

SPECIES LIMITS IN ANTBIRDS (PASSERIFORMES: THAMNOPHILIDAE): THE MYRMOTHERULA SURINAMENSIS COMPLEX

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ABSTRACT.—Current species-level taxonomy of Neotropical birds is in need of reassessment but lacks objective methodology and criteria for the ranking of allopatric populations. Previously (Isler et al. 1998), through empirical analysis of pairs of syntopic species, we developed methods and standards for employing vocalizations in determining species limits in the family Thamnophilidae. Building on this study, we now propose procedures for integrating vocal characters with morphology and geographic distribution in making species determinations in thamnophilids. We applied this methodology to populations of antwrens in the *Myrmotherula surinamensis* complex (including three subspecies of *M. surinamensis* and *M. cherriei*). Four diagnostically differentiated populations were identified, all of which corresponded to named taxa. Each population (some of which are narrowly sympatric) was distinguished unambiguously by morphology and vocalizations. Under these objective and conservative standards, we recommend that *Myrmotherula surinamensis*, *M. multistriata*, *M. pacifica*, and *M. cherriei* be recognized as distinct species. The level of differentiation found between *M. surinamensis* and *M. multistriata* illustrates the minimum threshold recommended for species status of allopatric populations of thamnophilid antbirds and should provide a useful reference point for future considerations of species limits. Received 16 September 1997, accepted 20 May 1998.

ALMOST WITHOUT EXCEPTION, current taxonomies of Neotropical birds at the species level are based solely on judgments of the significance of morphological similarities and differences. If species designations are to provide sound building blocks in ornithological, biogeographical, and conservation research, it is crucial that explicit and practical taxonomic standards be applied consistently and objectively. In the case of thamnophilid antbirds (one of the most numerically significant groups of Neotropical birds) and other suboscines, taxonomic reassessments should incorporate analyses of vocalizations, which appear to be innate in this group (Isler et al. 1998).

Isler et al. (1998) analyzed vocalizations of eight congeneric, syntopic pairs of thamnophilid antbird species to develop a threshold of vocal differentiation appropriate for definition of species limits of allopatric populations. Eleven principal characters were defined to reflect independent vocal features, and the presence of diagnosable vocal differences between syntopic pairs was tested using approximately 30

measures of these characters for each vocalization type. Members of all eight pairs were diagnostically distinguishable by at least three principal vocal characters (i.e. none was distinguished by only one or two characters). This finding led us to recommend three diagnosable characters as an objectively defensible reference point for establishing vocal differentiation at the species level for thamnophilids. In this paper, we integrate this guideline with analyses of morphological characters and geographic distribution in recommending a taxonomic standard for species-level recognition of thamnophilid antbird populations.

One component of the large (31 species recognized by Sibley and Monroe [1990]) thamnophilid genus *Myrmotherula*, which appears to be polyphyletic (Hackett and Rosenberg 1990), is a well-defined, presumably monophyletic group of "streaked antwrens." Within this group, four complexes may be recognized on the basis of the form of their loudsongs (Fig. 1) as well as morphology. Loudsongs of the *surinamensis* complex (Fig. 1A; includes *cherriei*) are a nearly evenly paced or decelerating series of abrupt notes that rises or remains constant in

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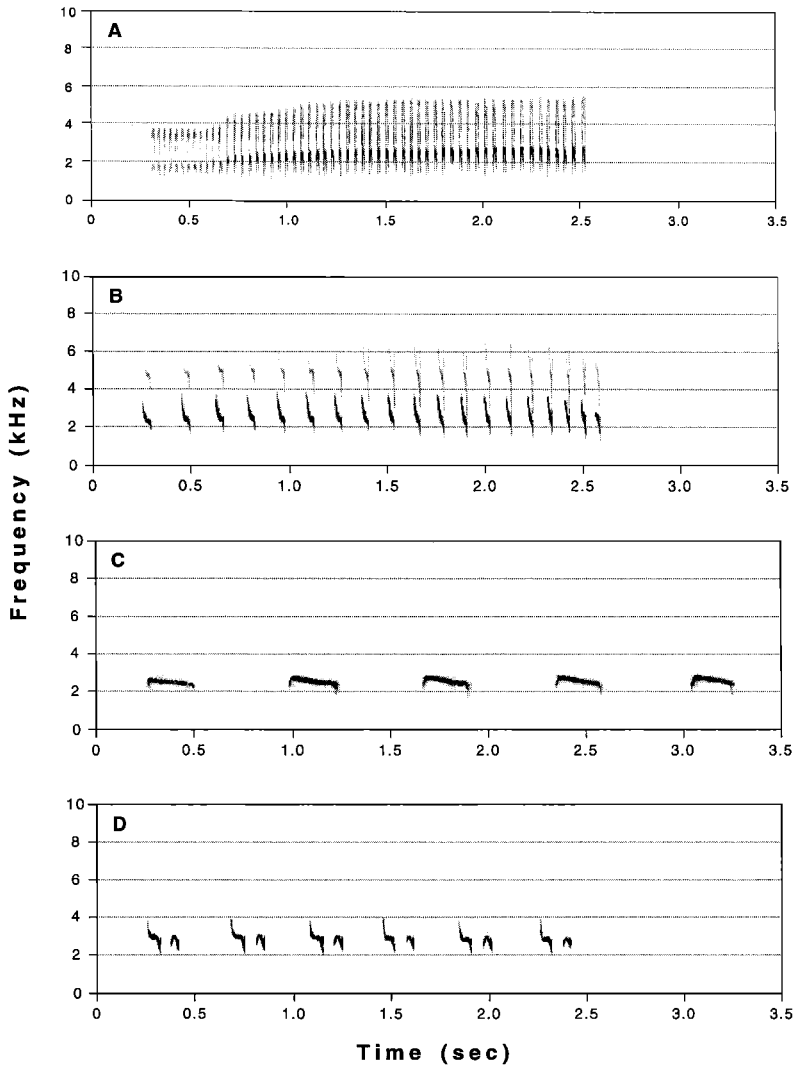


FIG. 1. Examples of loudsongs from four complexes of "streaked" antwrens. (A) *Myrmotherula s. surinamensis*, Raleigh Falls, Suriname (Whitney, ISL-BMW.115:20). (B) *Myrmotherula b. brachyura*, 4 km W Carolina Rd., Suriname (Davis, LNS 25302). (C) *Myrmotherula sclateri*, Alta Floresta, Mato Grosso, Brazil (Whitney, ISL-BMW.63:30). (D) *Myrmotherula l. longicauda*, Pilcopata, Cuzco, Peru (Parker, LNS 30052). Reference numbers explained in Isler et al. (1998: appendix).

