

THE RUFOUS CACHOLOTE (FURNARIIDAE: *PSEUDOSEISURA*) IS TWO SPECIES¹

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Abstract. New information on the vocalizations and behavior of populations of the Rufous Cacholote (*Pseudoseisura cristata*), combined with a morphometric analysis of museum specimens, reveal that it actually consists of two biological species: a form that is restricted to the arid *caatinga* region of northeastern Brazil (*P. cristata*), and a wider-ranging form (*P. unirufa*) that occupies seasonally flooded savannas and deciduous woodlands in northern and eastern Bolivia, northern Paraguay, and southwestern Brazil. Long considered a subspecies of *P. cristata*, *P. unirufa* is shown to be morphologically, vocally, and ecologically distinct from allopatrically distributed populations of *P. cristata*. Reciprocal playback experiments of tape-recorded vocalizations indicate that neither form responds to the other's vocalizations. The two species may also differ in their breeding systems and social structures. *P. cristata* is shown to be a cooperative breeder, with nonbreeding helpers assisting in territorial defense, nest-building, and care of nestlings. No evidence of cooperative breeding was found in *P. unirufa*.

Key words: cooperative breeder, duets, Furnariidae, *Pseudoseisura cristata*, *Pseudoseisura unirufa*, species limits, vocalizations.

INTRODUCTION

The genus *Pseudoseisura* as currently treated is comprised of three species of large, rather aberrant furnariids (the cacholotes) whose affinities outside of the genus are uncertain (Vaurie 1980). The three species of cacholotes are more or less allopatrically distributed through eastern and southern South America (Peters 1951, Vaurie 1980, Ridgely and Tudor 1994). Two of the species (*P. lophotes* and *P. gutturalis*) are considered monotypic. The third, *P. cristata* (the Rufous Cacholote), is currently treated as a polytypic species consisting of two disjunctly distributed subspecies: nominate *P. c. cristata* (hereafter *cristata*) of northeastern Brazil, and *P. c. unirufa* (hereafter *unirufa*) of northern and eastern Bolivia, northern Paraguay, and southwestern Brazil (Hellmayr 1925, Peters 1951, Ridgely and Tudor 1994). Although the Rufous Cacholote is a large, noisy, and generally conspicuous bird of open habitats, it has received slight attention from ornithologists, and little has been published of its basic biology (Vaurie 1980).

In this paper we present evidence that the subspecies of Rufous Cacholote are distinct biological species, which, although similar in general appearance, are morphologically, vocally, and ecologically differentiated and which appear to differ in their social structure.

METHODS

We made observations of "Rufous" Cacholotes at various sites in Mato Grosso, Brazil (August and October 1991, each September from 1993–1998), Pernambuco, Brazil (January 1996–1999 and February 1996), and Bahia, Brazil (January 1996–1999 and February 1996). All measurements used in behavioral data (distances, heights, etc.) are estimates. Mapped distributions (as they appear in this paper) are based entirely on label data from specimens that the senior author examined and by more recent records documented by tape recordings. These localities were entered into a Geographic Information System (Isler 1997) and mapped by Morton Isler (Division of Birds, National Museum of Natural History, Washington, D.C.).

We assume that vocalizations of cacholotes, like those of other suboscines, are mostly or entirely inherited (Kroodsma 1984, 1989, Kroodsma and Konishi 1991), and as such, provide po-

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tentially important characters for systematic study as in other suboscines (Bierregaard et al. 1997, Isler et al. 1997, Krabbe and Schulenberg 1997). To analyze vocalizations, we assembled recordings of *crystata* ($n = 41$ cuts involving 30 individuals, pairs, groups) and *unirufa* ($n = 23$ cuts involving 17 individuals or pairs). A "cut" contains one or more consecutive vocalizations from a given individual, pair, or group of cacholotes. Locations and recordists for all recordings examined are listed in Appendix 1. For comparison, vocalizations were categorized as loudsongs, duets, chatter, or calls. "Loudsongs" were consistently patterned multi-note vocalizations (Isler et al. 1997) given by an individual bird, seemingly in the context of territorial advertisement. These were given individually by both sexes (most commonly when individuals were separated by considerable distances), but were also incorporated into duets. "Duets" involved simultaneous singing by a pair or family group of cacholotes. Duets consisted of typical loudsongs of both sexes, combined with a "chatter" that was not given outside of a duet context. Vocalizations categorized as calls were of low amplitude and structurally simple (usually involving single notes) and were seemingly given in the context of contact vocalizations between mates or family members. Our tape recordings were made with Sony TCM-5000 recorders, and Sennheiser MKH-70, ME-66, and ME-80 microphones. All recordings have been or will be archived at the Library of Natural Sounds, Cornell University, Ithaca, New York. Spectrograms were made by Phyllis Isler (Division of Birds, National Museum of Natural History, Washington, D.C.) on a Power Macintosh 7500 computer using Canary version 1.2.1 (Bioacoustics Research Program, Cornell Laboratory of Ornithology, Ithaca, New York).

Playback experiments were conducted to determine the reactions of cacholotes of each subspecies to vocalizations of the other. In each case, an individual, pair, or group of cacholotes was first presented with 5–10 tape recordings of the other taxon, given at typical intervals of about 15 sec. After a "buffer" period of about 2 min, the cacholotes were then presented with 5–10 tape recordings of their own vocal type. This was done to account for potential seasonal influences by resolving the question of whether birds that were unresponsive in the first trials were discriminating between the different vo-

calizations, or were generally nonterritorial during the trial period and therefore unresponsive to playback of any kind. Failure to account for seasonal differences in responsiveness has been cited as a potential design weakness in other playback experiments (Kroodsmas 1986). Responses to playback were characterized as strong, moderate, weak, or none. A "strong" response involved immediate and repeated vocalizations (from previously nonvocalizing birds) as well as approach toward the sound source. A "moderate" response involved either a cautious approach without vocalizing, or sustained vocalizing without approach. A "weak" response involved single or unsustained vocalizations (from previously nonvocalizing birds) without approach. The "none" category includes instances in which birds remained silent (in the case of previously nonvocalizing birds) and did not approach the sound source, as well as instances in which already vocalizing birds neither changed the delivery or rate of their vocalizations, nor approached the sound source.

