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VOCALIZATIONS, BEHAVIOR AND DISTRIBUTION OF THE RIO BRANCO ANTBIRD

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ABSTRACT.—We here present the first detailed analysis and sonagrams of the vocalizations of the Rio Branco Antbird (*Cercomacra carbonaria*) and augment the scant literature concerning its abundance, habitat preferences, and behavior. Based on vocal similarities, we examine the possible relationships of the Rio Branco Antbird to other species in the genus. *Received 15 Aug. 1996, accepted 20 Feb. 1996.*

As currently recognized, the genus *Cercomacra* consists of 12 species (Sibley and Monroe 1993, Bierregaard et al. 1997, Graves 1997) of medium-sized antbirds. The genus is poorly known, as evidenced by the discovery of two new species of *Cercomacra* and the elevation of another subspecies to species in the last decade (Fitzpatrick and Willard 1990, Bierregaard et al 1997, Graves 1997). Fitzpatrick and Willard (1990) proposed that the genus contains two distinct species groups, with one species (*C. cinerascens*) intermediate. They labelled these two groups the "*nigricans*-group" (consisting of the species *C. nigricans*, *manu*, *melanaria*, *ferdinandi*, and *carbonaria*) and the "*tyrannina*-group" (then consisting of the species *C. tyrannina*, *serva*, *nigrescens*, and *brasiliana*) (Fitzpatrick and Willard 1990). A subsequent cladistic analysis of plumage and vocal characters of the "*nigricans*-group" by Silva (1992) supported the hypothesis that the group is monophyletic and that *C. cinerascens* is the sister taxon of all five included species but reached different conclusions from Fitzpatrick and Willard concerning the phylogenetic relationships of species within the complex.

The Jet Antbird (*C. nigricans*) is the most widely distributed species of the *nigricans*-group as defined by Fitzpatrick and Willard (1990), occurring both east and west of the Andes from Panama to western Ecuador and northeastern Venezuela (Ridgely and Tudor 1994). The recently described Manu Antbird (*C. manu*; Fitzpatrick and Willard 1990) is now known to be widely, but apparently locally, distributed south of the Amazon from southeastern Peru to east of the upper Rio Tapajós, Mato Grosso, Brazil (Parker et al. in press, Zimmer et al. in press). The remaining three species have limited distributions around the perimeter of the Amazon Basin (mapped in

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Fitzpatrick and Willard 1990). The Mato Grosso Antbird (*Cercomacra melanaria*) is found in northern and eastern Bolivia, southwestern Brazil in Mato Grosso and Mato Grosso do Sul, and in extreme northern Paraguay (Ridgely and Tudor 1994). The ranges of *C. carbonaria* (extreme northern Brazil along the Rio Branco and some major tributaries) and Bananal Antbird (*C. ferdinandi*) (largely Bananal Island in the Araguaia-Tocantins drainage) are among the smallest of all South American birds, and consequently, little is known of their vocalizations or natural histories.

In this paper we present the first published behavioral accounts and vocal analysis of *C. carbonaria*, the Rio Branco Antbird, and comment on its possible relationships to other species in the group, as suggested by vocal comparisons. We also attempt to determine why its distribution is so small.

STUDY AREA AND METHODS

Zimmer and Whittaker observed Rio Branco Antbirds between 1–3 Nov. 1994 along an approximately 10-km transect of the Rio Branco, from the city of Boa Vista, Roraima, Brazil, to just north of Ilha São Jose (ca 2°53′N, 60°33′W; Fig. 1). Whenever individuals or pairs of *C. carbonaria* were located, we followed them for as long as possible, summarizing foraging and other behaviors on cassette tape. Tape-playback was used to assess presence or absence of Rio Branco Antbirds in places where no spontaneously vocalizing birds were heard, and also to determine limits of territorial boundaries. All measurements included in such summaries (height above ground, territory size, distances, etc.) are estimates. Terminology for foraging behaviors follows Remsen and Robinson (1990). Two additional foraging terms used here are "hitching" and "side-to-side hitching." As used in this paper, "hitching" is a slight modification of the term as used by Whitney and Pacheco (1994) and is defined as movement in which both feet are moved sideways either simultaneously or in rapid succession, such that the axis of the body is held at an obvious angle (if not perpendicular) to the substrate (stem, vine, branch, etc.) and progression is made by a series of short advances. "Side-to-side" indicates hitching progression in which the orientation of the body relative to the substrate changes from one motion to the next, such that the bird leads first with one side, then with the other. We have also included observations made by Stotz 13–16 Oct. 1987 and Feb.–March 1992 on the distribution, abundance, and habitat of Rio Branco Antbirds near Boa Vista.

We recorded songs using Sony TCM-5000 recorders and Sennheiser MKH-70 and ME-80 microphones. All recordings by Zimmer have been or will be archived at the Library of Natural Sounds, Cornell Univ., Ithaca, New York. We made sonagrams on a Macintosh Centris 650 computer using Canary version 1.1 (Bioacoustics Research Program, Cornell Laboratory of Ornithology, Ithaca, New York), Canvas version 3.0.6 graphics software (Deneba Software, Miami, Florida), and a LaserWriter Pro 630 printer. We examined specimens of all species in the *nigricans* group, as well as *C. cinerascens*, at the Field Museum of Natural History (FMNH) and at the Los Angeles County Museum of Natural History (LACM). Neither instituition has female specimens of *C. ferdinandi* or *C. melanaria*.