frequency. Loudsongs of the *brachyura* complex (Fig. 1B; includes *obscura*) are an accelerating series of abrupt notes that rises and falls in frequency. Loudsongs of the *sclateri* complex (Fig. 1C; includes *ambigua*) are a slowly delivered series of relatively few long notes nearly constant in frequency. Loudsongs of the *longicauda* complex (Fig. 1D; includes *klagesi*) are series of paired notes, moderate in length and delivered deliberately at approximately the same fre-

quency. Morphologically, underpart coloration and tail morphology distinguish the four groups. In the *brachyura* and *sclateri* complexes, both sexes have pale yellow underparts, whereas males in the *surinamensis* and *longicauda* complexes are streaked black and white below, and females have ochraceous to yellowish-red-brown underparts. Short tail lengths distinguish the *brachyura* complex from the *sclateri* complex. Gyldenstolpe (1930) first pointed out

that *cherriei* was allied with *surinamensis* in having 12 rectrices and that *klagesi* and *longicauda* each had 10 rectrices. Thus, on the basis of vocal and morphological evidence, *surinamensis* and *cherriei* appear to form a complex that is appropriate for analysis exemplifying our approach.

CRITERIA FOR DEFINING SPECIES AND SUBSPECIES

Criteria for establishing species limits in thamnophilids were initially developed in a study of the Slaty Antshrike (*Thamnophilus punctatus*) complex (Isler et al. 1997) and have been refined based on the vocal analysis of eight syntopic pairs (Isler et al. 1998). Because this paper serves in the developing methodological base for subsequent studies examining species limits in antbirds, it is important to recognize that the following criteria are limited to vocal and morphological data and may be modified as additional studies are completed, particularly studies of molecular differences (e.g. Hackett 1993). Empirical studies, currently underway, should illuminate the concordance between measures of genetic differences between antbird populations and differences in vocal and morphological characters.

Taxa or populations treated as species.—(1) Sympatric taxa that are reproductively isolated. (2) Parapatric populations diagnosable by either morphology or vocalizations and with a lack of clinal intermediacy at the contact zone indicating that gene flow is absent or highly restricted. (3) Allopatric populations that are diagnosable by both morphology and vocalizations. In the case of parapatric and allopatric populations, differences in three vocal characters are employed as a reference point following guidelines developed in Isler et al. (1998). Thus, for allopatric populations, when vocalizations are the principal means of diagnosis at the species level, differences in three vocal characters are required, and a morphological character must identify individuals of at least one sex unambiguously to a particular taxon. Allopatry encompasses populations separated by wide portions of rivers and whose ranges are not known to extend to headwaters regions.

Taxa or populations treated as subspecies.—(1) Geographically isolated populations that are diagnosable either by morphology or vocaliza-

tions or weakly differentiated for both (e.g. not meeting the species-level guidelines for vocal characters developed in Isler et al. 1998). (2) Populations with the preceding characteristics that are undifferentiated over large areas and that come into contact in a manner in which intermediates occur in a steep, apparently stable cline.

Named taxa proposed to be synonymized.—(1) Taxa that are not unambiguously diagnosable by either plumage or vocalizations. (2) Populations that vary along an extensive cline.

Use of behavioral data.—Ancillary data with potential taxonomic value in antbird studies include stereotypic motor patterns such as tail movements (e.g. Isler et al. 1997), foraging behavior such as near-perch vs. aerial maneuvers (e.g. Schulenberg 1983, Whitney 1992), and nest placement and architecture (e.g. Wilkinson and Smith 1997). Behavioral data will be used to support species-level determinations and may play an important role in some cases. We remain cautious in incorporating differences in habitat preferences because there appears to be substantial undocumented and poorly understood geographic variation in habitat preferences of a number of antbird species.

METHODS

Taxa and distribution.—Currently, four taxa are recognized within the *Myrmotherula surinamensis* complex (Peters 1951): the monotypic species *cherriei* and three subspecies of *surinamensis* consisting of *pacifica*, *multostriata*, and the nominate form, hereafter referred to as *surinamensis*. Distributional maps were prepared using the methods described by Isler (1997). Ranges of *pacifica*, *multostriata*, and *surinamensis* are plotted in Figure 2. That of *pacifica* is isolated from the remaining taxa by the Andes. East of the Andes, *surinamensis* occurs in the Guianan region south to the Rio Amazonas and west to the vicinity of the Colombia-Venezuela border; *multostriata* is found mostly south of the Amazon but also occurs north of the Amazon in western Amazonia northward to central Colombia along the base of the Andes and also between the Rio Negro and Rio Solimões near their confluence. A gap of uncertain width between ranges of *multostriata* and *surinamensis* appears to extend from Amazonas, Brazil, in the region of the middle and upper Rio Negro, to east-central Colombia (an area poorly known ornithologically).

The known range of *cherriei* (Fig. 3) has been extended substantially in recent years to the Rio Tigre, Loreto, Peru (Alvarez 1994) and to the Anavilhanas Archipelago, lower Rio Negro, Brazil (M. Cohn-Haft

