent outbursts, the muted snarling why-songs, and the supplantings back and forth reminded me of the frequent feuding when two or more pairs of Bicolored Antbirds attend a swarm of ants. In Bicolored Antbirds, the pair on its own territory dominates other pairs and wandering birds but permits them to remain at peripheral sites at a swarm. The rheimtorhine antbirds probably have a similar form of territoriality, although I could not be certain without banding pairs and following them from one territory to another to see if there are reversals of dominance.

One male *melanosticta* waited to supplant another male until the latter finished chewing a prey item. A male *hoffmannsi*, food in his beak, did a bugling upright with his back toward a female who had supplanted him; she held her upright pose and then bill-wiped as he made his getaway. Another male *hoffmannsi* supplanted a juvenile male as it captured a long centipede; both faced in bill-down upright poses and the adult male retreated. I have recorded similarly polite conduct from Bicolored and other antbirds. The general rule seems to be that a bird dissecting food or with food in its beak is rarely attacked, except at the moment of prey capture.

One male *berlepschi* raised his crest now and then as a dominant male approached; then the first male bill-wiped, preened his belly, and shook his body. Eventually he was supplanted and moved away to forage, calling "chup" faintly. Retreating *hoffmannsi* were occasionally sleeked.

One male *berlepschi* gave several "chuc" notes as his mate approached, but she supplanted him anyway. I occasionally saw males supplant nearby females and vice versa, but could seldom tell if they were mated or not.

There were two other definite records: a male *gymnops* supplanted his mate; and a female *berlepschi* supplanted her mate after a courtship feeding.

At swarms, a pair converse with faint chirps, chup notes, and short faint-songs. They sometimes forage a meter or two apart, but closer approach is permitted only for courtship feedings. In this respect these birds are like the species of *Gymnopithys* and unlike *Phaenostictus*, *Phlegopsis*, and *Skutchia*, which tolerate the foraging mate within a centimeter or two.

REPRODUCTIVE BEHAVIOR

Adult females of all five species of *Rhegmatorhina* always seemed to be paired. One young female *hoffmannsi*, with brown feathers still along her malar region and on the side of her breast, had a male attending her at Coatá. Female Bicolored Antbirds of about this age (10 to 20 weeks since hatching) occasionally pair with wandering males for short periods, but the definitive pair bond is normally formed only after the female has lost all her brown juvenal feathers. There is a surplus of males among Bicolored Antbirds and perhaps among rhegmatorhine antbirds: there always seemed to be unmated adult males in all five species. However, it was not possible to be certain without banding birds.

Probably the pair bond is formed by courtship feeding, which is the pairing and precopulatory ritual in many genera of antbirds. In related antbirds, the female often gets nearly all her food from the male during the period when she is forming the eggs. I have seen courtship feeding only for *melanosticta* at Caraurá, *gymnops* at Palhão, and *berlepschi* at Maloquinha. Perhaps I arrived at Coatá too late in the breeding season (young out of the nest were common in early April) to see feeding in *hoffmannsi*. However, I watched many pairs for many hours; and such related species as Bicolored Antbirds occasionally perform courtship feeding even during the non-breeding season (the dry season). I watched the few pairs of *cristata* so briefly that they did not become tame enough for courtship feeding.

I watched two feedings of *melanosticta*. The female preened and loafed after the first one. On the second, she flew below the male, he bent down, and she took the prey. When she lowered her head he pecked at her, so she dropped into cover.

For the one observed feeding of Bare-eyed Antbirds, the male faint-sang and chirped as he wandered with food in his beak. Finally he found the female, loafing in cover as she had been at various times that morning. As she took the prey to the ground, he flicked his spread tail and returned to the swarm.

