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BEHAVIOR AND VOCALIZATIONS OF THE CAURA AND THE YAPACANA ANTBIRDS

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ABSTRACT.—The first detailed information on the vocalizations (including the first sound spectrograms) and natural history of the Caura Antbird (*Percnostola caurensis*) and the Yapacana Antbird (*Myrmeciza disjuncta*) are presented. The Caura Antbird was studied in the Serrania de la Cerbatana, edo. Bolívar, Venezuela, where it inhabits humid foothill forest dominated by large rocks. Caura Antbirds specialized in foraging on or beneath rocks, a behavior unusual among the Thamnophilidae. The Yapacana Antbird was studied at a site along the south bank of the Río Ventuari, edo. Amazonas, Venezuela. These antbirds were locally abundant in a specialized stunted woodland that grows on white sand soils. Based on newly described vocal characters, the closest relatives of *P. caurensis* appear to be *P. leucostigma* and *P. schistacea*, whereas *M. disjuncta* has no apparent close relatives and probably merits placement in a monotypic genus. *Received 9 July 1998, accepted 5 Jan. 1999.*

Among the least known members of the large antbird family Thamnophilidae are the Caura Antbird (*Percnostola caurensis*) and the Yapacana Antbird (*Myrmeciza disjuncta*). Both species are nearly endemic to southwestern Venezuela and have remained relatively unobserved by modern field ornithologists. The most extensive collections of both species (36 specimens of *P. caurensis* and 5 specimens of *M. disjuncta*) reside in the Coleción Ornitológia Phelps (COP), Caracas, Venezuela. Single specimens of each species collected near Pico Neblina (edo. Amazonas, Venezuela) in 1984 by Field Museum of Natural History (FMNH) personnel represent the only specimens of *P. caurensis* and *M. disjuncta* collected anywhere since 1972 and 1981 respectively. There is essentially no published information on habitat or behavior of the two species, and nothing is known of their vocalizations (Ridgely and Tudor 1994).

In February 1998 I observed the habitats and behaviors and tape-recorded the vocalizations of Caura Antbirds in the Serrania de la Cerbatana, edo. Bolívar, Venezuela, and of Yapacana Antbirds in Yapacana National Park, edo. Amazonas, Venezuela. This is the first detailed information on the natural history and vocalizations of these species and allows a more informed assessment of their possible generic affinities.

STUDY AREAS AND METHODS

I observed Caura Antbirds 10–15 February, 1998 in the Serrania de la Cerbatana near Hato Las Nieves (6° 34′ N, 66° 12′ W), edo. Bolívar, Venezuela (Fig. 1). The Serrania de la Cerbatana rings a large valley vegetated mostly by a mixture of savanna and tropical dry forest, transected by narrow bands of gallery forest along occasional streams, and dotted with groves of *Mauritia* palms in poorly drained areas. Three main rivers, Caño Las Nieves, Río Agua Fria, and Río Danta, drain the valley. The Serrania mountain range rises dramatically from the valley, and on the southern and western borders is covered with humid forest. The south facing slopes of the mountains to the north of the valley are noticeably drier. The tallest peak in the chain is Pico Las Nieves at 2080 m. I studied Caura Antbirds along a 1.5 km trail that began in humid forest at 280 m elevation and extended up the side of a ridge to 400 m.

I studied Yapacana Antbirds 22–27 February 1998 along a trail (hereafter the "Picua Trail") near the settlement of Picua (4° 5′ N, 66° 45′ W) in Yapacana National Park, edo. Amazonas, Venezuela (Fig. 1). Picua is a small settlement of Piaroa and Mako Indians, on the south (left) bank of the Río Ventuari at about 150 m elevation. The surrounding area contains a mosaic of different soil types that support a patchwork of distinct vegetation types. The Ventuari and its many small tributaries are flanked by bands (of varying width) of tall forest (15–25 m) that grow on yellow clay soils and are seasonally flooded. This várzea forest is characterized by a closed canopy with a fairly open understory and an abundance of vines and lianas. On higher banks above the river the várzea grades into a taller transitional forest with a denser understory. Much of the area farther removed from the river is dominated by white sand soils on which grow lower stature woodlands and grassy savannas. The savannas range in size from less than 1 ha to about 1 km², with scattered shrubs and small trees. Larger savannas in the area contained stands of *Mauritia* palms. Large, isolated patches of red clay soils support tall (>30 m),

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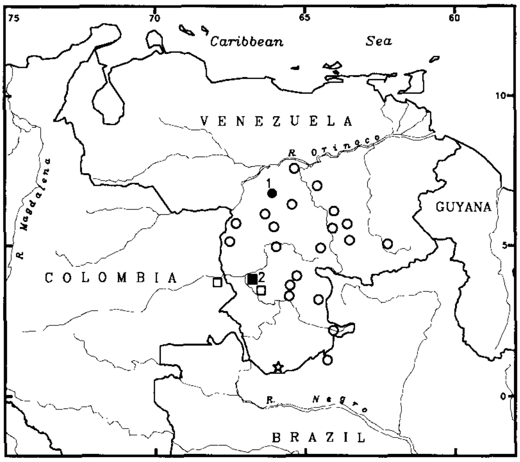

FIG. 1. Distributions of Caura Antbird (*Percnostola caurensis*) and Yapacana Antbird (*Myrmeciza disjuncta*): open circles = confirmed sites for *P. caurensis* (confirmation based on specimen records); open squares = confirmed sites for *Myrmeciza disjuncta*; open star = site near the base of Pico de la Neblina where both species have been collected in close proximity. The black circle and #1 indicates the site of the present study in the Serrania de la Cerbatana, edo. Bolívar, Venezuela where *P. caurensis* was studied. The black square and #2 indicates the site of the present study near Picua, in Yapacana National Park, edo. Amazonas, Venezuela where *M. disjuncta* was studied.

lush "islands" of humid tropical forest that are not seasonally flooded (= terra firme forest). Quartzite dome-like sandstone hills (cerros) and low outcroppings are scattered throughout the region.

Whenever individuals or pairs of *P. caurensis* or *M. disjuncta* were located, I followed them for as long as possible, tape-recording as many vocalizations as I could and summarizing foraging and other behaviors on cassette tape. Some of these behaviors were also documented on videotape. I used tape-playback of these recordings to assess presence or absence of antbirds in places where no spontaneously vocalizing birds were heard and to determine the limits of territorial boundaries. All measurements included in such summaries (height above ground, territory size, distances, times, etc.) are estimates. Terminology for foraging behavior follows Remsen and Robinson (1990).