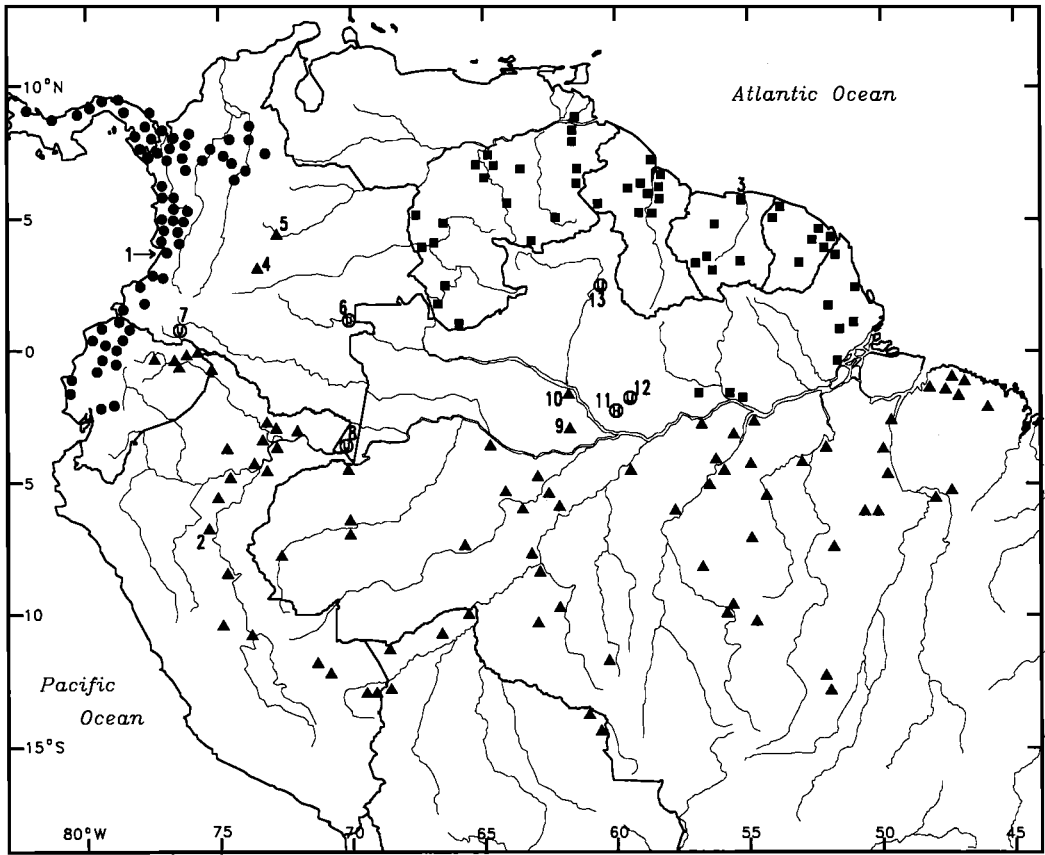


FIG. 2. Geographic ranges of taxa currently considered subspecies of *Myrmotherula surinamensis*. Black circles = *pacific*; black squares = *surinamensis*; black triangles = *multistriata*. U in a circle = taxon unknown; H in a circle = hypothetical record; narrowly spaced dots = cordilleran divides; more widely spaced dots = Brazil states. Symbols represent the occurrence of taxa within small geographic sectors (see Isler 1997). 1. Buenaventura, Colombia, type locality of *pacific*. 2. "Rio Ucayali," Peru, type locality of *multistriata*. 3. "Surinam," type locality of *surinamensis*. 4. Female specimen at AMNH from Rio Duda, Meta, examined and confirmed by authors to be *multistriata*. 5. Puerto Barrigón, Meta (Meyer de Schauensee 1946). 6. Mitú, Vaupés (S. L. Hilty pers. comm., sight record). 7. Near Puerto Umbria, Putumayo (S. L. Hilty pers. comm., sight record). 8. Near Leticia, Amazonas (S. L. Hilty pers. comm., sight record). 9. Specimens from Rio Manacapuru, Amazonas, at MZUSP examined and confirmed by authors to be *multistriata*. 10. Recordings (Cohn-Haft, ISL-MCH.2:03) of vocalizations from Parque Nacional de Jaú, Amazonas, are consistent with those of *multistriata*. 11. A sight record from 80 km north of Manaus, Amazonas (D. F. Stotz and Bierregaard 1989) is only tentatively identified as this species (D. F. Stotz pers. comm.). 12. Sight record for Balbina, Amazonas (Willis and Oniki 1988) was identified as "*surinamensis*" without subspecific designation. 13. Two males from Serra de Lua, Roraima, at FMNH cannot be identified with certainty, but they appear to be *surinamensis* (D. F. Stotz pers. comm.).

and B. M. Whitney unpubl. data). Syntopy is known for *cherriei* and *surinamensis* near the Rio Ventuari, Amazonas, Venezuela, where the two forms occupy separate but adjoining habitats, close enough to hear each other's vocalizations (K. Zimmer pers. comm.). We also consider *cherriei* and *multistriata* to be syntopic along the Rio Tigre, Loreto, Peru, where both taxa have been found in the same thickets, although

not at the same time (J. Alvarez and B. M. Whitney pers. obs.).

Analysis of morphology.—We previously described the methodology used to analyze morphology (Isler et al. 1997). In addition to museum inventories listed in Isler et al. (1997), we obtained records from the Museo de Zoología da Universidade de São Paulo (MZUSP) and Natural History Museum of Los An-

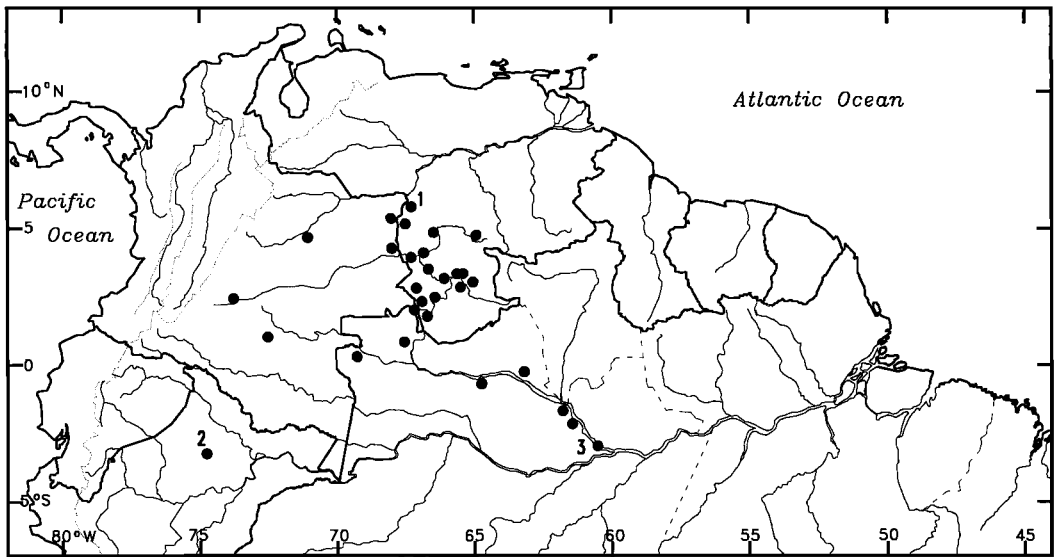


FIG. 3. Geographic range of *Myrmotherula cherriei*. Narrowly spaced dots = cordilleran divides; more widely spaced dots = Brazil states. Symbols represent the occurrence of taxa within small geographic sectors (see Isler 1997). 1. Perico = Puerto Ayacucho, Amazonas, type locality of *cherriei*. 2. Above Intuto, Rio Tigre, Loreto, collected and recorded (Alvarez 1994). 3. Arquipélago das Anavilhanas, Amazonas, tape recorded (Cohn-Haft and BMW).

geles County (LACM). Measurements were made of five males and five females of each population as references. Because we found no evidence of sexual dimorphism in measurements, we combined measurements for both sexes.