The senior author examined representative specimens of *crystata* (17) and *unirufa* (11). These specimens are housed at the Academy of Natural Sciences of Philadelphia, Philadelphia (ANSP), Carnegie Museum, Pittsburgh (CM), Field Museum of Natural History, Chicago (FMNH), Los Angeles County Museum of Natural History, Los Angeles (LACM), the Louisiana State University Museum of Natural Science, Baton Rouge (LSUMZ), and the National Museum of Natural History, Washington, D.C. (USNM). A list of specimens examined is provided in Appendix 2. A wing rule with a perpendicular stop at zero was used to measure flattened wing chord (wing), tail length (tail), and hind toe length without the claw (hind toe), and dial calipers were used to measure tarsus length (tarsus), culmen length from the anterior end of the nares to the tip (culmen), bill depth at the anterior end of the nares (bill depth), bill width at the anterior end of the nares (bill width), and hind claw length (hind claw). All measurements made with calipers were made to the nearest 0.01 mm, those taken with the wing rule were made to the nearest 0.5 mm. Measurement terminology conforms with that used by Pyle et al. (1987). General linear models were used to investigate age- and gender-corrected differences between the two subspecies for each of the eight characters measured. Residual diagnostics indi-

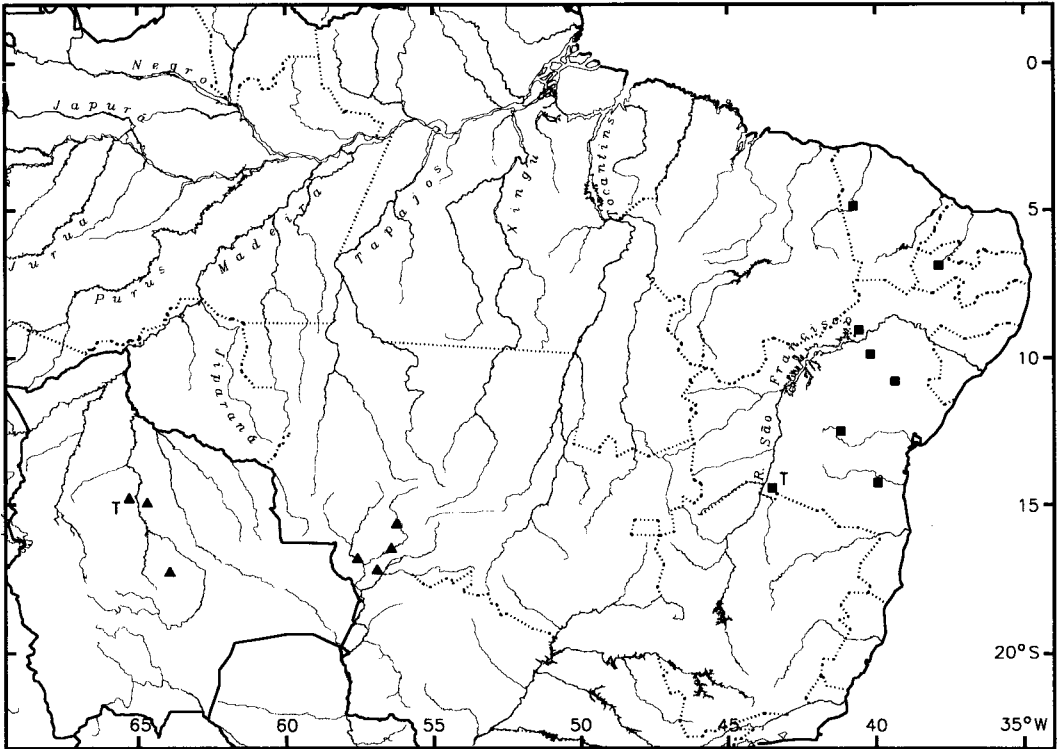


FIGURE 1. Distribution of Rufous Cacholote (*Pseudoseisura cristata*) as confirmed by examination of specimens or tape recordings: black squares = *P. c. cristata*; black triangles = *P. c. unirufa*. "T" next to a symbol indicates the type locality for that taxon. The Moxos, Bolivia type locality for *P. c. unirufa* pertains to a region, not a locality. Because this region was historically centered in the Trinidad area, Departamento Beni, the "T" is placed there.

cated no violations of the general linear model assumptions of error normality and constant variance. Plumage was described from museum specimens and compared to a standard color reference (Smithe 1975).

RESULTS

DISTRIBUTION

The two forms of "Rufous" Cacholote are allopatrically distributed (Fig. 1). Nominate *cristata* is endemic to the Brazilian states of Bahia, Ceará, extreme eastern Maranhão, Minas Gerais, Paraíba, Pernambuco, and Piauí (Peters 1951, Ridgely and Tudor 1994). *P. c. unirufa* occurs in two disjunct populations, one in northern Bolivia (Departamento Beni), and the other extending from eastern Bolivia (Departamento Santa Cruz) eastward through northern Paraguay (Alto Paraguay) to southern Mato Grosso and Mato Grosso do Sul, Brazil (Peters 1951, Ridgely and Tudor 1994).

PLUMAGE

Both forms of "Rufous" Cacholotes are some shade of uniform rufous-brown throughout, except for a contrasting grayish crown found in most *unirufa* (see below). The crown feathers of all individuals are highly elongate, forming a distinctive crest. As is typical of furnariids in general, males and females are not sexually dimorphic in plumage. Adults of both *cristata* and *unirufa* have bright yellow eyes (pers. observ.). Juvenile *cristata* have dusky scaling or barring on the sides of the face, throat, and breast, and show variable amounts of dusky streaking or barring on the crown (Vaurie 1980; pers. observ.). Juvenile specimens of *cristata* from LACM also showed whitish tips or fringes to some feathers of the throat and abdomen, a character which would be difficult to discern in the field. Juveniles of *cristata* are further distinguished in the field by their bluish-gray eyes (pers. observ.). We do not know the extent to

TABLE 1. Ranges (sample sizes) and means \pm SD of selected measurements (mm) of "Rufous" Cacholotes (*Pseudoseisura cristata*), followed by a statistical comparison of the means. Values of *P* derived from Analysis of Variance (ANOVA).

Characters	<i>cristata</i>	<i>unirufa</i>	<i>P</i>
Culmen	14.1–19.8 (15) 16.7 \pm 1.6	13.1–15.5 (11) 14.4 \pm 0.7	<0.001
Bill depth	5.9–7.1 (14) 6.5 \pm 0.4	5.0–6.4 (11) 6.0 \pm 0.5	<0.001
Bill width	4.4–6.2 (17) 5.1 \pm 0.5	4.4–5.4 (11) 4.8 \pm 0.3	ns
Wing chord	97.0–112.0 (17) 103.8 \pm 4.0	92.0–106.0 (11) 98.6 \pm 4.3	<0.01
Tail	94.0–107.0 (17) 99.8 \pm 4.5	87.0–101.0 (11) 93.9 \pm 4.9	<0.01
Tarsus	29.4–32.2 (17) 31.1 \pm 0.9	29.5–32.5 (11) 30.1 \pm 1.1	<0.01
Hind claw	8.3–10.6 (17) 9.5 \pm 0.7	9.4–10.8 (11) 9.9 \pm 0.4	ns
Hind toe	13.0–15.5 (17) 14.6 \pm 0.8	13.0–16.0 (11) 14.4 \pm 0.9	ns

which juveniles of *unirufa* share these plumage or soft-part characters (if at all). What appeared to be a food-begging juvenile bird accompanying two adults of *unirufa* near Pixaim (Mato Grosso, Brazil) had yellow eyes similar to those of the adults, and we saw no evidence of dusky barring on the face or underparts.