Tape recordings were made with a Sony TCM-5000 recorder and Sennheiser MKH-70 microphone. All recordings have been or will be archived at the Library of Natural Sounds, Cornell Univ., Ithaca, New York. Spectrograms were made by Phyllis Isler on a Power Macintosh 7500 computer using Canary version 1.2.1 (Bioacoustics Research Program, Cornell Laboratory of Ornithology, Ithaca, New York). Morton Isler compiled a comprehensive list of distributional records of the two species of antbirds as documented by specimens, tape recordings, or photographs (Isler 1997; Fig. 1).

PERCNOSTOLA CAURENSIS

Distribution and habitat.—The Caura Antbird is known only from the western portion of the "Pantepui" region (Mayr and Phelps 1967) south of the Río Orinoco in the Venezuelan states of Bolívar and Amazonas and in extreme northern Brazil (Fig. 1). *Percnostola caurensis* is well represented in museum collections, with 36 specimens (the most recent collected in 1972) in the Coleción Ornitológia Phelps (Caracas, Venezuela) alone (C. Rodner, pers. comm.). The most recent substantiated record was of a male collected in 1984 at 1250 m near the base of Pico Neblina (edo. Amazonas, Venezuela; Willard et al. 1991). The occurrence of *P. caurensis* in the Serrania de la Cerbatana represents a slight range extension to the northwest (Fig. 1).

The forest along the first 500 m of the trail was tall (ca 30 m), with an open understory dominated by slender palms. The terrain was flat and nearly devoid of large rocks. I could locate only one territory of *P. caurensis* along this portion of the trail, and it abutted the bottom of the hill. The hillside forest beyond 500 m was also fairly open, with an intermittent canopy of about 20 m. Few trees were larger than 30 cm dbh, and woody vines were abundant. Large stands of a narrow-leaved, nonspiny bamboo (1–2 m in height) occupied most light gaps. The entire slope was extremely rocky, with numbers of boulders up to 8 m tall and 15 m along their longest axis. These boulders were typically moss and fern covered, with terrestrial bromeliads, cacti, and bamboo growing over their tops and in the crevices (Fig. 2). Many were topped with small trees, the gnarled roots of which draped off the sides of the rocks like tendrils, trapping leaf litter and organic debris. I located 6 pairs of *P. caurensis* along about 1 km of trail through this rocky, hillside forest.

The Serrania de la Cerbatana was extremely dry in February 1998. Typical dry season conditions appeared exacerbated by ongoing El Niño related events. Leaf litter throughout the forest was extremely dry and many trees had shed large numbers of leaves. This was particularly evident in the hillside forest, where large patches (0.5–1 ha) of deciduous vege-

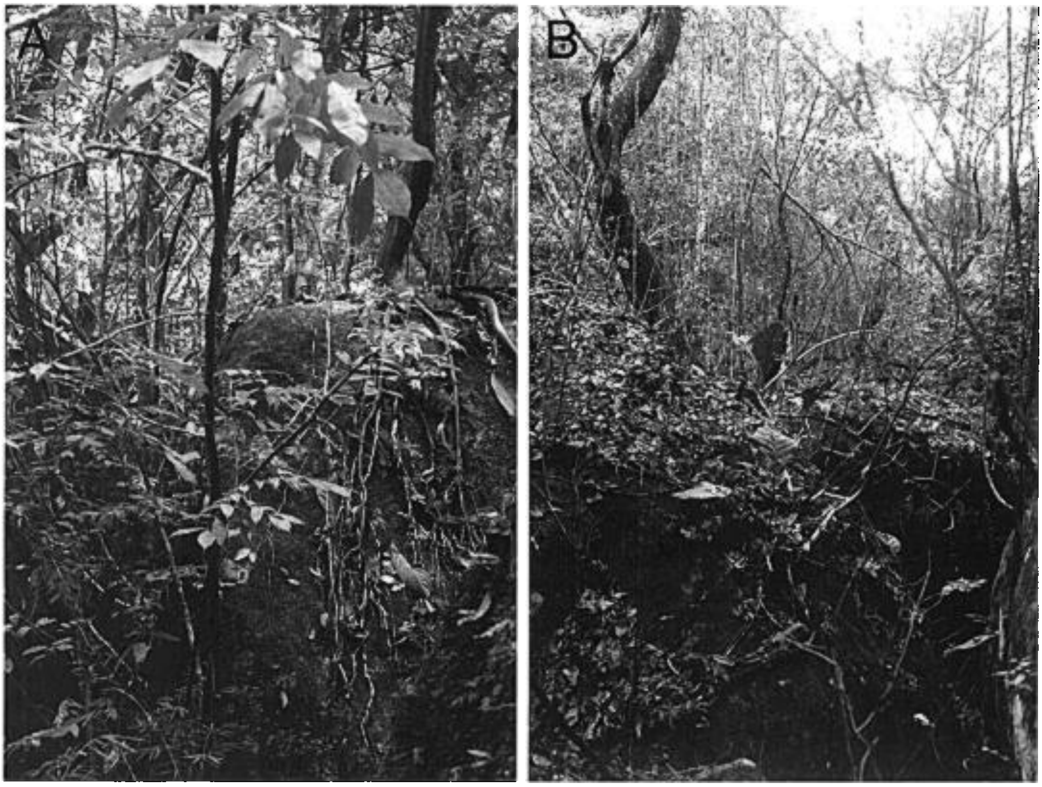

FIG. 2. Rocky hillside forest in the Serrania de la Cerbatana, edo. Bolívar, Venezuela. (A) Relatively open forest, with a broken canopy of about 20 m. The rocks were 2–3 m tall and 4 m in diameter. (B) A rocky alluvial fan along which were located two Caura Antbird territories. Note the highly deciduous state of the vegetation in this light gap, and the abundance of leaf litter trapped in the roots and vines overtopping the rocks.

tation were conspicuously scattered across the slope, usually coincident with the rock strewn alluvial fans at the bottom of ravines.

Morphology.—Soft-part colors were identical for both sexes. The iris was reddish-brown, the legs and feet were slate gray (a shade paler than the bill), and the bill was blackish. Plumage was as described by Ridgely and Tudor (1994).

Vocalizations.—Caura Antbirds were generally quiet during my fieldwork, as were most other species of insectivorous birds. Dawn choruses were both unremarkable and short, suggesting a low level of breeding activity for most species during the height of the dry season. There was a sustained rain during the early morning hours of 13 February; the two following mornings I noted increased spontaneous song from Caura Antbirds.

I recorded over 120 loudsongs (as defined by Isler et al. 1997) and 900 calls from 12 individual antbirds. The loudsong of *P. caurensis* is a far carrying series of 7–15 modulated and well spaced notes (Fig. 3A). The first notes are widely spaced, and the terminal notes are closer together and drop in pitch. Female songs (Fig. 3B) were similar in pattern to male songs, but differed in other characteristics such as mean number of notes, mean frequency, etc. Females sang less frequently than males.