I observed seven feedings of Harlequin Antbirds. On three the female growled faintly. On the last of these three the male backed off when she

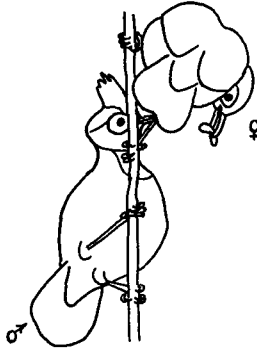


FIG. 7. Male Harlequin Antbird watching female eat after feeding her. Note his raised crest and spread tail. After a field sketch, Maloquinha.

gaped; he raised his crest and spread his tail. Finally he gave her the food and she stopped growling. Later she supplanted him. Just after she had captured her own prey later that morning, he arrived with food. He called "chee" faintly several times and presented the food to her twice before she gulped down her own prey and accepted his without growling. Another male spread his crest as he watched his mate eat the food nearby (Fig. 7). Another female, her head and body low in the usual food-chewing pose, spread her tail when her mate waited beside her and watched her eat his gift.

Males often lead their mates to swarms. The male flicks his tail and looks down at the trail of ants repeatedly as he flies along it toward the swarm. Faint chipping and chirping notes are interspersed with his faint-singing and serpentine-singing. The female usually tags along behind, but she may leapfrog with him as the two close in on the swarm. For *cristata* I recorded only "chup" and two-note faint-songs ("whierr, whew") as the male led his female (calling "whier," a one-note faint-song) about a swarm; however, an unmated male called serpentine-songs persistently one day.

The nests of these birds are unknown, but probably are inside low rotten stubs or similar sites as is the case for Bicolored Antbirds. One male *berlepschi* at Maloquinha performed "nest-showing" by flying to the top of a low stub, peering in as he flicked his spread tail, and calling repeatedly.

YOUNG

On 3 April a young *hoffmannsi* at Coatá, out of the nest and away from an ant swarm, fluttered short distances near the ground but was relatively easy to catch. It was dark brown all over, with a grayer belly, and had a dusky bare eye-ring and pale yellow gape angles. About half the size of the adult, it had a short black bill and blackish feet. The throat and neck were

rather bare. The half-length tail had wedge-shaped brown feathers with rather dusky tips. The young flicked the tail busily as it clung to a vertical sapling after release. It peeped loudly in the hand, bringing the adult female up. She had arrived, fed the young, and departed several times before I found it. The male arrived when the young was peeping loudly and the female chirring, but he soon departed. In related species, the female feeds one fledgling and the male feeds the other; this male may have been caring for another young bird off in the forest.

A nearly full-sized young *hoffmannsi* at an ant swarm with its parents near Borba, 29 March, was plain brown with pale gape angles and a dusky face. Other young at Borba and Coatá were catching at least part of their own food. One young female at Borba, 28 March, was brown but had a small bluish bare ring around the eye. She was barred on the back and underparts, and had a few white feathers among the brown ones on the lower cheeks, throat, and bib. A young male at Borba was similar, but lacked the barring and had large patches of white on the throat and bib. Several independent young males and females at Coatá showed various stages of the transition from the dusky faces and brown heads of young to the greenish-faced, white-bibbed adult stage, April 5 to 11.

These young birds were always supplanted by adults, and had to take the poorest foraging positions when adults were present. Young of many related species of antbirds are subordinate to adults, but young often supplant adults in the related *Gymnopithys lunulata*.

One nearly grown young *melanosticta*, giving a peeping song, followed two adults at Zatzayacu, 20 October. It had pale gape angles, a small bluish bare area around the eye, and a speckled back. It flew up and looked me over before following the adults off.

One young *gymnops*, with pale gape angles and a small bare bluish face area, followed the male of a pair at Palhão from 28 January to 3 February. The face was brownish-black, not dark black as in adults, and the body was dark brown. The bill was dark plumbeous, the iris dark reddish, as in adults. There was no sign of speckling. It fluttered the wings as it begged from the male on several occasions, but it was capturing some prey itself. On 31 January the male fed it and then pecked it.

Specimens of these birds in various museums (AMNH, American Museum of Natural History; CM, Carnegie Museum at Pittsburgh; CMNH, Chicago Museum of Natural History; MCZ, Museum of Comparative Zoology at Harvard; MG, Museu Goeldi at Belém, Brasil; PANS, Philadelphia Academy of Natural Sciences; examined by courtesy of the curators of the Departments of Ornithology) show the change from the juvenal to adult plumage and indicate that the first adult plumage is like following ones. The "immatures"

of specimen labels and faunal lists generally are birds molting from juvenal to adult plumage in this and related genera of antbirds.