Nominate *cristata* are noticeably paler above than are *unirufa*. Most specimens examined approximated Tawny (color #38; capitalized color names from Smithe 1975), and several specimens were paler still (closer to Cinnamon, color #39). Upperparts of *unirufa* are a darker, redder brown, closer to Ferruginous (color #41), with the tail being darker still (between Ferruginous and Chestnut, color #32). Only one specimen (USNM 16846) was contradictory to these patterns. That individual was identified as *cristata*, but had the upperparts darker and closer to *unirufa* in color. The label for this specimen lacked locality data. Contrary to Ridgely and Tudor (1994), there was no apparent difference in coloration between the two specimens from Departamento Beni, Bolivia, and other *unirufa*, apart from crown color (see below).

Crown colors differed significantly between *cristata* and *unirufa*. All adult specimens of *cristata* ($n = 12$) had crowns concolor with the mantles. This was consistent with our field observations. Three juvenile specimens of *cristata* had many crown feathers contrastingly grayish with dark longitudinal shaft streaks and dusky terminal bars, as did another juvenile specimen

from FMNH (D. Stotz, pers. comm.). Two other specimens of *cristata* had the crown feathers concolor with the mantle but had contrasting dark streaks along the shafts of some feathers. These birds also had some pale barring on the throat and abdomen, and had bill measurements intermediate between those of juveniles and adults examined. These two birds were presumed to represent older sub-adults. Most *unirufa* (8 of 11 specimens examined) had most crown feathers distinctly Glaucous (color #79), with a darker, more brownish-gray longitudinal streak along the shaft. Three of these specimens had the crowns somewhat variegated, the overlying feathers being Glaucous, but with many underlying or rear-crown feathers (the longest feathers of the crest) concolor with the mantle. These three specimens were from Departamento Beni (LSUMZ 124081) and Departamento Santa Cruz (LSUMZ 37649), Bolivia, and from Mato Grosso, Brazil (ANS 111616). The three remaining *unirufa* examined (LSUMZ 80296, FMNH 334462, and FMNH 180345) had the crown concolor with the mantle, with no trace of gray. These specimens were from Mato Grosso, Brazil, Departamento Beni, Bolivia, and Departamento Santa Cruz, Bolivia, respectively.

SIZE

In most measurable characters, *cristata* averaged larger than *unirufa* (Table 1). Several of these differences were statistically significant, although ranges for each character overlapped.

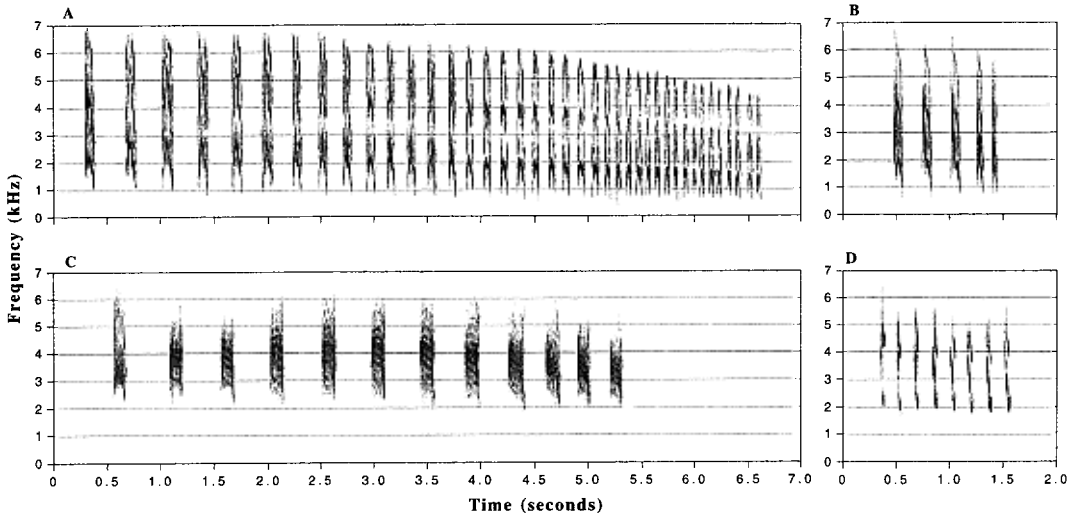


FIGURE 2. Loudsongs of Rufous Cacholotes. (A) *P. c. cristata* (presumed male) from Pernambuco, Brazil (K. J. Zimmer recording). (B) *P. c. unirufa* (presumed male) from Mato Grosso, Brazil (K. J. Zimmer recording). (C) *P. c. cristata* (presumed female) from Pernambuco, Brazil (K. J. Zimmer recording). (D) *P. c. unirufa* (presumed female), partial song from Departamento Beni, Bolivia (T. A. Parker recording, LNS # 38375).

There was little gender effect in any of the models, but there was a significant ($P < 0.05$) age effect introduced by the inclusion of three juvenile *cristata* in the analysis. These juvenile birds had the smallest bills of any of the *cristata* specimens. When only adult specimens were considered, culmen size was diagnostic. Culmen lengths (mm) of adults ranged from 15.7 to 19.8 for *cristata* and 13.1 to 15.5 for *unirufa*. Measurements from our sample fit well with those from an identically sized sample ($n = 17$ [*cristata*], $n = 11$ [*unirufa*]) reported by Hellmayr (1925).

VOCALIZATIONS

Spectrographic analysis confirmed our field impressions that *cristata* and *unirufa* differed strikingly and consistently in several aspects of their vocal repertoires. Both forms appear to have homologous, sex-specific loudsongs, which are delivered independently and as part of duets. What we believe to be the male loudsong in *cristata* is a descending series of notes that begins with 4–10 evenly spaced notes and then accelerates into a short rattle (“*chup chup chup chup chup chachachch . . .*”) (Fig. 2A). These loudsongs have a distinct “bouncing ball” pattern, in which introductory notes are widely spaced but between-note intervals rapidly diminish. What we believe to be the male loudsong of *unirufa*

is similar in pattern, but is shorter in length and differs in the shape of individual notes and in frequency (Fig. 2B). The presumed female loudsong of *cristata* is an evenly paced series of 15–35 well-spaced, frequency modulated “*zjeep*” notes with a particularly strident, buzzy quality (Fig. 2C). The presumed female loudsong of *unirufa* (Fig. 2D) is a similarly evenly spaced, long series of identical “CHEP” notes (“*chepchepchepchep . . .*”), all at essentially one pitch, but delivered at a much faster rate, and without the notably buzzy quality found in songs of female *cristata*. Both tonal differences in individual notes and rate differences in the loudsongs of these two taxa are immediately obvious to the human ear.