In response to tape playback and during territorial encounters, both sexes gave loud, buzzy "zhew" calls at varying levels of frequency modulation (Figs. 3C–E). On a few occasions, birds involved in territorial disputes uttered sharp "quip" notes (Fig. 3F) when neighboring birds approached closely. The most frequently heard vocalization, and one given by birds startled along the trail, was an abbreviated loud rattle (Figs. 3G, H), similar to the alarm calls of *P. leucostigma* and

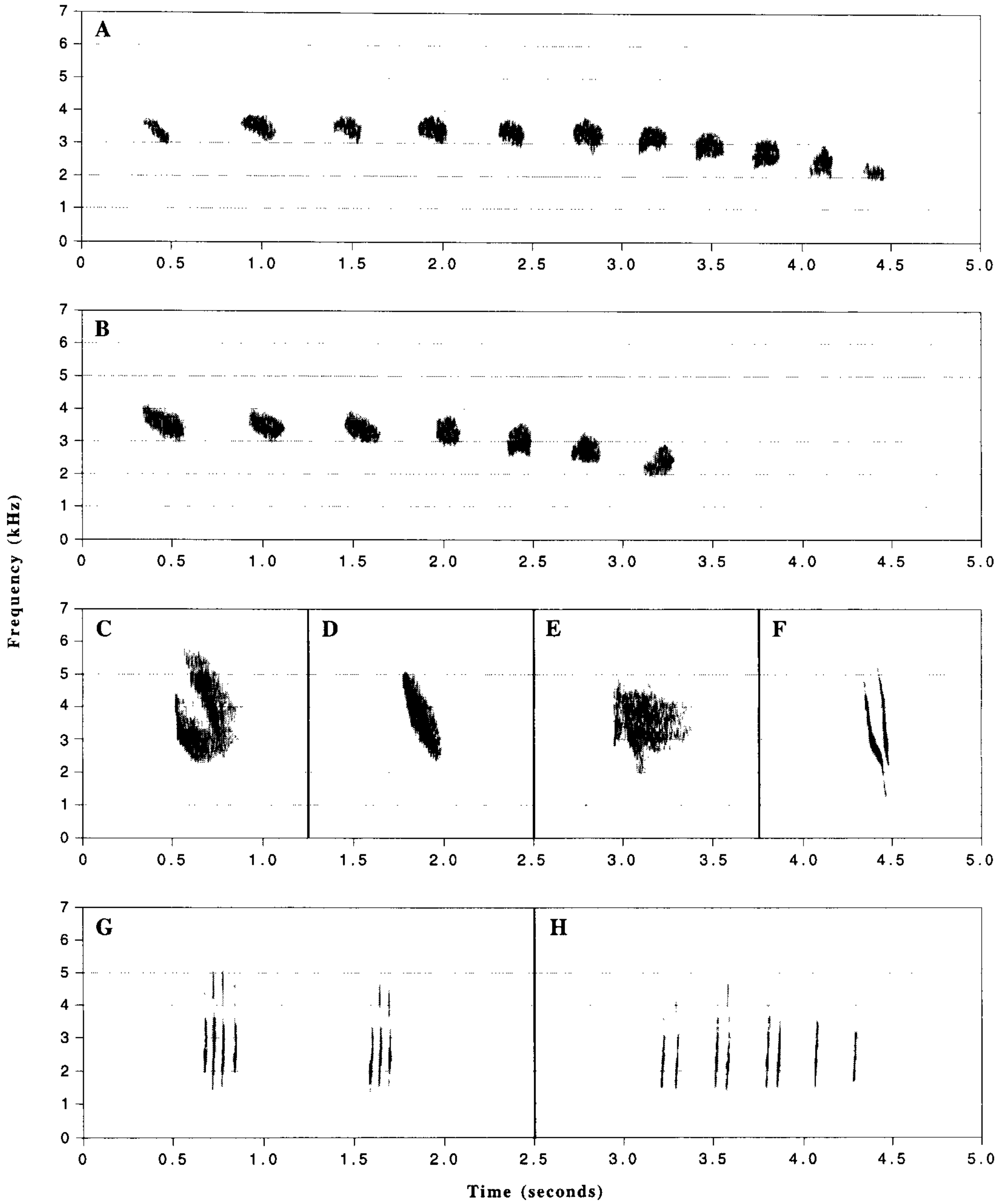

FIG. 3. Spectrograms of Caura Antbird (*Percnostola caurensis*) vocalizations: (A) male loudsong, (B) female loudsong, (C, D, E) "zhew" calls, which probably function as aggression calls, at various levels of frequency modulation, (F) "quip" call, (G) male alarm rattles, and (H) female alarm rattles.

several species of *Myrmeciza* antbirds (pers. obs.). A loud "chikit" (not tape recorded) was often given by Caura Antbirds at the moment they took flight. Birds alarmed by my presence gave this call immediately before flushing, as did birds chasing one another about in an aggressive boundary dispute.

Behavior.—Caura Antbirds were encountered singly or in pairs, but did not associate with mixed-species flocks. Mates foraging together were typically within 15 m of one another, and alarm calls from one bird elicited an immediate vocal response from the other. Foraging birds maintained a nearly horizontal posture, with the head held higher than the axis of the body. All individuals continuously raised their tails a few degrees above the plane of the body and then wagged them slowly downward in an arc 20–30° below the plane of the body. This tail movement was most exaggerated when the antbirds clung laterally to elevated perches or responded to tape playback, but was also used during terrestrial foraging. Mostly the tail appeared to be slightly fanned. Tail movements were occasionally accompanied by a simultaneous wing-flick.

Caura Antbirds foraged mostly on rocks or the ground. Both sexes spent long times creeping over the large boulders, often clinging laterally to nearly vertical rock faces and going in and out of the numerous crevices (often for minutes at a time) in the manner of Slaty Bristlefronts (*Merulaxis ater*; M. Isler and P. Isler, pers. comm.), Rock Wrens (*Salpinctes obsoletus*) or Canyon Wrens (*Catherpes mexicanus*). While creeping about the rocks, the antbirds frequently probed in the mosses and small ferns covering the surface, but spent most of their time inspecting the leaf litter trapped between the roots and vine tangles of trees overtopping the boulders. Arthropod prey (primarily orthopterans and hemipterans, as well as many arthropods too small to be identified) were gleaned from root and vine surfaces with quick stabbing motions. Curled dead leaves were carefully probed with the bill. Some antbirds inspected dead leaves without tossing them, others picked up leaves with the bill before tossing them aside. The antbirds routinely squeezed themselves into small spaces between the rock surface and overlying roots and vines, remaining in these somewhat "canopied" niches to forage for up to 60 s. When foraging on rocks, the antbirds tended to spend most of their time in somewhat protected locations, within the interior of vine tangles and root masses overtopping the rocks, within crevices in the rocks, or beneath rocky ledges and overhangs. The antbirds moved steadily over open rock faces, progressing by short hops of 5–10 cm and occasional longer wing-assisted hops or short, abrupt flights, often to low, overhanging branches or ledges. They frequently hopped from a rock up to a low branch or sapling to scan for 1–5 s before dropping back to the rock. Birds often dropped 1–5 m from the rocks to the ground. There, they hopped beneath the overhangs, probed in leaf litter and inspected rock surfaces. Antbirds spent many minutes inspecting fissures, crevices, and gaps within and between rocks, often retracing their routes.