Adult *gymnops* are so plain that it is difficult to tell the juvenal feathers from adult ones in young birds. A juvenile of "one third" the adult tail length (as one looks at it from the normal field distance of ten meters) from Miritituba, 20 March 1920 (CM-77563) has blackish from the dark and tiny bill to the auriculars, but the other feathers are dark reddish-brown. The throat is mostly bare, and new feathers at the sides are paler. The crest is fairly long and fluffy.

Older juvenile males (Santa Julia, Rio Iriri, 8 June 1914, MG-10834; Miritituba, 20 March 1920, CM-77558) show brown feathers along the sides of the chest and brown-tipped, blackish feathers on the belly to a greater extent than do adult males. The crown is mostly brown; the old feathers are short and broad and rather rufous, with darker centers, but new black sheathed crown feathers are scattered about. The back is a more russet brown than in the adult, the tail is browner, and the auriculars browner and less well feathered than in the adult. Several other males (AMNH-286724, Caxiricatuba, 16 May 1931; AMNH-286725, Caxiricatuba, 17 May 1931) seem young males finishing wing and body molt into the adult plumage. There are still a few brown-tipped feathers on the lower belly and crown, and the new inner primaries have duller, less rufous edges than do the old outer ones. The male taken on 17 May has a brown feather on the chest.

A juvenile but nearly full-sized female from Miritituba (20 March 1920, CM-77561) has short and broad crown feathers, uniformly brown or rufous-brown and colored like those of the back, instead of the long and pointed brown crown feathers of the adult female. The throat is well feathered in soft, pale brown rather than in the mottled blackish-brown of the adult female. The breast feathers form a band of a peculiar shiny and very dark rufous brown, not a plain brown with pale shaft streaks as in the adult female. The new feathers below the breast-band are paler and buffier brown, from the center of the chest down to the belly. Another young female (Miritituba, 20 March 1920, CM-77562) is slightly further in molt, with a few tiny blackish chin feathers and more brown feathers on the rufous-brown chest. Probably a similar bird from Caxiricatuba (12 May 1931, AMNH-286729) and one from Tauary (11 April 1931, AMNH-286730) are also juvenile females. All these young birds have black bills rather than the pale lower mandibles of adults; in life, the lower mandible of the adult is dark, but the pigment seems to disappear from specimens.

The young male *gymnops* thus seems to be browner than the adult male, especially on the short crown and on the belly and sides; but the black feathers appear on the face and chest very early. There is a rufous tinge to the dark brown areas of the plumage in both the juvenile male and female, especially on the pectoral band of the female. Certain adult females, taken in October to March, show a rather rufous tinge to the edges of crown feathers; it may be that these are first-year females. However, the juvenal plumage differs from the adult so subtly that I hesitate to attempt further separation of adults, which probably show individual variation.

The 30 specimens examined indicate that young *gymnops* appear in the early months of the year, or in the final months of the rainy season. They molt the body and then the wing feathers into an adult plumage in March to June. Molting adults have been taken March to November, and moderately worn adults from October to March. The schedule of molt and nesting is probably much the same as in Bicolored Antbirds, which start nesting with the rains but rarely get young out (because of nest predation)

until near the center or end of the rains several months later. Bicolored Antbirds have a protracted molt, from the middle of the rainy season to early in the dry season.

Of 30 available specimens of *berlepschi*, presumed adults in molt have been taken July to January, ones with slight or moderate wear from December to June. Three changing juveniles are available, a female from Vila Braga (21 January 1920, CM-76400) and males from there (1 July 1917, MG-13612) and Igarapé Bravo (16 June 1931, AMNH-286731). This species probably nests late in the rainy season, slightly later than do the *gymnops* across the river, and delays its molt to the dry or nonbreeding season and the beginning of the nesting season.

The young male from Vila Braga has double-barred feathers of the juvenal plumage among the new gray feathers on the center belly and lower chest. The brown bases and buff tips of single-banded feathers of the upper back and wing coverts are somewhat more rufous in hue than in the adult female, and other wing feathers are also somewhat more rusty. The black bars on dorsal and ventral feathers are narrower and smaller than in the adult female. The breast is rusty brown, the belly feathers and feathers of the lower back dull brown. The crown feathers are short and rusty, and lack the blackish sheen and edges of the feathers of the adult crest.