Because “Rufous” Cacholotes are sexually monomorphic, it was not possible in the absence of hand-sexed, color-marked birds to assign a particular vocalization to one sex with absolute certainty. However, birds of both forms which gave the more complex “bouncing ball” loudsong also were consistently the first members of a pair or group to respond aggressively to tape playback. These loudsongs also were more frequently delivered independent of a duet. Within duets by mated pairs, one individual consistently gave the bouncing ball loudsong, whereas the other individual consistently gave the repetitive long series. Thus, we can safely assume that the

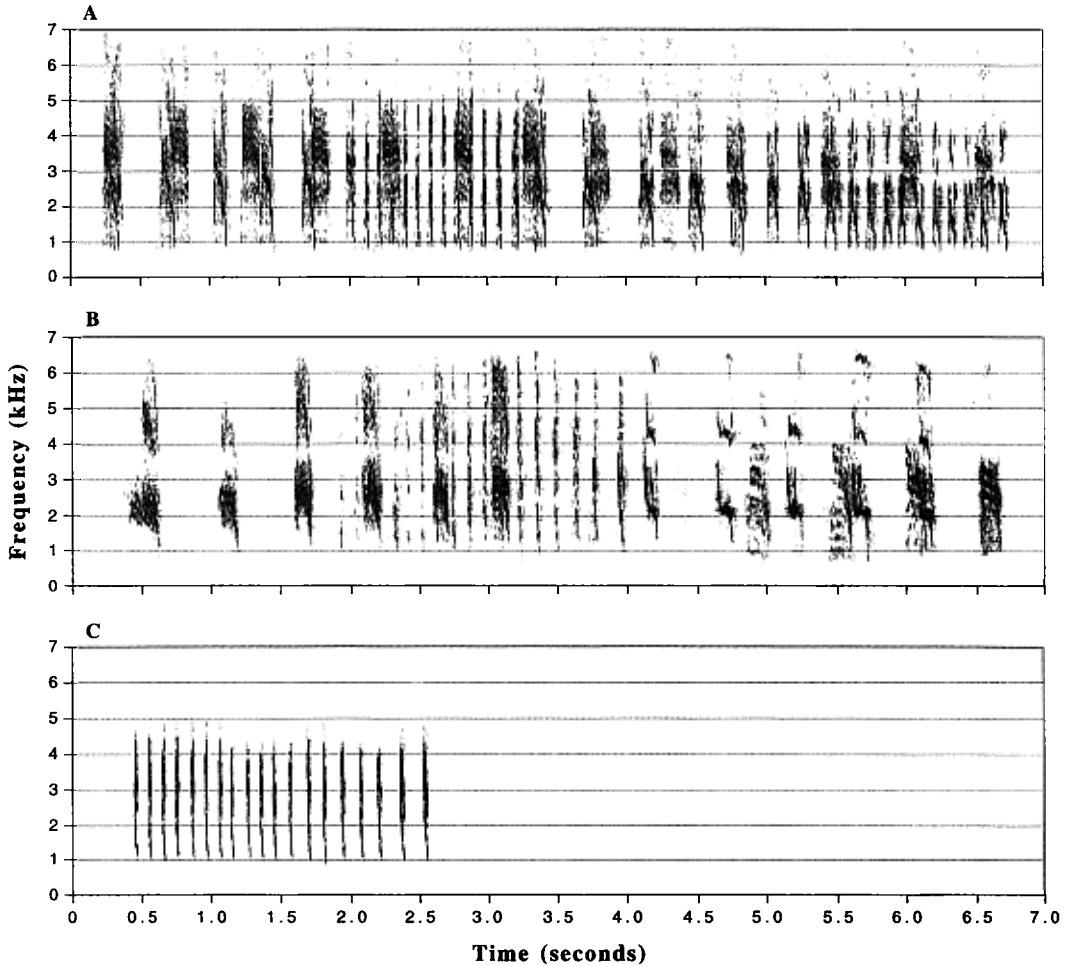


FIGURE 3. Duet vocalizations of *Pseudoseisura cristata cristata*. (A) partial male-female duet from Bahia, Brazil (T. A. Parker recording, LNS #35711). (B) partial male-female duet from Pernambuco, Brazil (K. J. Zimmer recording). (C) isolated duet chatter (presumed male) from Pernambuco, Brazil (K. J. Zimmer recording).

different types of loudsongs are specific to one sex or the other. The greater structural complexity of bouncing ball songs, along with their greater frequency of occurrence outside of duets and the more aggressive territorial response of individuals which gave them point to these being male songs.

The most frequently heard vocalizations from all "Rufous" Cacholotes were duets (Fig. 3 and 4). As in some other furnariids (e.g., *Cranioleuca vulpina*; Zimmer 1997), a song from one cacholote usually elicited an immediate duet response from its mate. Based on field observations, we would estimate that as much as 75% of male and female song bouts overlapped as

simultaneous duets. Duets were initiated by either sex, with the partner joining in immediately. The endings to duets were usually well-coordinated, and it was rare for a bird to sing more than one loudsong (males) or a few notes (females) after its mate had stopped.

The pattern of duets was similar between *cristata* and *unirufa*. In *cristata* (Fig. 3A, B), a typical duet involved the male and female simultaneously delivering their respective loudsongs, with the male filling many of his between-song intervals with a continuous, low, buzzy chatter (Fig. 3C). During periods in which the male was delivering the chatter, the strident notes of the female's loudsong stood out as the most con-