RESULTS

Cercomacra carbonaria is limited to the middle sections of the Rio Branco and its tributaries, in Roraima, extreme northern Brazil, and ad-

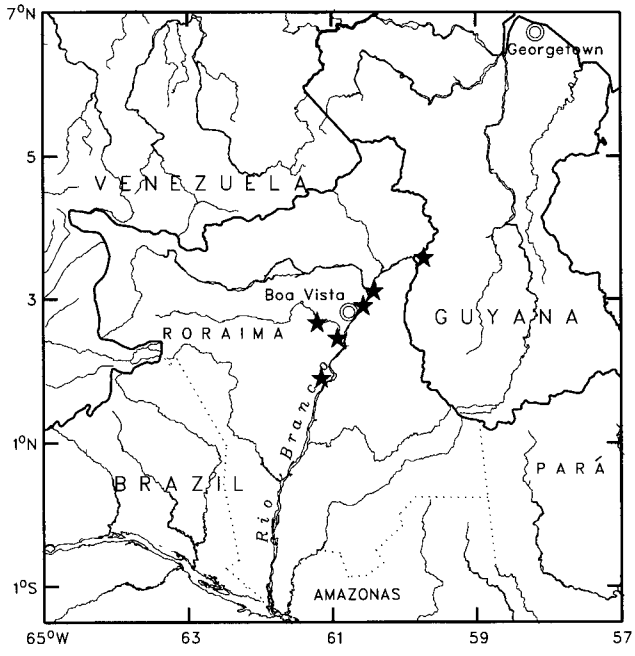


FIG 1. Distribution of Rio Branco Antbird (*Cercomacra carbonaria*): black stars indicate sites where specimens have been collected (all localities from Collar et al. 1992), or where the presence of Rio Branco Antbird has been documented by tape recordings (Guyana records from D. Finch recordings, LNS). The black star located immediately north of Boa Vista coincides with the sites at which the authors studied *C. carbonaria*.

jacent Guyana. It ranges from Caracarai in the south (Fitzpatrick and Willard 1990) north along the Rio Branco and Rio Tacutu to the Ireng River (Rupuruni District), Guyana, less than 2 km from its confluence with the Tacutu (D. Finch, pers. commun.). It has also been found on the Rio Mucajaí, a tributary of the Branco (Collar et al. 1992). In October 1987, Stotz found *C. carbonaria* at five sites near Boa Vista—the east bank of the Rio Tacutu ca 2 km above its mouth, the east bank of the Rio Branco 15 km northeast of Boa Vista, the west bank of the Rio Branco 10 km northeast of Boa Vista, Ilha Boa Água (on the Rio Branco north of Boa Vista); and on Ilha São José on the Rio Branco ca 10 km north of Boa Vista (Collar et al. 1992). Stotz also visited the type locality, Fortaleza de São Joaquim (28 km above Boa Vista), but found the habitat greatly altered and saw no signs of *C. carbonaria*. At least 18 birds were seen or heard during the 1987 survey, and the species appeared to be fairly common. In February and March 1992, Stotz found at least five

males along about 3 km of thickets lining a dry braid of the Rio Branco at Fazenda Santa Cecilia (directly across the river from Boa Vista).

In November 1994, Zimmer and Whittaker found *C. carbonaria* north of Boa Vista, where its distribution was patchy, on the sides of the river, with only four scattered pairs on either bank of the Rio Branco (west bank opposite the north end of Ilha São José, west bank ca 300 m south of Ilha São José, east bank ca 1 and 2 km south of Ilha São José). North of Boa Vista the Rio Branco is lined by a narrow band of gallery forest mostly less than 150 m wide. Beyond the immediate vicinity of the river, the predominant vegetation is savanna dotted with patches of low-canopied savanna woodlands on white sand soils and extensive stands of buriti palms (*Mauritia flexuosa*) in the lower-lying areas.

Pairs of antbirds along the banks of the river inhabited dense thickets at the edge of the gallery forest, within 100 m of the river. Systematic tape playback (every 50–100 m) along 300–500 m of suitable habitat at many points along both banks of the river did not elicit a response. Antbirds were either vocalizing spontaneously or were strongly responsive to tape playback, namely an immediate vocal response and approach. When no further playback was forthcoming, many birds continued to sing for several minutes. At no time did these extended song periods produce a vocal response from other birds. Similarly, we surveyed ca 2 km of tall-canopy (20–30 m) várzea forest along the Parana do Sulhão (a small tributary of the Rio Branco a few kms north of Boa Vista) by boat, presenting tape playback at 100-m intervals, with no response. We also surveyed an extensive stand of savanna woodland (canopy height of 20+ m) on the right bank of the Rio Branco separated from the strip of gallery forest by ca 500 m of open savanna. No *C. carbonaria* were found there, nor at the edge of tall forest a few hundred meters from the left bank opposite Boa Vista. In 1987, Stotz found *C. carbonaria* away from islands only in dense thickets along the river edge. They did not occur in other forested or semi-forested habitats. Similarly, birds were found only in thickets along a seasonally dry braid of the Rio Branco during an intensive two-week survey of the Fazenda Santa Cecilia.