The young male from Igarapé Bravo has some dull brown juvenal feathers on the rufous chest and a few brown ones in the gray areas of the sides of the upper chest; the brown breast-band of many young antbirds of this and related genera was evidently being replaced. The underparts are otherwise as in the adult male, except that the throat and cheeks are a dull sooty black rather than pure black. The rusty crown and barred back and covert feathers seem juvenal; however, the scapulars are greenish-brown and adult.

The juvenile female from Vila Braga is scrubby-plumaged and small. Although russet feathers are appearing on the chest, the feathers of the belly are a loose, fluffy brownish rather than double-barred as in the adult; however, the undertail coverts are doubly banded with blackish. The juvenal chest feathers are tinted buffy-brown, with blackish central spots. The face and loreal feathers are a dirty blackish. The crown has short rufous feathers, darker in the center and paler toward the nape. The tail is dusky brownish with a black subterminal band and pale buff tips, quite lacking in the adult. (However, the adult has a slight whitish-buff tip to each tail feather when it is new.) Feathers of the upper back and scapulars are marked like the tail feathers, and are duller than in the adult female. The juvenile female is thus less strongly barred than the adult female, except for the tail band and the chest feathers, while the juvenile male has dorsal and ventral barring that the adult male lacks.

Among the 14 available specimens of *hoffmannsi*, there are two juvenile males from Calama (AMNH-491346, 28 June 1907; AMNH-156290, 1 August 1907). The first has brown rather than gray underparts, many rufous feathers over the nape, one brown feather on the forecrown, and russet-brown upperparts and tail; it is otherwise adult. The second has a few brown feathers at the sides of the chest and on the gray underparts. The axillars are brown rather than gray as in the adult, and the under surfaces of the wings are duller and less rufous than in the adult. The mantle and tail are more rufous than in the adult. The feathers of the hind crown are very dark rufous brown and rather long; new sheathed black feathers are on the forecrown. There are a few brown feathers on the black auriculars and nape. There are some brown feathers on the lower cheeks, and a few yellowish-stained feathers on the white bib. On the new labels of two females with a few yellowish-stained bib feathers (AMNH-491347 and AMNH-

491353) C. E. Hellmayr has marked "juv.," but they may be adult. All juvenile females I saw in the field had brown feathers, especially on the underparts.

One male from Borba (AMNH-491342, November 29, 1906) is in wing molt, suggesting that this species molts before the breeding season in the fashion of *berlepschi*. June to August adults are not in molt. My records and the two juvenile males above indicate that young are out of the nest at least February to July, or in the final months of the rainy season.

The 56 available specimens of *melanosticta* are too widely scattered to tell much about molt and breeding. June to August specimens from Rosarinho and Humaitá, across the Madeira from the range of *hoffmannsi*, are in molt. Seven juveniles molting into adult plumage, taken from Humaitá north to the Amazon, span the period from April to August. Molt probably follows breeding, which is concentrated in the rainy season, rather than preceding breeding as in *berlepschi* and *hoffmannsi*. Closer to the Andes the seasons of molt and breeding are uncertain. On the Purús a juvenile was taken 11 November, and birds in molt have been collected from August to February. In Perú, both molting and nonmolting birds have been taken from July to October. The breeding seasons of birds in this and related genera are so closely tied to rainfall that I would expect breeding in the southern rainy season (January to June) toward the south and east and breeding with two annual peaks (April and October), corresponding to the two equatorial rainy seasons, in northern Perú to southern Colombia. Presumably *cristata* also shows the latter pattern, although the only known juvenile was taken in July.

Although adult male *melanosticta* are unspotted, juvenile males are spotted on the back like females. A young male from Santo Antonio de Guajará, near Borba on the Madeira (11 April 1930, AMNH-280637) has even larger black subterminal bars and rufous tips on the back feathers than does an adult female, although he has fewer and smaller spots on the wing coverts than do females. This young male has a very dull brownish crown, the feathers shorter and less filamentous than in the adult. There is a breast-band of deep rufous-brown, while the rest of the underparts are the grayer brown of the adult plumage. The face is black, much as in the adult. The tail and wings of this and a similar young male (11 November 1922, CM-93968) from Arimã on the Purús are more russet, less brown, than in the adult male. Some birds sexed as females (such as AMNH-491330, Humaitá, 17 August 1906) are quite like young males.