Analysis of vocalizations.—Methodology for vocal analyses and a complete list of characters and measures studied were described in Isler et al. (1998). We used all recordings available to us for *pacifica*, *surinamensis*, and *cherriei*, but selected approximately one-half of the larger sample of available recordings of *multostriata* from each locality based on recording quality. Localities and references for each recording are listed in Isler et al. (1998) except for *pacifica* and for additional recordings of *surinamensis*, which are provided in the Appendix. For each vocalization type for each population, we considered recordings from as few as three individuals to be the minimum acceptable for analysis, given that smaller samples faced rigorous statistical tests.

Tests of diagnosability.—Tests of diagnosability of characters and related aspects of methodology were described in Isler et al. (1998). In summary, in comparing populations, discrete characters had to be unambiguously distinguishable by distinct character states, and continuous variables were considered diagnosable only when the character distributions in the samples did not overlap and the distributions met statistical tests concluding that it was highly un-

likely that overlap would occur if sample sizes were larger.

RESULTS

Morphology.—The four taxa were readily diagnosable by female plumage but poorly diagnosable by male plumage (heterogynism; Hellmayr 1929). Plumage characteristics by which at least one pair of taxa differed are provided in Table 1. As noted, *surinamensis* females were either completely unstreaked below or had a breast band of fine streaks, but the localities of 19 museum specimens with fine breast bands did not suggest intermediacy with *multostriata* populations.

The only diagnostic character found among males was that the lower mandible of *cherriei* was black, whereas those of the other three taxa were pale. Although we believe that this difference provides a valid character, because few specimens of *cherriei* exist that identify soft colors, more specimen data and/or observations are needed to confirm that this coloration occurs consistently across age groups and seasons. In addition to bill color, some tendencies helped substantiate the identification of male

TABLE 1. Female plumage characters of taxa in the *Myrmotherula surinamensis* complex (*n* in parentheses). Comparisons of these characters revealed 31 diagnosable differences between pairs of taxa. Alphanumeric color notations were based on Munsell soil color charts.

Character	<i>M. pacifica</i> (>30)	<i>M. surinamensis</i> (>15)	<i>M. multistriata</i> (>15)	<i>M. cherriei</i> (>15)
White interscapular patch	Absent	Present	Present	Absent
Forecrown streaking	Absent (occasional faint hint)	Absent (occasional faint hint)	Absent (occasional faint hint)	Present
Color of crown streaks	Yellow-red-brown 5YR5/8 to 4/6	Yellow-red-brown 5YR5/8 to 4/6	Yellow-red-brown 5YR5/8 to 4/6	Pale-buff 10YR8/4
Crown and nape feathers	Dark centers typically narrower than combined width of light sides	Dark centers about equal to combined width of light sides	Dark centers about equal to combined width of light sides	Dark centers wider than combined width of light sides
Color of breast and throat	Yellow-ochre 10YR7/6 to 7/8, occasionally to 10YR6/8 on breast; becoming pale-buff 10YR8/2 on center of throat	Pale-buff 10YR8/4 to 10YR8/3; becoming whitish on center of throat	Pale-buff 10YR8/4 to 10YR8/3; becoming whitish on center of throat	Between buffy-yellow and pale buff 10YR8/6 to 8/4, including throat
Belly	Center pale-buff 10YR8/3 (rarely whitish), contrasting with breast	Center white, contrasting with breast	Center white, contrasting with breast	Underparts evenly colored throughout
Underpart streaking	Unstreaked	3 from French Guiana and 4 from Guyana lack streaks; 3 from Suriname, 8 from Rio Caura, 1 from Amazonas, Venezuela with band of fine streaks on breast	Numerous black streaks usually extend from throat to upper belly and flanks	Numerous black streaks usually extend from throat to upper belly and flanks
Width of underpart streaks	Absent	Absent or fine	Thin (1 mm or less on breast)	Broad (1.5 to 2 mm on breast)
Black malar streaks	Absent	Absent	Present, thin	Present, broad

specimens: the interscapular patches of male *cherriei* and *pacifica* typically were narrow (less than one-half the width between the scapulars, often only one feather wide), whereas those of *multostriata* and *surinamensis* typically were wide (nearly the entire width between the scapulars); the white tips of the outer rectrices typically were longest (usually 4 to 5 mm) in *cherriei*, shortest (usually 2 to 3 mm) in *multostriata*, and intermediate (usually 3 to 4 mm) in *pacifica* and *surinamensis*; and the black streaks of underparts tended to be narrow (<1 mm) in *multostriata* and wide (>1 mm) in males of the remaining taxa.

A reference set of measurements showed that the four taxa are closely similar in size (Table 2). Exceptions were differences in tail lengths between *surinamensis* and *cherriei* and between *surinamensis* and *pacifica*. Ranges of these pairs of measurements did not overlap, and distributions met our test of diagnosability, but measurement differences were not employed in the diagnosis pending the examination of additional specimens.

Vocalizations.—We identified five types of vocalizations: loudsong (Fig. 4), stereotyped call (Fig. 5A, B), short call (Fig. 5C–H, K), rattle call (Fig. 5I), and chit call (Fig. 5J). All taxa in the *surinamensis* complex delivered the loudsong and short call, the latter so named to distinguish it from the stereotyped call, which was only given by *multostriata* and *surinamensis*, and the rattle call, which was given solely by *surinamensis*. Differences in behavioral function among the five vocalizations were unknown. We found no sexual differences in measurements of vocalizations delivered by both sexes, and data derived from recordings of males and females were combined.

Because it is given by all taxa in the complex, we defined the series of abrupt rattle-like notes shown in Figure 4 as the loudsong. Only males of *multostriata* and *surinamensis* were recorded giving this vocalization, whereas it was delivered by both sexes of *pacifica* and *cherriei*. The stereotyped call (Fig. 5A, B), so named because it has the fixed pattern of a song, was found only in the repertoires of *surinamensis* and *multostriata* and was delivered by both sexes (contra Ridgely and Tudor 1994).