We found the Rio Branco Antbird to be common on Ilha São José, in a variety of habitats. In November 1994, individuals on the west side of the island were in dense second-growth (mostly in overgrown manioc plantations with widely scattered 20–30 m trees) similar to habitat favored by *C. nigrescens* south of the Amazon (pers. obs.). *Cercomacra carbonaria* seemed to be evenly distributed within this habitat, and at one point we located three calling pairs within 150 m of one another. On the east side of the island we located five pairs along ca 500–550 m of forest edge, with two more pairs heard calling distantly inside the forest. The

interior island forest was densely wooded, with a canopy of 20–30 m, and was bordered (at the southeast end of the island) by a uniform, ca 30 m wide band of a single species of tree (with leaf characteristics similar in appearance to *Inga* spp.) ca 8 m in height, with occasional overtopping *Cecropia* or other large trees. Although antbirds were seen foraging in this outer band of trees, and readily entered it in response to tape playback, they were spent most of their time in the floristically more diverse interior forest. The edge vegetation was used more in the first hour of the morning, when the birds were also most vocal.

Diameter of antbird territories, measured by walking along the sandbars bordering the forest edge and conducting playback trials, appeared to be no more than 100–150 m. We saw few interactions between males of adjacent pairs at territorial boundaries. None of these appeared to be particularly aggressive or sustained. Two males approached to within 1 m of one another, uttering staccato "kud-up" notes and subdued whiny sounds (see *Vocalizations*) while erecting their hindcrown feathers and exposing the normally hidden, white margins of the lesser coverts and the white interscapular feathers. This encounter did not result in any chase behavior, nor in a true song bout, and only one of the two males subsequently sang (and then only sporadically). Other interactions involved mutual approach to within 5–8 m, with one bird typically singing and the other remaining quiet and somewhat passive. The passive bird in such interactions frequently picked at bare branches seemingly devoid of prey, as if displacing aggression. Females responded to tape playback by vocalizing, but were generally more reluctant to approach than males. On one occasion we observed two pairs interacting at a territorial boundary. The two males approached to within 6 m of one another, and the respective females remained several meters farther back in the thickets. One male sang several songs, which elicited an excited duet from the other pair of birds. This was followed by closer mutual approach on the part of the males and some subdued aggression calls before both pairs retreated.

Apparent low density of Rio Branco Antbirds in seemingly suitable "mainland" habitats north of Boa Vista is puzzling, given the abundance of the species on Ilha São José. The discrepancy is particularly intriguing since antbirds on Ilha São José appear to be habitat generalists, occupying a variety of wooded and thicket habitats in high densities. Because our visit came well into the dry season, it is possible that failure to find *Cercomacra* reflected seasonal lack of territorial response rather than true scarcity. Few species were particularly vocal during our November visit, and several expected riverine species seemed to be curiously absent (=non-vocal). For most passerines, tape playbacks are most useful in eliciting a response early in the breeding season (pers. obs.). A drop-off

in song intensity between October and November could also account for the apparent higher densities of *Cercomacra* found by Stotz in 1987.

The distance between the known northern and southern range limits of *Cercomacra carbonaria* is about 210 km. Less than 20 km of the lower Rio Mucujaí has appropriate habitat (Stotz, pers. obs.). No Rio Branco Antbirds have been found along other main tributaries (such as the Rio Uracoeira) in the region (Stotz, pers. obs.). A maximum of 460 linear km of river edge, therefore, might be occupied by *Cercomacra carbonaria.* Suitable habitat within this belt is confined to within 0.5 km on either side of the river. Including the few (<10) river islands with significant vegetation between Boa Vista and the Rio Tacutu, this would give a total area potentially occupied by *Cercomacra carbonaria* as perhaps 250 km^2, or less. If densities of Rio Branco Antbirds on the mainland are estimated at one pair per 250 m of river edge (almost certainly greatly overestimated), and densities on the river islands are extrapolated from our estimates of territory size on Ilha São Jose, we would arrive at a maximum mainland population of 3700 birds, with perhaps another 500–1000 on river islands. These estimates are crude by any measure, but they do emphasize the tiny range and global population of *Cercomacra carbonaria,* as well as the linear nature of its habitat.

Molt and morphology.—In November 1994, several males were actively molting rectrices. A female collected by Stotz in October 1987 had small gonads and was in heavy molt (body, wings, and tail). This is consistent with singing patterns, and further suggests that the dry season is the non-breeding season for *Cercomacra carbonaria.* Soft-parts colors for both sexes were as follows: bill black; legs and feet gray; iris medium-brown.