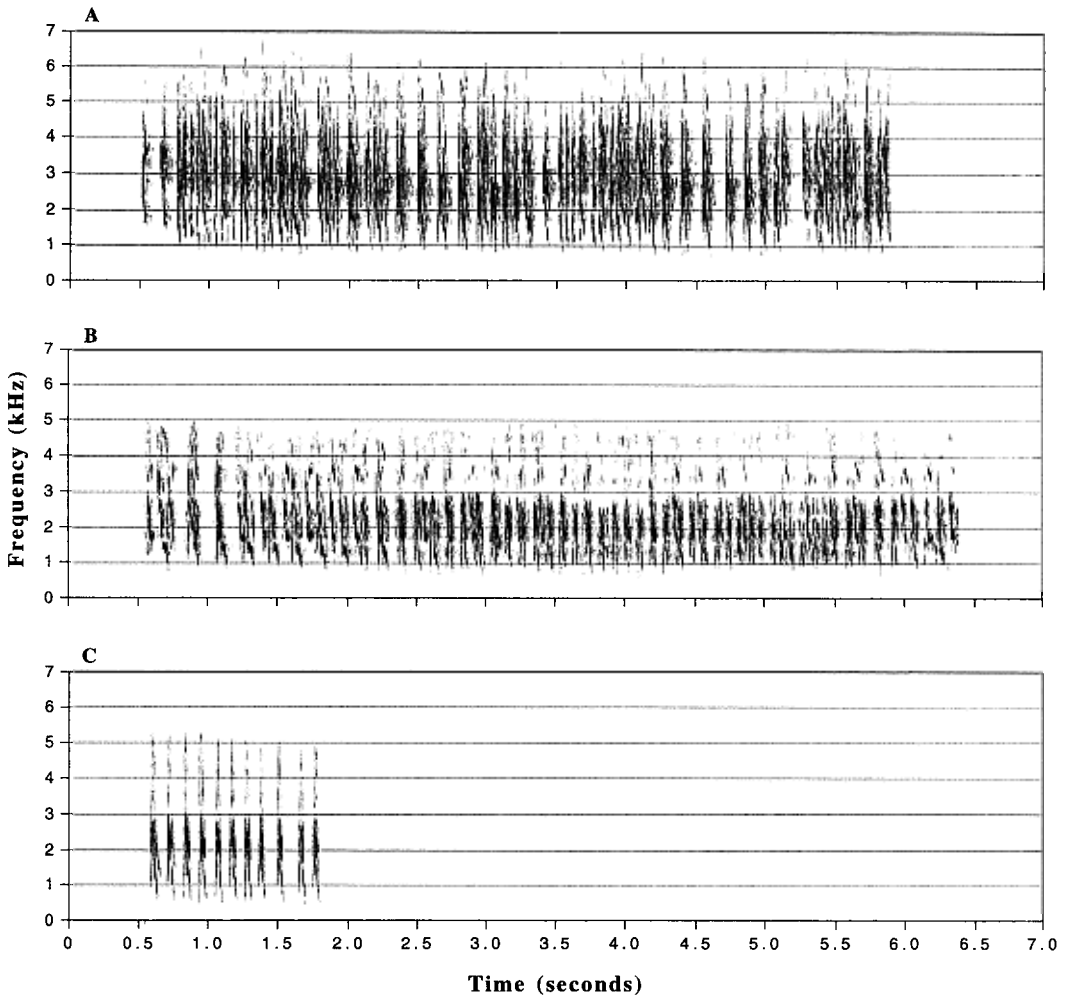


FIGURE 4. Duet vocalizations of *Pseudoseisura cristata unirufa*. (A) partial male-female duet from Mato Grosso, Brazil (K. J. Zimmer recording). (B) partial male-female duet from Departamento Beni, Bolivia (T. A. Parker recording, LNS #38375). (C) isolated duet chatter (presumed male) from Departamento Beni, Bolivia (T. A. Parker recording, LNS #38375).

spicuous element of the duet. When the male delivered his loudsong, the female continued to sing at the same rate, but her notes then became background to the male's louder song. Thus, although the male and female song bouts were simultaneous, the alternation by the male in switching from a far-carrying loudsong to a lower-amplitude chatter had the effect of making the duet sound antiphonal. This effect was accentuated by the evenly paced, relatively lengthy gaps between female notes. The male's ability to alternate from loudsong to chatter and back to loudsong without detectable pauses was remarkable. The pattern with which males

switched vocalizations also varied from one duet to the next. One duet might involve regular switching (loudsong, chatter, loudsong, chatter, etc.), whereas the next might be dominated by chatter with only one or two irregularly spaced songs. The male chatter was frequently a subdued prelude to a duet, particularly after separated birds had just reunited in response to tape playback. In these instances, a few seconds of male chatter appeared to be the synchronizing cue that precipitated a duet.

When juveniles joined parents in duets (see below), the adult male and female sang their respective songs, and the juvenile most frequently

provided the chattering backdrop that is normally delivered by the adult male. When groups of four–six *cristata* defended their territories with song bouts, it was common for two males and two females to sing typical loudsongs, with one or more birds providing constant chatter or for singing males to alternate between chatter and loudsong. In such instances, the two females displayed everything from near-perfect synchronization (complete overlap) of their notes to antiphonal coordination. Qualitative differences could usually be heard between songs of two females in a single song bout, one female giving the typical buzzy “zjeep,” and the other a more guttural “zherp.” Songs of two males within a single song bout usually only partially overlapped or not at all.

The duet pattern of *unirufa* (Fig. 4A, B) was similar to that of nominate birds, in that the male and female simultaneously delivered their respective loudsongs, with the male frequently filling his between-song intervals with a continuous chatter (Fig. 4C). As in *cristata*, the male pattern of switching between songs and chatter varied from one duet to the next. Duets of the two taxa sound distinctly different. Duets of *unirufa* sound like a uniformly loud, fast-paced jumble of chattering notes as the “chippering” female loudsong and the alternating male loudsong and chatter blur together. By contrast, the duets of *cristata* are distinctly slower and more antiphonal, and are characterized by the unique strident notes of the females, the tonal quality of which is unlike anything delivered by *unirufa*. We have not encountered more than two *unirufa* singing together.

Other calls by both taxa were limited to single “chuk” notes and subdued, short chatter, both of which appeared to be given by both sexes and all ages. These seemingly functioned as contact notes and in coordinating behaviors between mates and/or within family groups.

Tape recordings of the disjunct population of *unirufa* from Departamento Beni, Bolivia (Fig. 4B) sound identical to those of the more widespread population of eastern Bolivia, northern Paraguay, and southwestern Brazil. Similarly, we could find no geographic variation in the voice of nominate *cristata*.

PLAYBACK TRIALS

Playback experiments with *Pseudoseisura* recordings offer further evidence of the signifi-

cance of vocal differences among the taxa, and of their role as potential isolating mechanisms.