Data for characters that distinguished loudsongs of at least one pair of taxa are provided in Figure 6, and characters distinguishing each

TABLE 2. Reference set of standard measurements of taxa in the *Myrmotherula surinamensis* complex. Values are range, mean \pm standard deviation in mm. Sexes combined. Bill width measured as nares; bill length to nares; wing = chord; tail = central rectrix.

Species (n)	Bill width	Bill depth	Bill	Tarsus	Tail	Wing
<i>M. pacifica</i> (20)	3.3 to 3.9, 3.6 \pm 0.18	3.0 to 3.5, 3.4 \pm 0.15	9.6 to 10.4, 9.9 \pm 0.25	17 to 18, 17.7 \pm 0.50	27 to 30, 28.9 \pm 0.92	48 to 52, 49.6 \pm 1.23
<i>M. multostriata</i> (10)	2.9 to 3.3, 3.1 \pm 0.14	2.9 to 3.2, 3.1 \pm 0.08	8.3 to 9.2, 8.8 \pm 0.32	16 to 18, 16.9 \pm 0.58	24 to 28, 25.2 \pm 1.33	46 to 51, 48.5 \pm 1.47
<i>M. surinamensis</i> (10)	3.1 to 3.6, 3.3 \pm 0.13	2.9 to 3.4, 3.1 \pm 0.12	8.7 to 9.7, 9.1 \pm 0.32	17 to 18, 17.3 \pm 0.46	23 to 25, 24.5 \pm 0.57	46 to 50, 48.6 \pm 1.32
<i>M. cherriei</i> (10)	2.8 to 3.5, 3.2 \pm 0.22	2.9 to 3.3, 3.1 \pm 0.13	9.4 to 10.3, 9.9 \pm 0.26	16 to 17, 16.5 \pm 0.50	27 to 30, 28.7 \pm 1.20	45 to 50, 48.2 \pm 1.60

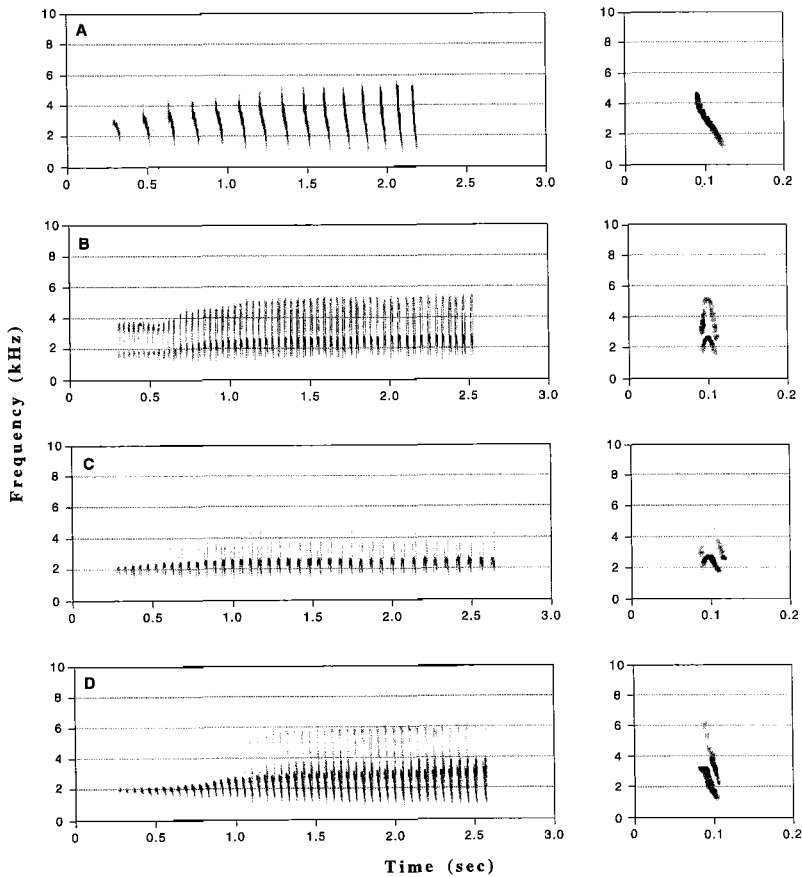


FIG. 4. Loudsongs of taxa in the *Myrmotherula surinamensis* complex. (A) *pacifica*: Rio Palenque, Los Ríos, Ecuador (Parker, ISL-TAP.24:12). (B) *surinamensis*: Raleigh Falls, Suriname (Whitney, ISL-BMW.115:20). (C) *multostriata*: Flor de Oro, Santa Cruz, Bolivia (Parker, ISL-TAP.26:10). (D) *cherriei*: Puerto Ayacucho, Amazonas, Venezuela (Zimmer, ISL-KJZ.21:18). To provide detail, the second-from-last note is shown on an expanded time scale.

pair are identified in Figure 7. Loudsongs of *surinamensis* (Fig. 4B) and *multostriata* (Fig. 4C) did not differ diagnostically. Characters that differentiated loudsongs of the remaining pairs primarily reflected aspects of pace, change in pace, and note structure/tonality. The loudsong of *cherriei* (Fig. 4D) was essentially evenly paced but was sometimes accelerated slightly in the middle; that of *pacifica* (Fig. 4A) accelerated throughout; and those of *multostriata* and *surinamensis* decelerated throughout. Note structure/tonality of *pacifica* and *cherriei* loudsongs were readily diagnosed from each other and from those of *multostriata* and *surinamensis* by note shape and the presence of overtones.

The frequency with which the stereotyped call was found in the recordings suggests that

it has an important, albeit unknown, behavioral function. In our inventory of 89 recordings of *multostriata*, the stereotyped call occurred more often than the loudsong (55 stereotyped calls vs. 43 loudsongs), although proportionately less often in the smaller ($n = 22$) sample of *surinamensis* (8 vs. 11). Stereotyped calls of *surinamensis* and *multostriata* differed diagnostically in note shape (Fig. 5A, B) and overall pace (Fig. 6). In addition, both taxa delivered a note between repetitions of the stereotyped call that we have termed an "interspersed" call, and although this call was not used as a character because of the small sample size for *surinamensis*, the notes of the two taxa appeared to differ in duration, as can be seen in the spectrograms (Fig. 5A, B).