Foraging behavior and sociality.—Rio Branco Antbirds were particularly difficult to follow, in part due to their secretive nature, and in part due to the nearly impenetrable nature of their preferred habitats. Both males and females flicked their wings frequently while foraging, and wagged their tails up and down in a shallow (ca 20°) arc, above and below the plane of the body. They generally traced a zigzag route through the foliage, progressing with several consecutive hops in a given direction before changing course. Hops carried the birds anywhere from 5 cm to 1 m at a time, and were separated by pauses of 0.5–2.0 seconds to peer about. Birds usually assumed a posture in which the body was held between horizontal and 45°. One male foraged from 1–7 m above the ground, but spent perhaps 75% of its time between 3.5 and 7 m above ground. It hitched rapidly along bare slender limbs without hitching from side-to-side. It picked three times at thin woody vines without visible success, and was seen to glean an unidentified arthropod from the underside of an overhanging green leaf by

stretching and reaching upward with a quick stab. Another male was seen to cling with its feet and reach downward to glean an unidentified medium-sized arthropod from the top surface of a green leaf 1 m above the ground in a shrubby forest border. This same male fluttered down suddenly from 2 m above ground to 1 m above ground to chase a flushed katydid. A pair of antbirds foraging within 5–7 m of one another gleaned a few small, unidentified arthropods from green leaves in the crowns of forest-edge trees ca 5–10 m above the ground.

Rio Branco Antbirds foraged individually or in pairs that remained in frequent vocal contact with one another. We did not find them associating with mixed-species flocks. Common insectivorous species found near *Cercomacra carbonaria* at all localities included *Picumnus spilogaster*, *Xiphorhynchus picus*, *Furnarius leucopus*, *Sakesphorus canadensis*, *Inezia subflava*, *Myiopagis gaimardii*, *Todirostrum maculatum*, *Thryothorus leucotis*, *Polioptila plumbea*, *Cyclarhis gujanensis*, and *Hylophilus pectoralis*.

Vocalizations.—We tape-recorded several different vocalizations from *C. carbonaria*. The primary, or territorial, song appeared to be a two-noted "hitch-COCK" repeated 4–10 times (most commonly 4–7 times) at the rate of about two couplets per second (Fig. 2A). This song was observed to be given only by males. When responding to tape playback, males increased the pace and sometimes lengthened the series of couplets, but otherwise sang identical songs.

Pairs engaged in duets (Fig. 2B) when responding to playback and when re-establishing contact during foraging. Such duets typically began with male two-noted songs, into which the female interjected (at any point in the male song) a loud, sharp "ECK" note. Typically, the female only "interrupted" 1–2 male song-couplets before the male switched from the two-note song to a single loud "OCK". Both birds then proceeded to deliver an antiphonal series of "ECK" (female) and "OCK" (male) notes in a rapid (3–4 combined notes per second) barking cadence that lasted 3–5 seconds. Thus, the introductory note of the female is not synchronized with the male, but it does lead to a synchronized duet. A peculiar feature of this duet is that the male always seemed to deliver the final note, often after a longer than average between-note interval.

In the few territorial interactions witnessed between two males, and in the single interaction witnessed between two pairs, birds of both sexes delivered a staccato "kud-up" or "kud-dudup" (Fig. 2C), often interspersed with single "kup" notes. Birds of both sexes also gave these aggression calls when they approached us closely following playback. A second contact call given both in territorial interactions as well as between mates when re-establishing contact following a separation, was a soft,

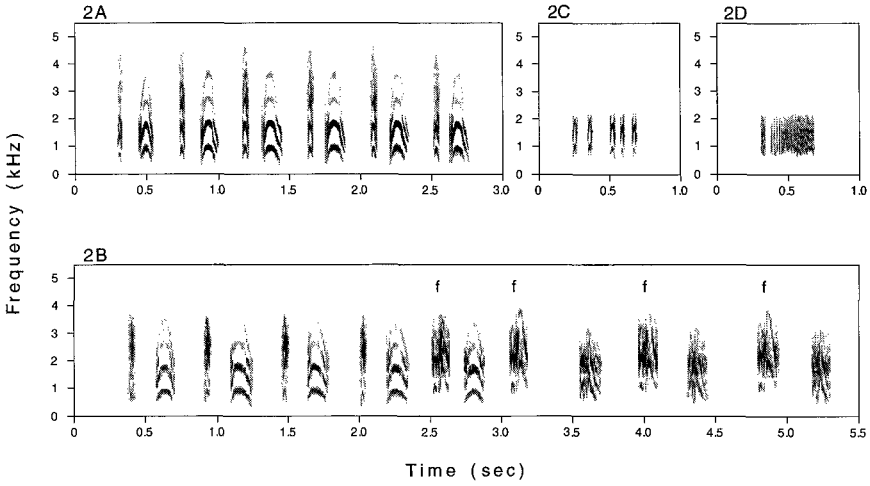


FIG. 2. Sonagrams of vocalizations of Rio Branco Antbirds, *Cercomacra carbonaria*: (A) male songs ("hitch-COCK'), (B) male song interrupted by single "ECK" notes of female and leading into male-female duet ("ECK-OCK"), (C) "kud-dup" and "kud-dudup" aggression calls of male (similar calls are also given by females), (D) "squeaking branch" contact call (this example delivered by a male, but similar calls are given by both sexes). All vocalizations recorded along the Rio Branco north of Boa Vista, Roraima, Brazil. All recordings by K. J. Zimmer.

whiny call that sounded like the subdued squeaking of a tree branch in the wind (Fig. 2D).