One male observed foraging for more than 30 minutes spent the bulk of this time foraging over, under, and between rocks, probing in moss and vine tangles. On three occasions the bird dropped to the ground at the base of large rocks and spent 1–5 minutes vigorously tossing dead leaves in the manner of a leaftosser (*Sclerurus* spp.). Large leaves (many larger than the bird) were picked up with the bill and tossed. Smaller leaves were frequently flipped by inserting the bill beneath the leaf and then giving a quick upward flaking motion. He also made an upward sally of 20–25 cm from the ground to take an unidentified arthropod from the underside of a green leaf. Other individuals occasionally made similar short upward sallies to glean prey from overhanging rocks.

One female antbird spent several minutes hopping around the periphery of a large emergent swarm of small, winged ants. Although she picked at the ground several times, it was not clear whether she was feeding on the ants. The bird flew off and returned to the antswarm twice. The male antbird was foraging nearby, but did not attend the swarm.

Territories appeared to be about 150–200 m in diameter. I witnessed only one territorial conflict. This was a prolonged encounter between pairs whose territories bounded a large rock-slide along the center of a ravine. The conflict was marked by several advances and retreats by both pairs. Both members of each pair countersang at length while gradually approaching their counterparts. Whenever the pairs approached to within about 20 m of one another, they tended to substitute "zhew" calls for songs. When they were in visual contact or close auditory contact, the pairs exchanged harsh calls for a few minutes before one individual or pair retreated, often with its rival in close pursuit. These abrupt retreats were always preceded by the loud, hard "chikit" call. The dispute lasted for more than 30 minutes. Eventually the pairs retreated to opposite ends of the rockslide, periodically singing.

Most species of passerines besides *P. caurensis* were encountered in mixed-species canopy and mid-level flocks. The apparent absence of terrestrial or semi-terrestrial antbirds (other than *P. caurensis*) or furnariids is noteworthy, although my failure to detect such species could be an artifact of depressed song activity during the dry season. The taller, less-deciduous forest below the mountains had a more diverse avifauna.

The presence of large rocks appeared to be a critical component of *P. caurensis* habitat. Of the 7 territories, 6 were in areas with abundant large rocks. The seventh territory was close enough to the bottom of the hillside to possibly have included some rocky terrain as well. The rocks provided microhabitats in which a diversity of plants flourished, and these plants, in turn, provided a wealth of potential foraging strata for a small terrestrial insectivore such as *P. caurensis.* Caura Antbirds spent more than 80% of their foraging time on rocks and overtopping vegetation, or on the ground directly beneath overhanging rocks. The importance of rocks as foraging sites for Caura Antbirds may be increased during the dry season, when favorable moisture-retaining microclimates are created along rock edges or crevices. Furthermore, the tendency for overtopping root masses and vine tangles to trap leaf litter is accentuated during the dry season, when many trees drop their leaves. Such accumulations of organic litter may provide attractive sites for arthropods when the forest is water-stressed. It is interesting that no other bird species was observed to exploit the extra resource dimensions created by the large rocks. The presence of Guianan Cock-of-Rock (*Rupicola rupicola*) in the area is almost certainly dependent on the availability of large rocks for nest sites (Snow 1982), but only the Caura Antbirds seemed to use the rocks as foraging substrates.

MYRMECIZA DISJUNCTA

Distribution and habitat.—The Yapacana Antbird was described in 1945 by H. Friedmann from two specimens collected near the base of Cerro Yapacana (edo. Amazonas, Venezuela) in April 1931. Five more specimens were collected from the same general locality in April–May 1947 (specimens COP). Cerro Yapacana is an isolated outlier of the western Tepuis, rising steeply above the Río Orinoco to an elevation of 1340 m. Meyer de Schauensee and Phelps (1978:218), perhaps describing the general habitat surrounding Cerro Yapacana, listed the habitat of *M. disjuncta* as "High rain forest at about 100 m in undergrowth and low bushes." Subsequent to its description, *M. disjuncta* has been documented from only three additional sites (Fig. 1). In March 1981, while working in sandy-belt forest near Puerto Inírida, depto. Guainía, Colombia, J. Dunning mist-netted an antbird later identified from photos as a female Yapacana Antbird (Hilty and Brown 1986; ANJP specimen 175723, R. Ridgely, pers. comm.; photo on file at VIREO). In February 1984 a single female *M. disjuncta* was collected at 140 m near the left bank of the Río Baría on the Venezuelan-Brazilian border (Willard et al. 1991). This extended the known range of *M. disjuncta* about 350 km south. There is no published description of the habitat in which this Yapacana Antbird was collected, but the nearby base camp was in "tall seasonal rain forest drained by both black-water and white-water streams" (Willard et al. 1991). J. Coons and D. Stejskal (pers. comm.) were the first to find *M. disjuncta* near Picua in January 1997. They reported seeing or hearing several individuals in savanna woodland on white sand soils along the Picua Trail.

The only habitat of the Ventuari in which I found *M. disjuncta* was what the local people refer to as "monte cerrado." I found this habitat only on the south bank of the Río Ventuari along the Picua trail. This is a stunted, virtually impenetrable woodland that grows on fine, compacted white sand soils that are seasonally saturated (Fig. 4). It is similar to the "savanna woodland" described from Campamento Junglaven located farther north (upstream) along the Ventuari (Zimmer and Hilty 1997) but has a greater density of vines, along with abundant sawgrass and bamboo scattered through the understory. The canopy varies from 6–10 m and is of generally uniform height with only occasional emergent trees of

FIG. 4. (A) Monte cerrado woodland along the Picua Trail, Yapacana National Park, edo. Amazonas, Venezuela. (B) Interior of the monte cerrado, depicting a typical Yapacana Antbird territory.

10–15 m. Few trees in this habitat have trunks thicker than 10 cm dbh.

A different type of "sandy belt forest" or savanna woodland occurred on the north bank. This woodland was partly deciduous, less diverse, and even more stunted than the monte cerrado. The understory was more open and lacked both bamboo and sawgrass. This forest grew on coarser, well-drained white sand soils atop low ridges or rocky outcroppings. *Myrmeciza disjuncta* and many other species typical of the monte cerrado were absent from this scrub woodland.