We performed tape playback experiments on pairs of *unirufa* at various points along the Trans-Pantaneira Highway near the settlement of Pixaim, Mato Grosso, Brazil (seven pairs in September 1996 and nine pairs in September 1998), and near Cuiabá, Mato Grosso, Brazil (three pairs in September 1996). Fifteen of the 19 pairs showed no response to tape playback of *cristata* duets, yet responded strongly to playback of *unirufa* duets. In most of these cases pairs of cacholotes flew in from distances of 50–100 m away, landed next to us, and duetted repeatedly in response to tape playback. Three pairs responded weakly to playback of nominate *cristata*. In each case, the pair of cacholotes responded to initial playback by moving to a higher perch in the same tree and singing a single duet. Additional playbacks failed to elicit further response. When we switched to playback of *unirufa* duets, each of the pairs approached us aggressively and duetted repeatedly. Another pair approached closely (without vocalizing) once after a single playback of nominate *cristata*, but did not respond to additional playbacks. This same pair responded immediately and aggressively five consecutive times to playback of *unirufa* vocalizations. In each case, we delayed the next trial until after the pair had ceased vocalizing and had left the immediate area.

We performed tape playback experiments on pairs or groups of nominate *cristata* in January 1997 (two pairs-groups near Exu and nine pairs-groups near Lagoa Grande, Pernambuco, Brazil; and two pairs-groups near Itaberaba and one group at Lencois, Bahia, Brazil), January 1998 (one group near Exu and another near Lagoa Grande), and January 1999 (one pair near Exu and nine pairs-groups near Lagoa Grande, and one pair near Canudos, Bahia, Brazil). Three of these pairs were completely unresponsive to playbacks of any kind. One pair gave a single duet after several playbacks of *unirufa* vocalizations, but did not approach or sing further, and the timing of their duet was such that we suspect it was incidental to our playback. When we switched to playback of *cristata* vocalizations, the pair flew directly at us from more than 100 m, landed in an adjacent tree, and gave several loud duets. The remaining 23 pairs or groups showed no response to repeated playbacks of

TABLE 2. Summary of playback trials (as detailed in the text) involving the two subspecies of *Pseudoseisura cristata* (*P. c. cristata* and *P. c. unirufa*). "Subject taxon (locality)" identifies the taxon of the bird on which the trial was being conducted, and the site. Locations where these trials were conducted were: Exu and Lagoa Grande (Pernambuco, Brazil); Itaberaba, Lencois, and Canudos (Bahia, Brazil); and Pixaim and Cuiabá (Mato Grosso, Brazil). Codes for Brazilian states are as follows: PE = Pernambuco, BA = Bahia, and MG = Mato Grosso.

Subject taxon (locality)	n	Response to playback of	
		<i>P. c. cristata</i>	<i>P. c. unirufa</i>
<i>P. c. cristata</i>			
Exu, PE	1	strong	weak
Exu, PE	3	strong	none
Lagoa Grande, PE	17	strong	none
Lagoa Grande, PE	2	none	none
Itaberaba, BA	1	strong	none
Itaberaba, BA	1	none	none
Lencois, BA	1	strong	none
Canudos, BA	1	strong	none
Totals	27	strong = 24 none = 3	none = 26 weak = 1
<i>P. c. unirufa</i>			
Pixaim, MG	13	none	strong
Pixaim, MG	2	weak	strong
Pixaim, MG	1	moderate	strong
Cuiabá, MG	2	none	strong
Cuiabá, MG	1	weak	strong
Totals	19	none = 15 weak = 3 moderate = 1	strong = 19

unirufa, yet responded strongly and immediately to playbacks of *cristata* (Table 2).

SOCIALITY AND BEHAVIOR

In January 1996 near Lagoa Grande (Pernambuco, Brazil), we found on a telephone pole an active *cristata* nest which was being attended by four birds. The open terrain allowed us to visually track the movements of foraging birds as they made trips to and from the nest to feed young. After verifying that each of the birds was bringing arthropod prey to the same hole in the large stick nest, we played tape of *cristata* in an attempt to confirm our count of nest attendants. Four birds, each of which appeared to be adult, responded by immediately flying to the crossbar of the pole on which the nest was placed. They gave several excited song bouts before flying off. In February 1996, A. Whittaker returned to the same spot and found a group of five birds, at least two of which were juveniles, engaged in constructing a new nest less than 100 m from the pole nest, which appeared to be unoccupied. One of the juveniles was seen carrying a stick ca. 30 cm in length from the pole nest to the

new nest. Whittaker found a second territory along the same road which was defended by four birds, all apparently adult in eye color and plumage.

In January 1997 and 1998, we performed playback experiments in 16 *cristata* territories (as detailed above) in Pernambuco and Bahia. Birds at two of the territories were unresponsive to playback. At five of the territories, tape playback resulted in territorial defense by a single pair of birds, although in some instances other cacholotes (which may have been occupants of the same territory) also responded vocally from more than 100 m distant without approaching. At five territories, playback resulted in close approach and repeated song bouts from four–six birds (two groups of four, two groups of five, and one group of six). At four other territories, playback resulted in defense by two adults and a single juvenile. In all instances, the vocalizing birds climbed around in the same trees and bushes while responding to our tapes and exhibited no agonistic behaviors toward one another. After they ceased calling, each group flew off together. Some groups with four or more birds included

one or more juveniles, although others appeared to be comprised of all adults. The subtle characters that distinguish juveniles are difficult to see except at close range and in good light, and thus, exact group composition was frequently difficult to determine. In all cases of group (more than two birds) territorial defense, all birds actively joined in the posturing and singing. Juveniles often responded by flying in and landing immediately next to one adult bird and appeared somewhat more timid than did adults.

In January 1999, playback experiments at 11 territories in Pernambuco and Bahia resulted in only one case of group territorial defense, that by three birds. All other territories were defended by either pairs or lone birds.

In contrast to our experiences with *crystata*, we have never had more than two *unirufa* in a territory respond to tape playback. More than 90% of all of our encounters with this form have involved two closely associated birds that were strongly territorial. On a few occasions in August–October visits to the Pantanal, we have encountered three–four *unirufa* foraging closely together in what we took to be family groups, but these groups were nonvocal and unresponsive to tape playback.

HABITAT

The two types of “Rufous” Cacholotes occupy markedly different habitats. Nominate birds are inhabitants of arid and semi-arid caatinga scrub and woodlands (Vaurie 1980, Ridgely and Tudor 1994, pers. observ.). Within this formation, the densest populations of cacholotes appear to be in some of the most arid regions of Pernambuco and Bahia. Even there, the distribution of cacholotes appears somewhat clumped, with some seemingly suitable areas unoccupied. Remarkably, areas subjected to relatively severe grazing pressure by goats often have larger cacholote populations than more pristine areas in the same region (pers. observ.).

P. c. unirufa occupies deciduous woodland, gallery forest edge, and seasonally flooded savanna with “islands” of swampy woodland (Ridgely and Tudor 1994, Parker et al. 1996). We have found it to be relatively evenly distributed throughout these habitats in the northern Pantanal of Mato Grosso, Brazil, but at lower densities than we have found *crystata* in its center of abundance.