DISCUSSION

The two analyses of species relationships among the *C. nigricans* group (Fitzpatrick and Willard 1990, Silva 1992) have emphasized plumage pattern and color (especially females), and vocalizations. Fitzpatrick and Willard (1990) hypothesized that *C. manu* and *C. melanaria* were sister species, "possibly close enough to be recognized as a superspecies," based on extremely similar female plumages and narrower white tips to the rectrices in both sexes compared with other members of the *C. nigricans* group. They further considered *ferdinandi*, *nigricans*, and *carbonaria* to be each other's closest relatives based on streaked throats in females, a character they called "unusual (presumably derived) among female antbirds." Silva (1992), in his cladistic analysis of the *nigricans* group, also used the narrow white tips to the rectrices to join *manu* and *melanaria*, distinguishing this condition from the broad white tail tips that characterize the other members of the *nigricans* group, as well as *cinerascens*. However, he treated the character of streaked throats in females differently

TABLE 1
LENGTH (MM) OF WHITE TIPS OF RECTRICES FOR VARIOUS TAXA IN THE *CERCOMACRA NIGRICANS* GROUP

Taxon	Mean	(SD; N)
C. cinerascens cinerascens	3.9	(1.04; 6)
C. cinerascens sclateri	7.7	(0.91; 6)
C. cinerascens immaculata	3.0	(0.73; 10)
C. melanaria	2.8	(1.31; 3)
C. manu	4.7	(1.30; 9)
C. carbonaria	7.2	(0.76; 5)
C. nigricans	7.8	(1.16; 12)

from Fitzpatrick and Willard. Silva considered *carbonaria* to have an unstreaked throat, and *manu* and *melanaria* to have "slightly marked" throats in contrast to the "well marked" throats of *ferdinandi* and *nigricans*.

Based on our examination of specimens at FMNH and LACM, we believe that Silva's analyses of both the white tail tips and the underpart pattern (including throat streaking) of females need modification. Although Silva (1992) treated *C. cinerascens* as having broad white tips to the rectrices, the width of the white tips in *C. cinerascens* shows substantial geographic variation (Table 1). The subspecies *sclateri* has white tips fully as wide as *C. carbonaria*, a species treated by Silva as having broad tips, but *C. c. immaculata* and nominate *cinerascens* have white tips that are narrower than in *C. manu*, one of his species with narrow white tail tips. As a result of this variation within a species, it seems inappropriate to use the width of the white tail tips as a character in a phylogenetic analysis within this group of *Cercomacra*.

Similarly, although Silva treated *cinerascens* as lacking throat streaks in contrast to the "slightly marked" throats of *manu* and *melanaria*, we find that the pattern of *cinerascens* is quite similar to that of *manu*. Four female specimens of *manu* have medium-gray underparts with the rachis of some feathers of the throat and upper breast white, forming a subtle, narrow streaking. In *cinerascens*, females (15 specimens) typically show a pale rachis, contrasting with darker barbs, on feathers of the throat and upper breast, but because the pale rachis is buff and the remainder of the feather is ochraceous, the contrast appears less strong than in *C. manu*, even though the pattern is the same in the two species. Silva's treatment of *carbonaria* females as having unstreaked throats appears questionable as well. The female of that species has much whiter underparts than any other *Cercomacra*, and these underparts are variably streaked, spotted,

and blotched with black, gray, and buff. The throat of one FMNH female specimen is largely whitish, marked irregularly with black and gray, and three others (LACM) have white throats moderately to heavily streaked with black and gray. Feathers on the upper breast closely resemble the white streaked feathers of females of *C. nigricans* with broad white centers edged with dark gray or black. This agrees with our field observations, none of which indicate that female *carbonaria* have anything other than streaked throats. Because of this, we propose that females of *C. carbonaria* are best treated as showing the streaked pattern of *nigricans* and *ferdinandi*, as was done by Fitzpatrick and Willard (1990).

In addition, interpretation of relationships within the *Cercomacra nigricans* group have been hampered by lack of recorded, comprehensive vocal repertoires for each species (Fitzpatrick and Willard 1990, Silva 1992). None of these workers had access to tape recordings of *C. carbonaria*, and only Silva (of the three) had field experience with the bird. Furthermore, in 1990 there were almost no known recordings of *C. ferdinandi* available for study, and the voices of the just-described *C. manu* and the range-restricted *C. melanaria* were only marginally better represented in sound collections.