The russet or dull brown breastband and the dull crest feathers are among the last of the juvenal feathers to be replaced; in the above young female and one other (AMNH-282110, Rosarinho, 28 June 1930) the new whitish feathers are restricted to the front of the crown, indicating replacement from front to back. For young *Rhegmatorhina*, the dull and short crests and the brown feathers on the breast, as well as the dull and small eye rings, perhaps reduce attacks by adult birds, as probably is the case for the brown chests of the related Bicolored Antbirds (Willis, 1967). However, the differences between young and old are difficult to detect when the adult is mostly brown, as is true for *melanosticta* and *gymnops*.

DISCUSSION

In behavior, rhegmatorhine antbirds are very much like Bicolored Antbirds and ant-following birds in several other related genera (*Phlegopsis*, *Skutchiea*, *Phaenostictus*, and *Pithys*). The major peculiarity of *Rhegmatorhina* is the behavior pattern of crest-raising, associated with strong development of a crest in all five species. One could argue that the genus *Rhegmatorhina* should

be a subgenus of *Gymnopathys*, for the two genera are morphologically very close. However, *Pithys albifrons* and species of the other genera are also closely related to these in behavior and morphology. Through *Hylophylax*, these genera grade into *Myrmotherula* and into *Thamnophilus*. There has been more evolutionary divergence in plumage and morphology than in reproductive and vocal behavior in the ant-following antbirds. It is uncertain whether they should all be put in one genus (*Pithys* has priority) or left in the present narrow genera. I prefer to wait for a revision of the Formicariidae. There is not much point in lumping two genera at a time, such as *Rhegmatorhina* with *Gymnopathys*, and creating several successive combinations of names, if all are eventually going to be lumped as the large genus *Pithys* or eventually into *Thamnophilus*.

The species of *Rhegmatorhina*, so far as is known, are allopatric. They differ mainly in color pattern, so that some might wish to consider them well-marked forms of one species. *R. melanosticta* clearly diverges from the others in the structure of the crown feathers. It probably should not be placed as a subspecies unless it is found to hybridize with *cristata* in Amazonian Colombia. *R. cristata* looks more like the other species of the genus, despite its rather long crest and its different song. However, it is more isolated geographically and morphologically than are the other three.

The forms *gymnops*, *berlepschi*, and *hoffmannsi* are practically identical in behavior. Oddly, *berlepschi* looks like a hybrid between *gymnops* to the east and *hoffmannsi* to the west. However, no intergrades have yet been discovered, and the juvenal plumages of the three are very different. At Maloquinha and along the wide Tapajoz, *gymnops* and *berlepschi* are separated by the river. If savannahs or other unsuitable habitats do not prevent their spread, the two may occur together around the headwaters of the Tapajoz.

The relationship of *berlepschi* and *hoffmannsi* is even more puzzling. Both species occur between the Tapajoz and Madeira, without any large river or other unsuitable habitat to prevent their meeting. How could two forms or species have evolved? There are isolated species on the west bank of the Tapajoz in several other genera of antbirds, and in marmosets as well (Hill, 1957). There are several theories that could account for evolution of these species.

One theory (Haffer, 1969) suggests that such species evolve in isolated forest "islands" when savannah areas widen during dry interglacials, then spread to meet relatives when forests increase during wet glacial periods. Another theory is that high sea levels during interglacials flood the river basins of the lower Amazon, cutting off islands because of the peculiar river pattern between the Madeira and Tapajoz. De Boer (1966) reports marine