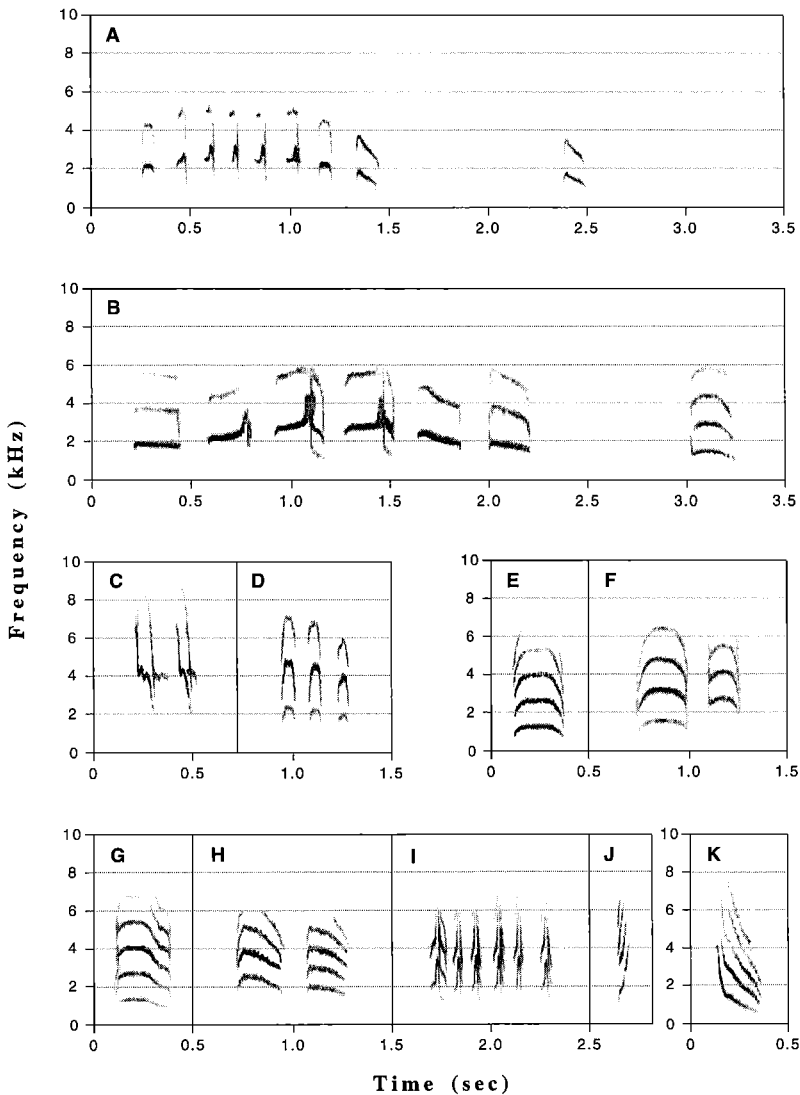


FIG. 5. Calls of taxa in the *Myrmotherula surinamensis* complex. (A) *surinamensis*: stereotyped-call followed by an interspersed-call; Surama, Guyana (Whitney, ISL-BMW.151:14). (B) *multistriata*: stereotyped-call followed by an interspersed-call; Liborio, Loreto, Peru (Whitney, ISL-BMW.93:12). (C) *pacifica*: short call 1 (downslurred and modulated); Cana, Darién, Panama (Whitney, ISL-BMW.11:29). (D) *pacifica*: short call 2 (hill-shaped and unmodulated); Cana, Darién, Panama (Whitney, ISL-BMW.11:29). (E) *multistriata*: short call given singly; Rurópolis, Pará, Brazil (P. Isler, LNS 47945). (F) *multistriata*: short call in a doublet; P. N. Jaú, Amazonas, Brazil (Cohn-Haft, ISL-MCH.2:03). (G) *surinamensis*: short call given singly; Raleigh Falls, Suriname (Whitney, ISL-BMW.20:28). (H) *surinamensis*: short call in a doublet; Guyana Trail, Bolívar, Venezuela (Whitney, ISL-BMW.15:20). (I) *surinamensis*: rattle call; state unknown, Venezuela (Schwartz, LNS 61936). (J) *surinamensis*: chit call; Junglaven, Amazonas, Venezuela (Zimmer, ISL-KJZ.7:36). (K) *cherriei*: short call; Junglaven, Amazonas, Venezuela (Zimmer, ISL-KJZ.18:03).

Short calls were delivered by both sexes of all taxa. The short call of *cherriei* (Fig. 5K) was downslurred, unlike short calls of *surinamensis* and *multistriata*, which were hill-shaped (Fig.

5E–H). Notes of *cherriei* short calls were always given singly, whereas those of *surinamensis* and *multistriata* were delivered in groups of two to four (most often two) as well as singly. Short

Loudsongs	<i>M. cherriei</i> N = 15 individuals and 54 songs	<i>M. s. pacifica</i> N = 27 individuals and 93 songs	<i>M. s. multistriata</i> N=19 individuals and 57 songs	<i>M. s. surinamensis</i> N=11 individuals and 24 songs
Number of Notes				
Number of notes	37-78 [53±8]	8-23 [16±2]	24-102 [40±16]	18-73 [51±15]
Pace				
Overall pace (notes/sec)	19.65-25.56 [22.17±1.24]	6.45-9.18 [7.56±0.62]	13.77-21.48 [16.99±1.77]	17.29-25.41 [21.04±2.02]
Pace of Section 3; loud-song divided into thirds	19.23-24.55 [21.84±1.25]	6.65-10.67 [8.42±0.69]	11.33-19.05 [14.47±1.70]	15.32-23.03 [18.43±2.07]
Change in Pace				
Pace of first section divided by pace of second section	0.90-1.06 (0.97±0.03)	0.84-1.02 (0.91±0.03)	1.07-1.27 (1.16±0.03)	1.09-1.42 [1.17±0.09]
Pace of first section divided by pace of third section	0.91-1.11 (1.01±0.04)	0.60-0.95 (0.82±0.06)	1.23-1.53 (1.34±0.05)	1.16-1.50 [1.31±0.09]
Note Structure/Tonality				
Note Shape	Sharply downslurred, wide frequency band	Sharply downslurred, narrow frequency band	Abrupt chevron	Abrupt chevron
Presence of overtones	Overtones very sharp, almost vertical	No overtones	Overtones reflect note shape	Overtones reflect note shape
Stereotyped-calls	<i>M. cherriei</i> N = 28 recordings	<i>M. s. pacifica</i> N = 21 recordings	<i>M. s. multistriata</i> N = 26 individuals and 72 calls	<i>M. s. surinamensis</i> N = 9 individuals and 34 calls
Presence/absence	Absent	Absent	Present	Present
Pace				
Overall pace			2.4-4.3 [3.4±0.3]	5.9-9.0 [7.2±0.6]
Note Structure/Tonality				
Note shape			Flat "mesa" with complex center notes containing an inverted V towards end of note	Abrupt inverted U or even more sharply peaked inverted V
Short-call Characteristics	<i>M. cherriei</i> N = 14 individuals	<i>M. s. pacifica</i> N = 5 individuals	<i>M. s. multistriata</i> N = 34 individuals	<i>M. s. surinamensis</i> N = 25 individuals
Note Structure/Tonality				
Note shape	Downslurred	Sample inadequate (see text)	Hill-shaped	Hill-shaped
Rattle-call Characteristics	<i>M. cherriei</i> N = 28 recordings	<i>M. s. pacifica</i> N = 21 recordings	<i>M. s. multistriata</i> N = 89 recordings	<i>M. s. surinamensis</i> N = 19 recordings
Presence/absence	Absent	Absent	Absent	Present