Both Fitzpatrick and Willard (1990) and Silva (1992) identified the characteristic two-syllable element in the primary song as a phylogenetically informative character. It unites the *nigricans* group in Fitzpatrick and Willard (1990), and Silva (1992) used it as a character to identify the clade including the *nigricans* group and *cinerascens*. Fitzpatrick and Willard (1990), in their analysis, reported a "staccato whinny" vocalization for *C. manu*, and noted that "only *manu*, *melanaria*, and *ferdinandi* are known to have the staccato whinny in their repertoire." Based on these statements, Silva (1992) used the presence or absence of the "staccato whinny" as a character in constructing his cladograms for the *C. nigricans* group. He scored the character as being absent in *C. carbonaria* (based on his own field experience) and present in *manu*, *melanaria*, and *ferdinandi* (based apparently on the statements of Fitzpatrick and Willard). The resulting cladogram was discordant with the hypotheses of Fitpatrick and Willard with respect to the phylogenetic position of *C. ferdinandi*, which Silva (1992) considered as the sister species of the *manu-melanaria* clade.

While acknowledging that verbal transcriptions of bird vocalizations often lose something in the translation from one observer to the next, we remain unclear as to which of *C. manu*'s many vocalizations is the "staccato whinny." The vocalization that sounds closest to Fitzpatrick and Willard's (1990) description (Fig. 3A) does appear to have analogous elements in the repertoires of *C. melanaria* (Fig. 3B) and *C. ferdinandi*

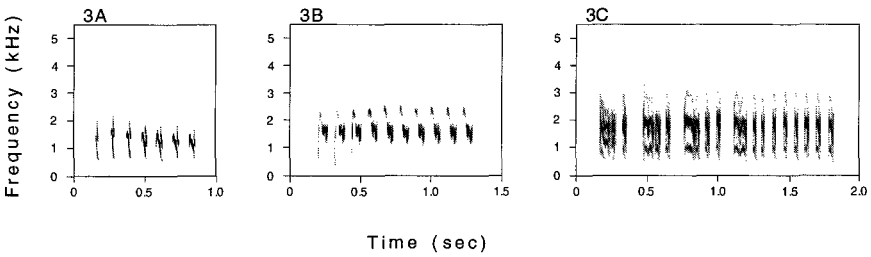
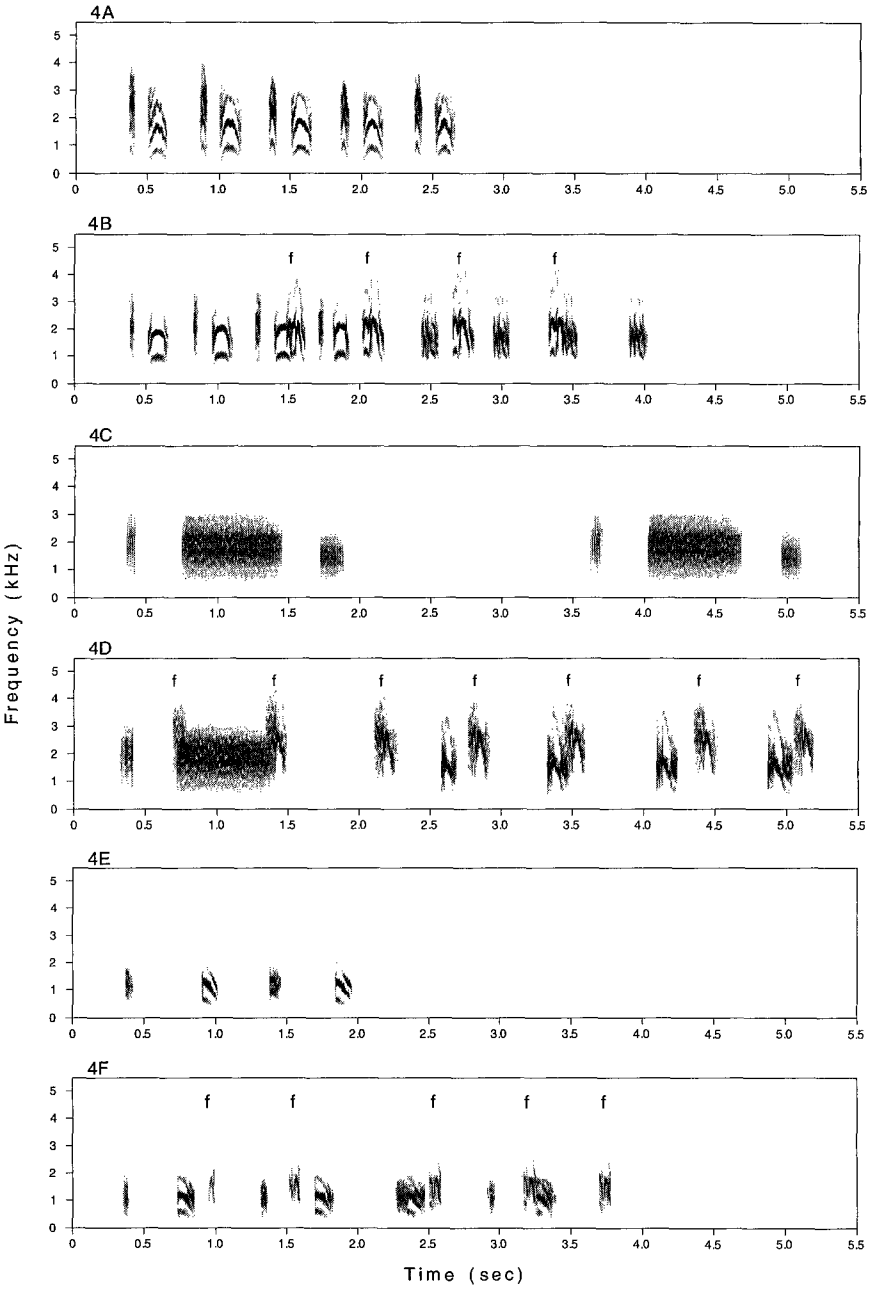