Both types of “Rufous” Cacholotes frequent

homesteads and ranches, often placing their nests close to human habitations.

DISCUSSION

Nominate *crystata* and *unirufa* differ significantly in their male and female loudsongs and consequently, in their duets. None of these vocalizations are known to vary geographically within the two forms. The northern Bolivian population of *unirufa*, which is nearly as geographically isolated from other *unirufa* as are the latter from *crystata*, appears to be vocally identical to eastern populations of *unirufa*. A primary challenge in applying the biological species concept to allopatrically distributed taxa is the need to judge whether or not the two taxa are sufficiently differentiated as to prevent extensive hybridization in the event of secondary contact. Carefully designed and systematically conducted playback experiments provide convincing evidence of whether vocal differentiation confirmed by spectrographic analysis is a sufficient barrier to interbreeding.

In our study, these experiments strongly suggest that neither taxon of “Rufous” Cacholote recognizes nor reacts to the vocalizations of the other. The five inter-taxon responses (four of which involved only a single song or duet without approach or subsequent vocalization, and the other, which involved unsustained approach without vocal response) are almost certainly taxonomically insignificant. During our observations of cacholotes, we found that many of the duetting species of furnariids in Mato Grosso and northeastern Brazil seem to share an intergeneric response to any loud, chattering duet. On several occasions we found that a duet from a pair of Greater Thornbirds (*Phacellodomus ruber*), Rufous Horneros (*Furnarius rufus*), or Pale-legged Horneros (*F. leucopus*) would result in an immediate vocal response from a pair of *P. c. unirufa* that we were watching. The horneros (and to a lesser extent, the thornbirds) were similarly responsive to any duets by the cacholotes. Similarly, *P. c. cristata* in northeastern Brazil routinely responded to noisy duets of Band-tailed Horneros (*F. figulus*) by delivering a single duet of their own. All of these species (particularly the cacholotes and horneros) have some structural similarities to their duets, possibly evolved in response to acoustic characteristics of their common environment. Interspecific recognition of disturbance duets from neigh-

boring species could be important in decreasing the risks of predation for species which have permanent pair-bonds and territories. During our playback trials, we frequently set-off duet "chain reactions" of neighboring pairs of horneros simply by playing back cacholote tape. The four "weak" responses that we observed in our trials were no stronger than the responses given by the same cacholotes to neighboring furnariids of different genera. The one inter-taxon response (out of 46 trials) that was rated as "moderate" came when a pair of *unirufa* approached briefly at the first playback of a *cristata* duet, but did not vocalize and quickly retreated. Subsequent inter-taxon playbacks to this pair produced no response.

Duets serve multiple functions, including coordinated defense of territory and pair-bonding. In "Rufous" Cacholotes, as in the majority of duetting species, the same types of duets are used during bouts of territorial defense, as a prelude to copulation or nest building, and when pairs reunite following visual separation (Farabaugh 1982, pers. observ.). In sexually monochromatic species (most Furnariids), sexual specificity of duet contributions probably serves in mate attraction as well as in identifying the sex of a territorial trespasser (Farabaugh 1982). A likely by-product of sexual specificity of duet roles is the strengthening of reproductive isolation. In an habitually duetting genus such as *Pseudoseisura*, vocal differences between taxa would seem to present major obstacles to reproductive or social compatibility.

Morphological distinctions between *cristata* and *unirufa* are less obvious than the vocal differences, but are nonetheless significant. Crest color is the most conspicuous distinguishing character, and one that has been confused in the literature. Hellmayr (1925) stated that *unirufa* was "very similar to *cristata*, but averaging smaller with slenderer bill; general coloration of plumage deeper cinnamon rufous, and feathers of pileum always more or less tipped (or edged) with ashy." This statement leaves as ambiguous the crest color of nominate *cristata*, particularly in light of Hellmayr's (1925) following comment that "I find the western race to be separable after all, although single examples are not always distinguishable." Vaurie (1980) noted only that *cristata* was "somewhat paler and brighter than the birds of southwestern Brazil, northern Paraguay and Bolivia." In his description of *P. cris-*

tata, Vaurie (1980) made no subspecific distinctions, and reported that "the distal half, or more, of the longer crest feathers has grayish edges, and is brown or brownish at its center or along the shaft, the base of the crest feathers being rufous." Ridgely and Tudor (1994) describe Rufous Cacholote (without distinguishing between *cristata* and *unirufa*) as having the "crest feathers ashy gray." They go on to state that birds from Beni, Bolivia "appear paler and more cinnamon and lack gray in crest." The implication of this description is that all populations of Rufous Cacholotes except those from Beni, Bolivia are gray-crested.

There are two obvious sources for the conflicting literature regarding crest color. The first is that crest color is variable in at least some populations of *unirufa*, perhaps especially in the Beni population. Although in Mato Grosso, Brazil we have encountered only gray-crested *unirufa*, examination of specimens revealed that birds from Departamentos Beni and Santa Cruz (Bolivia), and Mato Grosso could have crests that were rufous-brown, gray, or variegated brown-and-gray. Examination of a small sample of specimens could easily suggest that all birds from Departamento Beni were brown-crested, or that all other *unirufa* were gray-crested. The second source of confusion is that juveniles of nominate *cristata* are gray-crested, which could lead investigators to the conclusion that all populations of *cristata* and *unirufa* were equally variable with respect to crest color.

In addition to crest color, *cristata* and *unirufa* differ more subtly in overall color, and in several mensural characters (notably bill size).

Particularly intriguing is the evidence of differing social structures between *cristata* and *unirufa*. Our field work demonstrates that for at least part of the year it is common for nominate birds to live in groups, in which there appears to be an alpha-pair with 1-4 helpers. These helpers not only assist in territorial defense by joining in cooperative duets, but, at least in some instances, actively share in nest building and care of young. The presence of juveniles in some of the groups that we encountered suggests that helpers are offspring from previous nestings that remain on their natal territories to assist their parents in raising younger siblings. Similar cooperative breeding systems have been documented for a number of Neotropical taxa (Brown 1978). We found juvenile *P. c. cristata*

joining adults in duetting in response to playback, and in construction of new nests. Hudson (1920) reported that after fledging, juvenile White-throated Cacholotes (*P. gutturalis*) remained with their parents until the next breeding season, and that these birds were most frequently found in family groups of five or six. Similarly, Nores and Nores (1994) found that juvenile Brown Cacholotes (*P. lophotes*) in Argentina remained in the natal territories for 5–13 months, frequently joining in the defense of the parental nest, and occasionally aiding in nest construction or repair. Although this was considered as a possible “step toward cooperative breeding,” no care of younger siblings was reported (Nores and Nores 1994). Brown Cacholotes also were reported to breed before becoming adult (Nores and Nores 1994).