Using tape playback I located at least 24 pairs of *M. disjuncta* along 1350 m of the Picua Trail. No birds were detected farther than 50 m from the trail. Territories were evenly spaced along both sides of the trail and appeared to be no more than 50–75 m in diameter. Near the savanna edge the monte cerrado was particularly stunted, with a more open canopy and more sawgrass in the understory. I found only two territories of Yapacana Antbirds along more than 150 m of trail transecting this more grassy woodland.

Morphology.—There has been some confusion in the literature regarding plumage characters of *M. disjuncta.* Central to the confusion is the type specimen of *M. disjuncta,* an immature male molting into adult plumage (Friedmann 1945, 1948), which displayed a combination of adult and immature plumage characters. Thus, Meyer de Schauensee (1970: 249) wrote that the male has "upperparts blackish-gray, crown and nape tinged brown" and "sides of head gray, chin white; rest of underparts white, strongly tinged ochraceous buff; center of abdomen white." Similarly, Meyer de Schauensee and Phelps (1978:218) described the male plumage as having the "throat and breast white suffused with ochraceous tawny, strongly so on breast and sides of throat, middle of abdomen white, undertail coverts dark gray." They described the female as differing from the male by "dark ochraceous buff spots on wing coverts and ochraceous under tail coverts." This description was essentially repeated in Hilty and Brown (1986). Ridgely and Tudor (1994:332) were much more nearly correct in both their illustration of the male and in the description of the plumage, but still suggested that the underparts of the male are "tinged with creamy buff."

None of the 20 or more male Yapacana Antbirds that I saw showed any hint of tawny, ochraceous buff, or creamy buff color on the underparts, nor did they have the crown or nape tinged brown. Instead they were uniformly dark gray (with an almost steely blue cast) above (except for the usually concealed white interscapular patch) and on the sides of the face, with the chin, throat, breast, belly, and undertail coverts white. The sides and flanks were washed with gray, but these areas were often concealed by the wings. The wing coverts were blackish, with the lesser and median wing coverts fringed white. The tail was blackish and the rectrices were either narrowly tipped or fringed white. This character is not mentioned in any of the previous descriptions, possibly because the narrow white tips/fringes were lost to wear in the few existing specimens. The legs were pinkish gray, the iris blackish brown, the maxilla blackish, and the mandible whitish. Females differed in having a slightly brownish cast to the upperparts, particularly the crown and nape, which contrasted with the gray sides of the face. The underparts were a bright ochraceous buff (almost pale orange) from the throat to the undertail coverts, and were only slightly paler on the chin and upper throat. I did not note pale tips or fringes on the rectrices of females, nor could I confirm the presence of a contrastingly colored interscapular patch.

All birds that I saw had proportionately short, broad tails that appeared graduated. This could have been influenced by molt, but, if so, all of the individuals in this area were highly synchronous in the regrowth of their outer rectrices.

Vocalizations.—J. Coons and D. Stejskal (pers. comm.) tape recorded some single-note harsh calls of *M. disjuncta* during their January 1997 visit to Picua, but did not encounter singing birds. Yapacana Antbirds were also generally quiet during the period of my field work. Even at dawn there was little spontaneous singing, suggesting that the level of breeding activity was low. However, birds were highly responsive to tape playback, which often elicited singing from one or more neighboring pairs in addition to the resident pair. Both males and females responded vocally to playbacks, although males were much more aggressive in approaching the speaker. All types of vocalizations that I recorded were given by both sexes of Yapacana Antbirds. I tape recorded over 350 loudsongs and 230 calls from 34 individuals.

The typical loudsong of *M. disjuncta* consisted of two prolonged, harsh, heavily frequency modulated notes separated by a short pause, into which were inserted one or two "pip" notes (Fig. 5A). The first harsh note was the longest, and increased in intensity while rising in pitch. The second harsh note was shorter and had a more uniform amplitude. A typical loudsong could be transcribed as "cchhhhhhh pipizhhhh". On many occasions birds sang songs with no discernible "pip" notes between the harsh elements, although spectrograms of such songs reveal a distinct spike at the beginning of the second harsh note (Fig. 5B). Less frequently birds sang songs with three harsh elements instead of two (Figs. 5C, D). The third harsh note in such series was usually the shortest. Loudsongs varied in duration, depending largely on the number of harsh elements included. I could find no consistent differences between male and female songs, although males more frequently inserted two "pip" notes between harsh elements and females more frequently sang songs with no "pip" notes.

The most commonly heard calls were long, harsh, single notes, at a somewhat higher pitch than the harsh elements of the song, and with a peculiar, slightly nasal quality (Figs. 5E, F). These "harsh calls" were given by both sexes, although those of females were higher pitched. "Harsh calls" seemed to be aggression calls given in response to tape playback or by a bird disturbed by my presence. Birds occasionally gave a soft rattle (Fig. 5G) in a similar context. When Yapacana Antbirds of either sex were suddenly startled or strongly agitated, they gave one or more sharp and somewhat squeaky "squip" notes (Fig. 6A). These notes were similar in tonal quality to the notes inserted between the primary harsh