FIG. 3. Sonagrams of "staccato whinny" vocalizations of *Cercomacra* antbirds: (A) "whinny" of Manu Antbird (*C. manu*) from Madre de Dios, Peru (K. J. Zimmer recording), (B) "whinny" of Mato Grosso Antbird (*C. melanaria*) from Mato Grosso, Brazil (R. Behrstock recording), and (C) song with "whinny" element of Bananal Antbird (*C. ferdinandi*) from Goias, Brazil (P. Donahue recording).

(Fig. 3C). However, the "whinny" elements of each of the three species appear only tenuously related. The "whinny" of *manu* is a frequently heard vocalization (but given at irregular intervals) that may be repeated several times in succession, independent of other vocalizations (Zimmer, pers. obs.). It is often given by foraging birds visually separated from their mates and is more commonly heard in mid-day or afternoon (Zimmer, pers. obs.). The "whinny" element of *ferdinandi* does not appear to stand alone as a distinct vocalization, but rather, is joined to the end of the two-note element to produce a more complex primary song (Isler and Whitney 1996, Fig. 3C). We do not know the context of the "whinny" vocalization in *melanaria*. In our collective field experience with *melanaria*, we have not noted any similar vocalization, and we could only locate a single archived recording of this call (Fig. 3B). Whatever the function, the "whinny" does not seem to be a commonly used part of the vocal repertoire of *C. melanaria*. Our work with *C. carbonaria* certainly supports Silva's (1992) contention that no such vocalization is included in the vocal repertoire of that species; however, it could be present but rarely used (as in *C. melanaria*). We would argue that too much weight has been given to the presence or absence of the "staccato whinny," given that the vocalization seems to differ widely in both function and frequency of use between taxa.

At the same time, some vocal similarities between *C. carbonaria* and other species in the group have been overlooked. The primary, "hitch-COCK" song and the male-female duets of *C. carbonaria* sound closest to recordings of the analagous vocalizations of *C. nigricans* (Fig. 4A, 4B), observations that fit well with the hypotheses of both Silva (1992) and Fitzpatrick and Willard (1990). However, there are also some vocal similarities between *C. carbonaria* and *C. melanaria* that could suggest


4A
4B
4C
4D
4E
4F
f
Frequency (kHz)
Time (sec)

a closer relationship between those taxa than previously suggested. The primary song of male *C. melanaria* is a three-note "rek-RURRRR-rock," with the middle note much longer than the other two (Fig. 4C). Females sing a nearly identical song that differs slightly in pitch. Although these songs are quite different from the primary song given by males of *C. carbonaria*, qualitative similarities in tone and note shape are evident between the middle note of the *melanaria* song and the "squeaking branch" calls (Fig. 2D) given by both sexes of *carbonaria*. More striking are the similarities in the duets of the two species. Duets of *C. melanaria* typically begin with one or more male songs, after which the female begins interjecting a loud, sharp "ECK" note (Fig. 4D) similar to that of female *carbonaria*. This "ECK" note may be inserted anywhere in the middle of the male's song or immediately after the third note of the song. As in *C. carbonaria*, a few notes by the female *C. melanaria* typically results in the male switching from its song to a single loud "OWP," which is less squeaky and slightly lower-pitched than the female's "ECK" (Fig. 4D). Both birds then proceed to deliver an antiphonal duet of alternated "ECK" and "OWP" notes at the rate of about 3–4 combined notes per second for 4–8 seconds. Occasionally the roles will be reversed, with females singing the primary song and the male initiating the duet of single notes. As can be seen from comparing sonagrams in Figures 2 and 4, the duets of *C. carbonaria*, *C. nigricans*, and *C. melanaria* are similar in overall pattern and cadence, and in the shape and pitch of the individual notes of both the males and the females. As is the case with *C. carbonaria*, duets of *C. melanaria* usually end with the male delivering the terminal note.