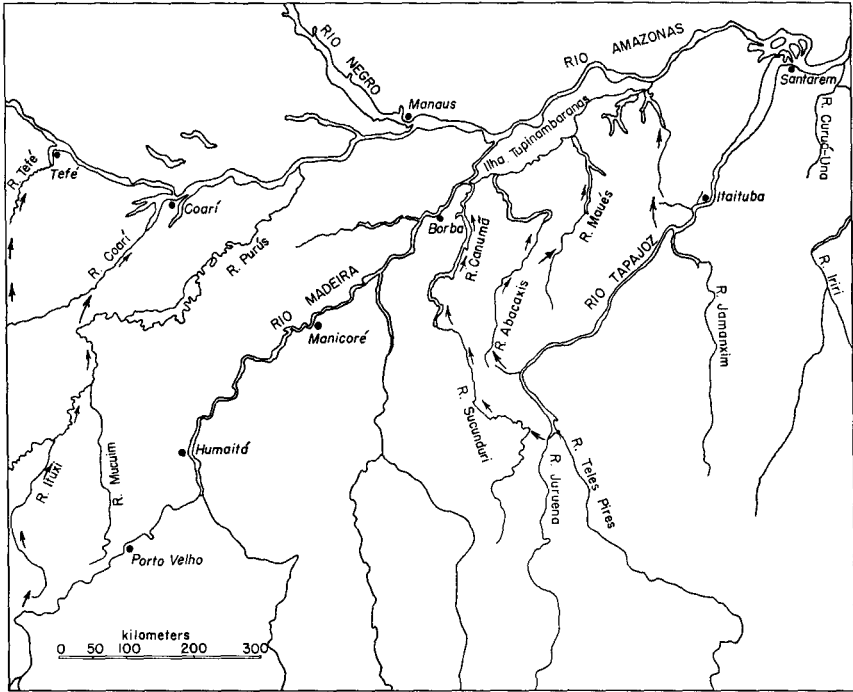


FIG. 8. Central Amazonia, showing possible former courses of the Rio Madeira (arrows on left of present-day Madeira) and Rio Tapajoz (arrows on right).

sediments well up the lower Amazon in the Tertiary and earlier. The peculiar river pattern probably derives in part from a crisscross fracture pattern that seems to develop in river basins where there is considerable sedimentation (Sternberg, 1950) but in part may derive from what may be called the third theory, that of river piracy creating islands as the Tapajoz and Madeira shifted their lower courses eastward after the Andes rose in the late Tertiary.

Probably the Tapajoz and Madeira flowed northwest off the Brazilian Shield until well after the Andes rose, and did so even after the Amazon became a strong river rather than an occasionally flooded lowland between the Guianan and Brazilian Shields. On a map of Amazonia, one sees huge finger lakes along the Amazon, pointing toward sharp bends in the upper courses of the Tapajoz and Madeira (Fig. 8): Lagoa de Tefé, Lagoa de Coari west of the Madeira; and the lagoons of Canumã, Abacaxis, Maués-Acu, Uaicurapá, and Arapuins between the Tapajoz and Madeira. Possibly small rivers cutting back from the northeast captured the headwaters of the Madeira and Tapajoz by a series of river piracies. If so, the Madeira may once have

flowed to the Amazon at Tefé and jumped to its present exit near Nova Olinda do Norte by way of a temporary exit at Coarí. The lower Tapajoz, which once flowed out through the Canumã to the mouth of the present-day Madeira, may have jumped eastward from lagoon to lagoon and ended flowing out from its present exit at Santarém. In this way the Madeira and Tapajoz, which probably feathered west into the Amazon when it first became a strong river, now feather east into it. After seeing the Lagoa de Tefé several times from the air and traveling the lower Canumã by boat, I doubt that these wide, steep-sided lagoons were carved by the tiny rivers that now flow to them. From the air, the upper end of the Tefé Lagoon, now silted in by the winding little Rio Tefé, seems the swampy former channel of a large river far to the south of the present lake.

Glacial periods, when sea levels were low and the cutting powers of rivers great because of high rainfall, are likely times for shifts in the lower courses of these rivers. River channeling or river subsidence because of deposits in glacial periods could allow flooding in interglacials, creating islands; or the Tapajoz may have had two exits at times, creating a large forested island on which *berlepschi* and other animals now restricted to the west bank of the Tapajoz could have evolved. Investigation of the geologically and ornithologically unknown region between the Tapajoz and the Madeira may show whether or where *berlepschi* and *hoffmannsi* come near each other and thus specify what the western boundary of such an island may have been.