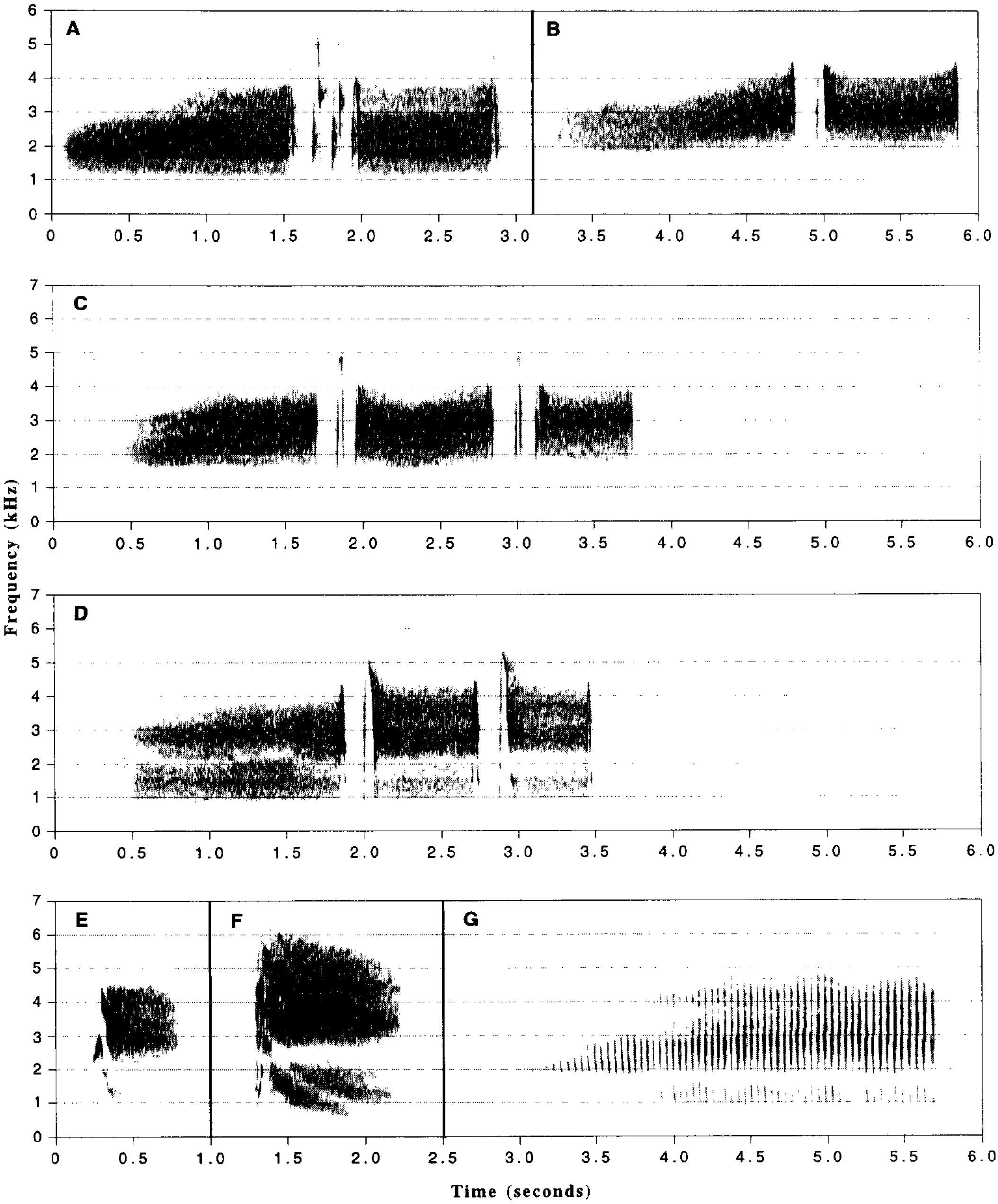

FIG. 5. Spectrograms of Yapacana Antbird (*Myrmeciza disjuncta*) vocalizations: (A) male loudsong with two "pip" notes inserted between the primary harsh elements, (B) loudsong variant with no discernible "pip" notes between harsh elements (sex of singing bird unknown), (C) loudsong variant with three harsh elements and single "pip" notes (sex of singing bird unknown), (D) loudsong variant with three harsh elements and no "pip" notes (sex of singing bird unknown), (E) male harsh call, probably an aggression call, (F) female harsh call, probably an aggression call, and (G) soft rattle call, given in an aggressive context.

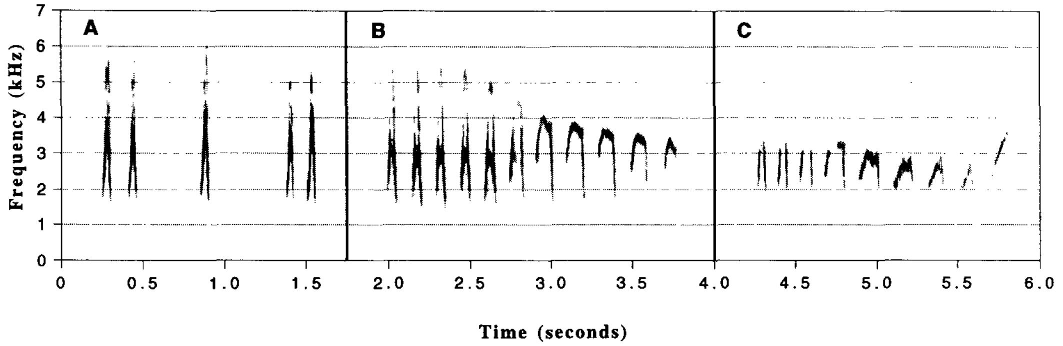

FIG. 6. Spectrograms of Yapacana Antbird (*Myrmeciza disjuncta*) calls: (A) "squip" notes given by a startled or alarmed bird, (B) rarely heard complex call (sex of calling bird unknown), and (C) variant complex call (sex of calling bird unknown).

elements of most loudsongs. Occasionally birds of either sex gave a more complex call that began with several "squip" notes and ended with a descending series of soft, whistled "wheee" or "whew" notes (Figs. 6B, C). These complex calls had a distinct tailing off quality, as in "squip squip squip wheee wheee wheee whew whew." The function of these calls was not clear.

Behavior and sociality.—Yapacana Antbirds were encountered singly or in pairs and did not associate with mixed-species flocks. Given the relatively small size of their territories, members of pairs were rarely far from their mates. An alarm call or song from one bird almost invariably brought an immediate vocal response from its mate. I did not witness any confrontations between neighboring pairs of antbirds, although on several occasions a singing pair of birds stimulated an adjacent pair to approach the apparent boundary and countersing for several minutes.

Yapacana Antbirds typically maintained a horizontal posture, with the head held higher than the axis of the body. Singing birds usually maintained a more upright posture. The tail was held within a few degrees above or below horizontal, and often was kept slightly fanned. Foraging birds often quickly flicked the tail up and down in a shallow arc of less than 10°, but just as frequently dipped the tail slowly downward at about a 30° angle before flicking it back up more rapidly. Singing birds frequently shivered the tail up and down more rapidly throughout a song. Some individuals wagged their tail sideways in a slow, somewhat jerky manner. Such motions involved the entire tail being swung a few degrees away from the axis of the body, held briefly in that position, then swung still further in the same direction before being swung back into alignment. This jerky motion is similar to some of the tail movements employed by the Silvered Antbird (*Sclateria naevia*; pers. obs.). Whether foraging or singing, Yapacana Antbirds flicked their wings at least once during virtually every pause between hops. Wing-flicks occurred both independent of and in synchrony with tail movements. Singing birds rarely sang consecutive songs from the same perch. In response to tape playback males often exposed a white interscapular patch.

Yapacana Antbirds foraged mostly on or near the ground, always lower than 1.5 m. They were restless, active foragers, moving by short hops (often wing assisted) and seldom pausing for more than 2 s in one spot. When moving above the ground they clung laterally to slender vertical saplings or perched across horizontal limbs and vines, progressed in an often erratic, zigzag course, and frequently moved up and down. They were adept at clinging to the thinnest stems, including slender bamboo stalks and vines. On a few occasions I saw birds hop headfirst down nearly vertical stems or branches, almost in the manner of a nuthatch (*Sitta* spp.). Birds frequently took several hops on the ground before jumping up to a low perch and then back down to the ground. Small arthropod prey were gleaned from stems and from tops and bottoms of live leaves by reaching out, up, or down on extended legs and with neck craned. Prey were captured with a quick stabbing motion of the bill and swallowed entire. Larger prey items were bashed against the perch and mandibled one or more times before being swallowed. Antbirds typically wiped their bill on the perch after swallowing prey. Most prey items that could be identified were small orthopterans (katydids and crickets), hemipterans, and geometrid larvae.