Our observations of *cristata* suggest some differences from the social structure reported for *P. gutturalis* and *P. lophotes*. We did not find evidence of paired juvenal-plumaged birds independent of adults. Also, groups defending territories did not always include juvenal-plumaged birds. In some groups, all of the birds appeared to be adult-plumaged with yellow eyes. This was the case in the group of four birds that were cooperatively feeding nestlings near Lagoa Grande (Pernambuco, Brazil). Based on specimens examined at LACM, we believe that there is at least one transitional plumage between juvenal and adult, in which birds have slight amounts of dusky streaking along the shafts of crown feathers and have some pale-fringed feathers on the throat and breast. If this is the case, then observed groups of 4–6 apparent adults could be composed of an alpha pair plus older sub-adults. Such birds would be difficult to distinguish from adults in the field. This would suggest that sub-adult *P. c. cristata* delay breeding for longer than young of other cacholotes. They also would appear to play a larger role in breeding activities by assisting in the feeding of nestlings. However, the general lack of group territorial response to playback trials in 1999 (only 1 of 11 territories being defended by more than two birds) may be indication that *cristata* group structure is not permanent.

The apparent lack of cooperative breeding in *P. c. unirufa* is interesting given that some form of this behavior is found in every other taxon in the genus. Cooperative breeding in many species has been linked with ecological constraints, par-

ticularly oversaturation of preferred habitat by established breeders (Koenig and Pitelka 1981). Species that live in stable environments are better candidates for the evolution of cooperative breeding systems than are species that occupy less stable environments, where periodic resource bottle-necks result in lower densities and more vacant potential territories (Gill 1990). Our observations of *unirufa* are from the Pantanal region of Mato Grosso, a 150,000 km² alluvial area in the upper Paraguay Basin. The region has a highly seasonal climate, with a pronounced midwinter dry season (July–October) followed by a November–April rainy season with 1,000–1,400 mm of rain (Dubs 1992). Each year the major rivers in the region overflow their banks during the rainy season, flooding much of the basin and constantly altering the topography of the landscape. Annual flooding and drying cycles in this region may create sufficient resource instability to inhibit the development of cooperative breeding systems in *unirufa*. By comparison, the caatinga inhabited by *P. c. cristata*, the arid lowland scrub inhabited by *P. gutturalis* (Parker et al., 1996), and the chaco woodland and scrub occupied by *P. lophotes* (Ridgely and Tudor 1994) would appear to be more seasonally stable environments. More detailed investigation into the reproductive biology of *P. c. unirufa* is needed to confirm the absence of cooperative breeding. Of particular interest would be comparisons of populations of *unirufa* from dry woodlands to those of the Pantanal.

CONCLUSIONS

The two described forms of “Rufous” Cacholote are allopatric in their distribution and occupy different habitats. *P. c. cristata* are diagnosable from all *P. c. unirufa* by marked differences in male and female loudsongs and duets, and adult *cristata* may be separable by culmen length alone. Nominant birds are further generally distinguished by their overall larger size, paler Tawny or Cinnamon plumage (as opposed to Ferruginous), and crests which are concolor with the body. Juveniles of *cristata* have plumage characters and eye color different from adults. There is as yet no indication that juveniles of *unirufa* exhibit such differences. Extensive tape playback experiments demonstrated that neither form of “Rufous” Cacholote responds to vocalizations of the other. Cooperative breeding has been determined to be common in *cristata*,

whereas it appears to be absent in *unirufa* populations studied to date. The sum of these differences points to *cristata* and *unirufa* as being separate species. Thus, we submit that the complex consists of two species as follows:

Pseudoseisura cristata (Spix), the Caatinga Cacholote

Pseudoseisura unirufa (d'Orbigny and Lafresnaye), the Gray-crested Cacholote

The traditional English name of "Rufous Cacholote" is not appropriately applied to one form over the other. Therefore, we suggest the English name of "Caatinga Cacholote" for *P. cristata* (highlighting the unique habitat in which it occurs) and "Gray-crested Cacholote" for *P. unirufa*, which emphasizes the best plumage character for separating most individuals of the two forms. In choosing the latter name we recognize that not all individuals of *unirufa* have gray crests, but attempts to incorporate the geographic range or habitat preferences of this form into a name were unsatisfactory.

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APPENDIX 1

Recording locations and recordists. Numbers following each name represent the number of recordings from the recordist at each site.

cristata—BRAZIL: Boa Nova, Bahia (T. A. Parker, 1); Lencois, Bahia (K. J. Zimmer, 6); Uricuri, Pernambuco (K. J. Zimmer, 1); Lagoa Grande, Pernambuco (A. Whittaker, 2; K. J. Zimmer, 33).

unirufa—BOLIVIA: 8 km south of Trinidad, Departamento Beni (T. A. Parker, 1). BRAZIL: Trans-Pantaneira Hwy. between Pixaím and Porto Jofre, Mato Grosso (K. J. Zimmer, 22).

APPENDIX 2

List of localities and lending institutions for specimens examined. All specimens were from one of the follow-

ing institutions: Carnegie Museum, Pittsburgh, Pennsylvania (CM); Field Museum of Natural History, Chicago, Illinois (FMNH); Los Angeles County Museum, Los Angeles, California (LACM); Louisiana State University Museum of Natural Science, Baton Rouge, Louisiana (LSUMZ); Academy of Natural Sciences of Philadelphia, Philadelphia, Pennsylvania (ANSP); and the National Museum of Natural History, Washington, D.C. (USNM).

cristata (10 males, 5 females, 1 sex unknown)—BRAZIL: Bahia, Barra (LACM, 2 males, 1 female), Rio do Peixe (CM, 1 female; FMNH, 3 males), unspecified locality (USNM, 1 sex unknown). Ceará (USNM, 1 male). Paraíba, Coremas (LACM, 2 males, 1 female), Santa Luisa (USNM, 1 female), Souza (USNM, 1 male, 1 female). Piauí, Ibiapaba (FMNH, 1 male).

unirufa (5 males, 5 females, 1 sex unknown)—BOLIVIA: Departamento Beni, 6 km southeast of Trinidad (LSUMZ, 1 female), 10 km southwest of Trinidad (LSUMZ, 1 male). Departamento Santa Cruz, Buena Vista (FMNH, 1 male), Puerto Suarez (CM, 1 female, 1 sex unknown), unspecified locality (LSUMZ, 1 female). BRAZIL: Mato Grosso, Descalvados (ANSP, 1 male, 1 female; FMNH, 1 male, 1 female), Fazenda Santa Rosa (LSUMZ, 1 male).