In our experience, *Cercomacra manu* has the most extensive vocal repertoire of any species in the *nigricans* group. We have recorded several vocalizations of *C. manu* for which there seems to be no analogs in the repertoires of the other species. The primary song given by males is a two-noted "uck OCK," with the individual notes spaced about 0.5 sec apart (Fig. 4E). These notes may be repeated monotonously, or the ca-

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FIG. 4. Sonagrams of vocalizations of *Cercomacra* antbirds: (A) songs of male Jet Antbird (*C. nigricans*) from Darién, Panama (T. A. Parker recording, LNS #25923), (B) Jet Antbird: male songs leading into male–female duets, from Miranda, Venezuela (P. Schwartz recording), (C) songs of male Mato Grosso Antbird (*C. melanaria*) from Mato Grosso, Brazil, (D) Mato Grosso Antbird: male song leading into male-female duet, from Mato Grosso, Brazil, (E) songs of male Manu Antbird (*C. manu*) from Mato Grosso, Brazil, and (F) Manu Antbird: male song leading into male-female duet, from Mato Grosso, Brazil. Unless otherwise noted, sonagrams are from recordings by K. J. Zimmer.

dence may be varied, as in "uck OCK OCK, uck OCK." Males also routinely sing a faster series of 3-6 "uh-oh" couplets, at a lower pitch. Although these songs are recognizably similar to those of other species in the *nigricans* group, they also differ markedly in frequency and pace (Fig. 4E). Duets often consist of females inserting loud, single "OUK" or "CLOCK" notes into typical male songs, the notes being placed either immediately after the second male note, in between the notes, or superimposed over one of the male notes (Fig. 4F). This usually stimulates the male to switch from the two-note song to a cadenced series of single notes, as is the norm for other species in the *nigricans* group. At this point however, females often switch from single notes to a series of 2–5 "uh-ouk" couplets, the notes of which are more nasal in quality and much more closely spaced than the two-noted songs of males (Fig. 4F). Contrary to the pattern seen in duets of *C. carbonaria*, *C. nigricans*, and *C. melanaria*, duets of *C. manu* routinely end with the female delivering the terminal note or notes.

In overall duet pattern, frequency band of individual notes, and stereotyped behavior of males in delivering terminal notes, the duets of *carbonaria*, *nigricans*, and *melanaria* are all more similar to one another than any of them is to *manu*. Unfortunately, the scarcity of tape recordings of *C. ferdinandi* precludes any assessment of duets or vocal repertoires of that species, making hypothesized relationships tenuous.

A cladistic analysis of relationships within the *C. cinersascens* complex may be premature, even with the addition of the vocal characters discussed above. However, we will discuss some preliminary thoughts on relationships within the group. The complex can be recognized as a clade within *Cercomacra* as described by Silva (1992). Two characters, white tail-tips, and a distinctive form of the primary vocalization, support this clade. Furthermore, Silva's placement of *cinerascens* as a sister species to the remainder of the group appears sound. The other species can be joined as a clade based on females with grayish, rather than brownish underparts, and with male plumage largely blackish. Beyond this, the only informative character that has been detected in the plumage analysis thus far is the heavy streaking on the throats of females of *nigricans*, *carbonaria*, and *ferdinandi*. This unites these species in a group that cannot be further resolved at present. This clade, *manu*, and *melanaria* form a trichotomy that cannot be resolved with plumage characters. The close similarity between *manu* and *melanaria* in female plumages is due to sharing primitive features within the group, rather than evidence of a sister relationship as hypothesized by Fitzpatrick and Willard (1990). The vocal characters discussed above, especially similarities between *melanaria* and *carbonaria*, and in the duet pattern of those species and *nigricans*, suggest

that *melanaria* is more closely related to the *nigricans*, *carbonaria*, *ferdinandi* group than to *manu*. The lack of information for *ferdinandi* as well as limited material for some other members of the genus (especially of duets) makes this a tentative suggestion. Biochemical data and further analysis of vocal data will be necessary to completely understand relationships within the *Cercomacra nigricans* group. Particular attention should be paid to male-female antiphonal duets, which are a conspicuous feature of the genus *Cercomacra*, and which may prove important indicators of relationship.

The gallery forests which *Cercomacra carbonaria* inhabits are part of a complex of open habitats, locally called "lavrado", dominated by dry grasslands in northeastern Roraima (Vanzolini and Carvalho 1991). Besides *C. carbonaria*, the region holds another endemic bird, Hoary-throated Spinetail (*Poecilurus kollari*), and the only Brazilian populations of several other species of birds. Other groups of organisms also have endemic taxa restricted to this region (Vanzolini and Carvalho 1991). These open habitats are almost completely unprotected, the exception being small patches of grassland totaling less that 1000 ha at the Maracá Ecological Station. Neither endemic bird occurs at Maracá.

Cercomacra carbonaria is treated by Collar et al. (1992) as "vulnerable", indicating "taxa believed likely to move into the Endangered category in the near future if the causal factors continue operating." The small range of *Cercomacra carbonaria* contributes to its vulnerable status, as does the complete absence of habitat protection. The most critical problem facing this species is the restricted area of gallery forest in the region and the potential threats to that habitat. Although there do not appear to be serious immediate threats to the gallery forests, they appear to be most at risk among the habitats within the lavrado of Roraima. There has been some conversion to agriculture, especially rice cultivation, and some trees in the gallery forest are used for their wood. In addition, however, our studies suggest that attention should focus on river islands with extensive gallery forest, where *Cercomacra carbonaria* is much more common than in mainland gallery forest sites, as described above. We urge protection for at least Ilha Boa Agua and Ilha São Jose, where *Cercomacra carbonaria* is most abundant, together with areas of gallery forest on the adjacent mainland. This would protect a major population of *C. carbonaria*, as well as other species restricted to the gallery forest of this region.

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