I encountered Yapacana Antbirds foraging in the open along the main trail on only three occasions. Two of these encounters involved pairs, and the other involved a lone female plumaged bird. In each case the birds were working the edge of the dense monte cerrado vegetation, as well as shrubs and clumps of grass growing in parts of the trail. All foraged mostly on the ground, progressing by a series of short hops with minimal pauses in between, and always with wings (and frequently the tail) flicking. The most frequent attack maneuvers were gleans from the surface of the leaf litter or brief probes with the bill beneath the leaf litter. The next most frequent technique was reaching up to glean from the undersides of overhanging green leaves and grass blades. On several occasions birds jumped 6–15 cm upward to glean prey from the undersides of leaves. The two pairs of antbirds encountered in the open were found in the early morning before the sun had illuminated the trail. The lone female plumaged bird (possibly a subadult male) was found in midmorning, when the entire trail was sunlit and temperatures were already above 30° C. I followed this bird as it foraged steadily at the edge of the woodland for more than 20 minutes and covered more than 50 m. It crossed at least one known territorial boundary, but remained silent and did not attract attention from any other antbird.

On one occasion I found a female Yapacana Antbird attending a foraging swarm of army ants (*Eciton* sp.) within the monte cerrado. I observed this bird over 20 minutes during which it was the only bird attending the swarm. The female antbird employed two strategies in the vicinity of the ants. Part of the time she scanned the swarm from perches within 0.3 m of the ground, dropped to the ground to seize fleeing arthropods (orthopterans, hemipterans, and spiders) and then returned to a low perch to beat the prey on a branch before swallowing. Slightly more time was spent hopping on the ground between the columns of ants and tossing dead leaves in the manner of a leaftosser (*Sclerurus* spp.). Most leaves were tossed by inserting the bill beneath the leaf and lifting it with a quick flaking motion. Occasionally the bird picked up a leaf in its bill and tossed it aside. David Wolf (pers. comm.) observed another female antbird (away from ants) that remained in one spot tossing leaves in a similar manner for 1–2 minutes.

I observed no other species of terrestrial or semi-terrestrial antbirds in the monte cerrado. The Black-throated Antbird (*Myrmeciza atrothorax*) and the Black-chinned Antbird (*Hypocnemoides melanopogon*), both of which routinely forage below 1.5 m (Hilty and Brown 1986; pers. obs.), were locally common in nearby forest or edge habitats, but were not found in the monte cerrado. The only other passerine (besides *M. disjuncta*) in this habitat that I found foraging below 1.5 m was the Buff-breasted Wren (*Thryothorus leucotis*), which foraged everywhere from the ground to the canopy.

DISCUSSION

Habitat and conservation.—My field work indicates that both the Caura Antbird and the Yapacana Antbird are habitat specialists, occurring in subtypes of more widely distributed macrohabitats. *Percnostola caurensis* has been recorded over a broad elevational range, 100–1300 m (Meyer de Schauensee and Phelps 1978). In the Pantepui region this range of elevations often spans the distance between tall, seasonal humid forest and elfin cloud forest. An antbird that occurs across such a spectrum of habitats might normally be considered an ecological generalist. However, if the critical ecological factor determining its distribution is the presence of large rocks within forest regardless of elevation, then *P. caurensis* is very much a specialist. This could, in part, account for the absence of the species from so many seemingly suitable lowland sites in Bolívar and Amazonas (Campamento Junglaven: Zimmer and Hilty 1997; Brazo Casiquiare: Paynter 1982).

Percnostola caurensis may have evolved as something of a rock-specialist to occupy a niche that is locally abundant in parts of the highly eroded Guianan Shield. Mayr and Phelps (1967:277) described the tepuis (table top mountains) of this region: "many are actually strongly dissected and strewn with isolated blocks, some more than 100 m high, and with a large variety of other rock forms." Most Caura Antbirds have been collected from the slopes of tepuis (Zimmer and Phelps 1947, Phelps and Phelps 1963, Meyer de Schauensee and Phelps 1978). The most recently collected specimen, from 1250 m at the base of Pico Maguire (edo. Amazonas, Venezuela), was from a site described as "A hanging valley in dense cloud forest with moderately tall trees, and rocky forest floor covered with thick moss" (Willard et al. 1991: 6). The apparent absence of *P. caurensis* from much of the eastern portion of the tepui region of Bolívar is a mystery.

Myrmeciza disjuncta appears to be restricted to woodlands growing on white sand soils. White sand habitats are widely but patchily distributed throughout Amazonia, with their center of distribution in the upper Río Negro region (Pires 1974, Stotz et al. 1996). White sand soils support many different types of vegetation, from scrub to tall forest (Anderson 1981). Several distinctly different types of vegetation were found growing on white sand soils in the Picua region but I found *M. disjuncta* only in the monte cerrado. Similarly, surveys of two nearby sites in Amazonas (Campamento Junglaven and Pto. Ayacucho) have failed to record *M. disjuncta* in spite of the prevalence of white sand woodlands (Zimmer and Hilty 1997). The Yapacana Antbird may therefore be restricted only to a particular type of white sand woodland, the monte cerrado. This would indicate an even patchier distribution than previously suspected and would help explain how this species has escaped detection for so long.

Both the Caura Antbird and the Yapacana Antbird appear to be locally common within their preferred habitats. The distributions of both species are centered in the lowlands or foothills of Amazonas and western Bolívar, which are among the least populated regions in Amazonia. Thus, neither species is under immediate threat of extinction. However, their patchy distributions and apparent restriction to particular microhabitats make them more vulnerable than most other birds of the Guianan lowlands. Stotz and co-workers (1996:4) have noted that "... the first major waves of extinctions in the Neotropics are not occurring in centers of diversity such as the Amazon. Rather, extinctions are occurring within centers of local endemism, especially among species that have evolved ecological specializations that limit their ability to adapt to human modifications of their habitats."

Before the conservation threats facing *P. caurensis* and *M. disjuncta* can be adequately assessed, we must first confirm their dependence on or preference for the microhabitats in which I found them, then attempt to quantify just how much appropriate habitat exists within their ranges. More comprehensive survey work within the region is clearly needed. Continued protection of existing parks or reserves, such as Yapacana National Park, is vital, particularly with regard to threats posed by illegal gold-mining.