J. Haffer (1969) suggests that the Amazonian rivers are poor barriers unless competing species occupy different banks. Changes in river courses and occasional flights across have permitted some colonizations even for poor-flying antbirds. Gene exchange could make the origin of species on separate banks unlikely unless wide marine or savannah areas added to isolation. I agree that competition from related forms may help keep rhegmatorhine and other antbirds from successfully crossing rivers, but think that clearing-avoiding species like these probably are effectively isolated by large rivers and could evolve separate species on the two sides because active crossings would be very rare. However, it is likely that evolution of species has involved both riverine and savannah "forest islands" in this region, and it may be difficult to compare the relative effects of the two kinds of isolating processes.

Even if evolution of these birds and others may be difficult to trace, comparison of ant-following and other "guilds" of species on the different banks of the Madeira and Tapajoz and Xingú should be very exciting for ecologists. The ant-following guild to the west of the river is in each case slightly more complex in numbers of species, yet geological and climatic conditions on the two banks often differ less than conditions 100 kilometers apart along the same side of a river. Evidently the rivers are a strong barrier

to spread even when there is no competing species beyond. The banks of these tropical rivers, often infertile for agriculture, should be fertile ground for ecologists and others interested in sudden changes in species diversity with little environmental diversity.

SUMMARY

All five allopatric species of plump, short-tailed antbirds of the genus *Rhegmatorhina* follow army ants and capture arthropods flushed by the ants low in the undergrowth of lowland forests along the Amazon. The most common foraging motion is sallying to the ground, as in birds of the related ant-following genera *Gymnopithys* and *Phlegopsis*.

Rhegmatorhine antbirds chirr and mob the observer. Freezing, and a sound of "keening" in some species, seem a reaction to distant danger. Single-note chipping, panicking, and hyperactivity result from the appearance of hawks and other nearby danger. The tail is flicked when a bird is excited.

Submissive behavior has not been noted, but there is a strong aggressive display, "challenging." The bird stands upright, ruffs up the crest (characteristic of the genus), and partly spreads the wings and tail. The bright blue bare areas around the dark eyes then show prominently against black faces, reminding one of the eyespot patterns of moths and other animals. Supplantings are frequent when several individuals of a species attend a swarm of ants. Two pairs or more attend a swarm at times, suggesting that there is a territorial system in which the pair on its own territory dominates other birds.

Interspecific aggression is frequent. Rhegmatorhine antbirds supplant smaller species, up to the size of woodcreepers of the genus *Dendrocincla*. Larger woodcreepers and large antbirds, such as members of the genus *Phlegopsis*, exclude rhegmatorhine antbirds from the best places over the ants.

Courtship feeding has been seen in three species and probably is the main courtship ritual in all. All adult females seemed to be paired, for there is apparently a surplus of males. Males lead their mates to swarms. A "nest-showing" display was noted for one male *berlepschi*.

In most behavioral aspects other than crest-raising, these antbirds resemble the noncrested antbirds of the related genus *Gymnopithys*. These and other ant-following genera have diverged less in behavior than in morphology.

Of the five species of *Rhegmatorhina*, *melanosticta* (ranging through upper Amazonia) is the most distinct in morphology and behavior. The isolated *R. cristata*, from the Uaupés River in northern Brasil and nearby Colombia, differs from other species in its loud-song but in few other respects. *R. berlepschi*, the Harlequin Antbird of the west bank of the Tapajoz in central Brasil, looks like but probably is not a hybrid between the white-throated *R. hoffmannsi* of the east bank of the nearby Madeira and the black-and-brown *R. gymnops* from the east side of the Tapajoz; juvenal plumages differ strongly. Possibly the presence of *berlepschi* and *hoffmannsi* rather than one species of the genus in forests between the Madeira and Tapajoz resulted from river piracy shifting the mouth of the Tapajoz eastward, creating for a time a forested island on which *berlepschi* evolved. The forested island may have been additionally isolated during dry interglacials by savannahs or by marine flooding up former and present river channels.

The different banks of the Tapajoz and Madeira and Amazon, with their rather

different species and guilds and communities, should be fertile ground for ecological studies of changes in species diversity in areas of low environmental diversity.

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