FIG. 6. Vocal characters and measures that distinguish at least one pair of taxa within the *Myrmotherula surinamensis* complex. Other characters studied are not shown. Not all pairs are differentiated on all measures; see Figure 7 for findings of diagnostic differences.

calls of *multistriata* and *surinamensis* could not be distinguished. Two types of short calls were recorded for *pacifica*, but their relative commonality was unclear due to small sample sizes. Short-call 1 notes of *pacifica* (Fig. 5C) were downslurred and almost always frequency-modulated but lacked overtones. Short-call 1 was recorded singly (two individuals), in a doublet (two individuals), and in a triplet (one individual). Short-call 2 of *pacifica* (Fig. 5D), the notes of which were hill-shaped and unmodulated but included overtones, was recorded once in a doublet and twice in a triplet. The downslurred short-call 1 of *pacifica* differed from the downslurred call of *cherriei* in lacking overtones and (not perfectly but typically) being shorter and frequency-modulated. The hill-shaped short-call 2 of *pacifica* was more abrupt than the short calls of *multistriata* and *surinamensis*, but sample sizes for *pacifica* short calls were deemed insufficient for the difference to be considered diagnostic.

In addition to short calls, it appeared that most taxa deliver an abrupt chit call. An example is provided in Figure 5 for *surinamensis* (Fig. 5J), and a similar call was recorded for *multistriata*. A possibly homologous call of a slightly different form was on a *cherriei* recording, but we could not be sure that it was not given by another species. Consequently, we did not attempt to use the chit call in the diagnoses.

A rattle call, a series of four to six rapidly delivered, hard notes (Fig. 5I), was delivered by *surinamensis* (*n* = 6). The rattle call was not recorded for other taxa in the complex. A single recording of *multistriata* included a hill-shaped note followed by abrupt notes somewhat resembling the notes of a rattle. We do not believe that this vocalization of *multistriata* is homologous to the rattle call of *surinamensis*, but if it were, it would differ diagnosably in a number of characters.

In summary (Fig. 7), between five and eight vocal characters, some represented by multiple

Plumage Characters	<i>cherriei</i> & <i>surinamensis</i>	<i>cherriei</i> & <i>multostriata</i>	<i>pacifica</i> & <i>surinamensis</i>	<i>pacifica</i> & <i>multostriata</i>	<i>pacifica</i> & <i>cherriei</i>	<i>multostriata</i> & <i>surinamensis</i>
Female						
Interscapular patch	Diagnosable	Diagnosable	Diagnosable	Diagnosable		
Forecrown streaking	Diagnosable	Diagnosable			Diagnosable	
Crown streak color	Diagnosable	Diagnosable			Diagnosable	
Relative width of crown streaks	Diagnosable	Diagnosable	Diagnosable	Diagnosable	Diagnosable	
Underpart coloration	Diagnosable	Diagnosable	Diagnosable	Diagnosable	Diagnosable	
Underpart streaking	Diagnosable	Diagnosable	Diagnosable	Diagnosable	Diagnosable	Diagnosable
Malar streak	Diagnosable	Diagnosable		Diagnosable	Diagnosable	Diagnosable
Male						
Bill color (see text)	Diagnosable	Diagnosable			Diagnosable	

Vocal Characters	<i>cherriei</i> & <i>surinamensis</i>	<i>cherriei</i> & <i>multostriata</i>	<i>pacifica</i> & <i>surinamensis</i>	<i>pacifica</i> & <i>multostriata</i>	<i>pacifica</i> & <i>cherriei</i>	<i>multostriata</i> & <i>surinamensis</i>
Loudsongs						
Number of Notes						
Number of notes					Diagnosable	
Pace						
Overall pace			Diagnosable	Diagnosable	Diagnosable	
Pace of Section 3; loud-song divided into thirds		Diagnosable	Diagnosable	Diagnosable	Diagnosable	
Change in Pace						
Pace of first third divided by pace of second third		Diagnosable	Diagnosable	Diagnosable		
Pace of first third divided by pace of final third	Diagnosable	Diagnosable	Diagnosable	Diagnosable		
Note Structure/ Tonality						
Note shape	Diagnosable	Diagnosable	Diagnosable	Diagnosable	Diagnosable	
Presence of overtones			Diagnosable	Diagnosable	Diagnosable	
Stereotyped-calls						
Presence/Absence	Diagnosable	Diagnosable	Diagnosable	Diagnosable		
Pace						
Overall pace						Diagnosable
Note Structure/Tonality						
Note shape						Diagnosable
Short-calls						
Note Structure/Tonality						
Note shape	Diagnosable	Diagnosable				
Rattle-calls						
Presence/Absence	Diagnosable		Diagnosable			Diagnosable

FIG. 7. Diagnostic plumage and vocal characters that distinguish pairs of taxa within the *Myrmotherula surinamensis* complex.

measures, distinguished all pairs of taxa except *multostriata* and *surinamensis*, which differed in three vocal characters.

DISCUSSION

This paper and its companion (Isler et al. 1998) propose objective methodology and criteria for employing vocal and morphological characters in designating populations as species and subspecies. In relation to the continuing debate concerning species concepts (e.g. Haffer 1992, O'Hara 1993, Zink and McKittrick 1995), aspects of our methodology and findings may be viewed as relevant to the biological species concept or the phylogenetic species concept. Regardless of which concept is employed, we believe that our methodology and the cri-

teria provide a pragmatic means for objectively defining antbird species.