Intrafamilial relationships.—The Caura Antbird was described by Hellmayr (1906) and placed in the genus *Sclateria.* The Caura Antbird was subsequently transferred to *Schistocichla* (Zimmer and Phelps 1947), which was later subsumed into *Percnostola* without elaboration by Peters (1951). Subsequent authors (e.g., Meyer de Schauensee 1966, 1970; Sibley and Monroe 1990; Monroe and Sibley 1993) have continued this treatment, recognizing five species: *P. rufifrons, P. schistacea, P. leucostigma, P. caurensis,* and *P. lophotes.* Ridgely and Tudor (1994) resurrected the genus *Schistocichla* for *schistacea, leucostigma,* and *caurensis* on the basis of their rounder, uncrested heads (crested in *P. rufifrons* and *P. lophotes*) and spotted rather than fringed wing coverts.

On purely morphological grounds, *P. caurensis, P. leucostigma,* and *P. schistacea* would appear to comprise a natural grouping. Plumage differences between *P. caurensis* and *P. leucostigma* are especially subtle, with size and soft part coloration being the most important field characters for visually distinguishing the two species (pers. obs.). Vocal similarities are less apparent, in part because of pronounced geographic variation in the vocalizations of the various named subspecies of *P. leucostigma* (pers. obs.). Indeed, some vocal differences within the *P. leucostigma* complex are as great as the between species differences in the *Schistocichla* group. Given this, I feel that resolution of the intrageneric relationships of the five species currently included in *Percnostola* should await molecular comparisons, as well as a closer evaluation of vocal and morphological differences as they relate to the *P. leucostigma* group.

Almost since its description, there has been speculation regarding the placement of the Yapacana Antbird in *Myrmeciza.* Friedmann (1948:478) offered that "the species is not too distantly related to *Myrmeciza atrothorax* but is clearly specifically distinct from that form." He went on to note that Zimmer had examined the type and the paratype and had pointed out that "the general plumage has about the texture of *Cercomacra carbonaria*" (Friedmann 1948:478). Friedmann (1948) further noted Zimmer's suggestion that a fully adult male *M. disjuncta* might show a closer relationship to *Cercomacra* than was suggested by the type specimen. He also commented that "The pattern of the markings of the upperwing coverts is very like that of some forms of *Cercomacra* (*serva* for example), but the bill is that of *Myrmeciza*" (Friedmann 1948:478). Peters (1951) alluded to the seemingly polyphyletic nature of *Myrmeciza* as he defined it and made several recommendations for the placement of various species, but did not mention *M. disjuncta.* Ridgely and Tudor (1994:333) also noted the heterogeneous nature of *Myrmeciza* and suggested specifically that *M. disjuncta* may not belong in the genus and "perhaps is more closely allied to *Sclateria*". They also seemed to suggest somewhat indirectly, that *M. disjuncta* was or should be included in the formerly recognized genus *Myrmoderus.* However, I can find no evidence that *M. disjuncta* was included in the various shifts of species between *Myrmeciza* and *Myrmoderus* by Hellmayr (in Cory and Hellmayr 1924), Todd (1927), or Peters (1951).

Morphological, vocal, and behavioral characters offer contradictory clues to the possible generic affiliations of the Yapacana Antbird. *Myrmoderus* is not currently recognized, but both Todd (1927) and Peters (1951) advocated that it be reserved for [*Myrmeciza*] *loricata* and *squamosa.* The latter are clearly sibling species that share several distinctive morphological, vocal, and behavioral characters, and they are distant in all respects from *M. disjuncta* (pers. obs.). In some morphological respects, *M. disjuncta* is reminiscent of the monotypic *Sclateria,* as suggested by Ridgely and Tudor (1994), but it has fringed rather than spotted wing coverts, white tail tips, an interscapular patch, and differs greatly in both vocal and behavioral characters. The song of *M. disjuncta* is mildly reminiscent of that of various members of the *Cercomacra nigricans* group (as defined by Fitzpatrick and Willard 1990), and the plumage pattern of males, largely gray with white-fringed wingbars and white tail-tips, and females ochraceous below, fits several members of the *C. tyrannina* group. However, *Cercomacra* antbirds tend to be slender and proportionately long-tailed (Ridgely and Tudor 1994), whereas *M. disjuncta* is relatively compact and short-tailed. No *Cercomacra* approaches the white underparts of male *M. disjuncta*; the genus as a whole has gray or blackish underparts. More importantly, male-female antiphonal duets are an important component of the vocal repertoires of virtually all species of *Cercomacra* (Zimmer et al. 1997), but are not found in *M. disjuncta.*

In size, proportions, and some aspects of plumage *Myrmeciza disjuncta* is somewhat suggestive of *Hypocnemoides.* However, neither species of *Hypocnemoides* is nearly as sexually dimorphic as is *M. disjuncta,* and they lack any suggestion of the ochraceous coloration found in female *M. disjuncta. Myrmeciza disjuncta* lacks the black throat and pale eye found in *Hypocnemoides.* Vocal differences between *M. disjuncta* and *Hypocnemoides* are much greater than the morphological differences (pers. obs.). By themselves, the two species of *Hypocnemoides* form a natural grouping, with great similarities in plumage, voice, foraging behavior, and habitat use. Almost none of these characters are shared with *M. disjuncta.*

I feel that *Myrmeciza* as currently constructed is paraphyletic, with various subgroupings that do not appear to be closely allied on the basis of morphological, vocal, or behavioral characters (e.g., Peters 1951, Ridgely and Tudor 1994). None of these subgroups is a good fit for *M. disjuncta. Myrmeciza atrothorax* has been suggested as a close relative of *M. disjuncta* by Friedmann

(1948), but the males of the two species differ dramatically in plumage, and the two species share no vocal similarities that I can detect. No compelling morphological similarities clearly ally *M. disjuncta* with any other *Myrmeciza,* nor with any other antbird. Similarly, I have compared songs and calls of *M. disjuncta* to the other 18 species currently placed in *Myrmeciza* (Isler and Whitney 1999; Zimmer, unpubl. data) and can find nothing to suggest a close relationship between *M. disjuncta* and any of the other species. Relationships suggested by one or two morphological characters in one sex are contradicted by morphological characters in the other sex, vocal characters, behavioral characters, or by some combination of the three. Although past descriptions of genera have been based largely on plumage characters which may or may not have phylogenetic relevance, the addition of vocal and behavioral data adds important evidence in redefining these relationships (e.g, comments in Remsen 1997, Remsen and Schulenberg 1997). In the absence of a molecular based phylogeny the most conservative approach would be to leave *M. disjuncta* where it is, as yet another poor fit in a genus understood to be heterogeneous. However, in my opinion, the sum of morphological, vocal, and behavioral evidence would suggest that the Yapacana Antbird is monotypic, deserving of its own genus.

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