The two sympatric pairs, *cherriei*/*surinamensis* and *cherriei*/*multostriata*, were distinguished by 13 and 14 plumage and vocal characters respectively (Fig. 7). Twelve plumage and vocal characters distinguished *pacifica* from each of *cherriei*, *surinamensis*, and *multostriata*. The diagnostic characters distinguishing *pacifica*, comparable in number and type to those distinguishing the sympatric pairs, provide a solid basis for consideration of species status.

Diagnostic plumage and vocal differences between *multostriata* and *surinamensis* were fewer (Fig. 7). These differences are of particular interest because they constitute a minimal example of the satisfaction of the proposed criteria for species designation. Plumages of fe-

males of the two taxa were considered diagnosable despite the presence of two conditions that require discussion. First, fine streaks were found on the breasts of some *surinamensis* females that might suggest intermediacy, but this was contraindicated by the scattered geographic distribution of these finely streaked specimens. Second, a contact zone with hybridization between *multostriata* and *surinamensis* might occur in eastern Colombia, which is poorly known ornithologically. Although such a contact zone is a possibility, it seems more reasonable to assume that an interstitial region in which neither taxon occurs will be found because of the apparent presence of such a region in the adjoining Rio Negro region of Brazil, which is relatively well studied. It may also be relevant that neither species was found in an extensive ornithological survey by the Museo Paraense Emílio Goeldi (MPEG) along the Rio Japurá, which lies about halfway between the upper Rio Negro and Leticia, Colombia. Better knowledge of the geographic relationship between *surinamensis* and *multostriata* would contribute to an understanding of the pattern of interface between Guianan and Amazonian birds, which is among the least known aspects of Amazonian avian biogeography.

With regard to vocalizations, the presence or absence of a rattle call, one of three diagnostic characters for separating *multostriata* and *surinamensis*, also requires further consideration. The absence of a vocalization must be used with care in diagnoses because of the possibility that it is a sampling artifact. We believe that the evidence is overwhelming in this case, because the rattle call was absent in all 89 recordings of *multostriata* but present in 6 of 19 recordings of *surinamensis*. The probability that this difference occurred by chance is extremely slight.

In light of the minimal differences between *multostriata* and *surinamensis*, however, we suggest that efforts be made to develop more information about this pair of taxa including: (1) molecular analyses; (2) additional vocalization recordings for *surinamensis*; (3) greater understanding of the behavioral functions of the different types of vocalizations, especially the stereotyped call and rattle call that distinguish *multostriata* and *surinamensis*; (4) additional specimens as well as vocalization recordings of the population of *surinamensis* in Amazonas,

Venezuela, which has the greatest likelihood of being intermediate between the two forms; and (5) more distributional knowledge, especially in eastern Colombia, to verify the apparent gap between the geographic ranges of the two taxa.

While this paper was in press, M. Lentino and R. Restall (pers. comm.) identified (based on plumage characters described herein) in the Colección Ornithological Phelps females of *surinamensis* and *multostriata* collected near San Fernando de Atabapo, Amazonas, Venezuela. The apparent sympatry of the two taxa suggests that additional fieldwork in this region should confirm or refute species status.

CONCLUSIONS

Analysis and discussion of phylogenetic relationships among the four taxa must await additional study of related groups. However, it is noteworthy that the same number of characters separated *pacifica* and *cherriei* as distinguished *pacifica* from *surinamensis* and *multostriata*, and the assumption, implicit in current taxonomies, that *pacifica* is closer to *multostriata* and *surinamensis* than to *cherriei* is not supported. On the other hand, the likelihood of a sister relationship between *multostriata* and *surinamensis* is supported by the data.

Myrmotherula cherriei, *M. pacifica*, *M. multostriata*, and *M. surinamensis* differ from one another in diagnosable vocal and morphological characters of sufficient magnitude, under our proposed criteria, to be considered distinct species. Thus, we submit that the complex consists of four species as follows:

Myrmotherula cherriei Berlepsch and Hartert
Cherrie's Antwren

Myrmotherula pacifica Hellmayr
Pacific Antwren

Myrmotherula multostriata Sclater
Guianan Streaked-Antwren

Myrmotherula surinamensis (Gmelin)
Amazonian Streaked-Antwren

With regard to the English name of *pacifica*, we recommend Pacific Antwren rather than Pacific Streaked-Antwren, suggested by Ridgely and Tudor (1994), which implies that *pacifica* is closely related to *surinamensis* and *multostriata*. The maintenance of streaked-antwren in the English names for *multostriata* and *surinamensis*

seems appropriate because our results suggest that they are sister species.

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APPENDIX. Vocalization recordings examined. The inventory of recordings examined for all taxa was provided in Isler et al. (1998; appendix) except for *Myrmotherula pacifica* and for new recordings of *M. surinamensis* that are provided below. Acronyms for recording archives: FSM = Florida State Museum Sound Archive, Gainesville; LNS = Library of Natural Sounds, Cornell Laboratory of Ornithology, Ithaca, New York; ISL = recordings not yet archived in an institutional collection but that have been copied into the inventory maintained by the Islers.

Myrmotherula pacifica PANAMA: Canal Zone: (K. Zimmer 1, ISL; B. Whitney 1, ISL). Darién: Cana (B. Whitney 2, ISL). San Blas: Nusugandi (B. Whitney 1, ISL). COLOMBIA: Córdoba: Rio Verde del Sinú (S. Hilty 1, ISL). Valle: Anchicayá (B. Coffey 1, ISL). Buenaventura (B. Whitney 1, ISL). ECUADOR: Esmeraldas: Cerro Mutilus (T. Parker 1, ISL), Lita (B. Whitney 2, ISL, LNS). Pichincha: Tinalandia (R. Behrstock 1, ISL; G. Clayton 1, FSM; B. Coffey 2, ISL; J. Hardy 1, FSM; G. Rosenberg 1, ISL; A. van den Berg 1, LNS; K. Zimmer 1, ISL). Los Ríos: Rio Palenque (T. Parker 1, ISL). Departamento unknown (J. Fjeldså 1, ISL).

Myrmotherula surinamensis Recordings added since Isler et al. (1998); GUYANA: (B. Whitney 3, ISL).
