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USE OF VOCALIZATIONS TO ESTABLISH SPECIES LIMITS IN ANTBIRDS (PASSERIFORMES: THAMNOPHILIDAE)

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ABSTRACT.—We introduce an empirically derived methodology for the definition, measurement, and application of vocal characters in assessing species limits in the numerically important Neotropical family Thamnophilidae. On the basis of available evidence, we assume that vocalizations are innate and that all vocal characters have a role in maintenance of species integrity in thamnophilids. Vocalizations of eight syntopic pairs, the members of which resemble one another in both plumage and voice, were analyzed to identify diagnosable vocal characters. To be diagnosable, characters had to distinguish members of a pair unambiguously. Three of the eight pairs were diagnosable by three vocal characters, four pairs by four characters, and one pair by seven characters. Vocalizations differed most consistently by characters reflecting loudsong note structure, loudsong pace, and note structure of calls. In establishing species limits for allopatric antbird populations, we suggest that three vocal characters, the minimum number distinguishing the syntopic pairs, be used as a point of reference. Keeping this point of reference in mind, we recommend that multiple diagnosable vocal characters be present when vocalizations are a major factor in determining species limits in thamnophilid antbirds. To the extent that populations differ strongly in other characters (e.g. morphological, molecular, other behavioral), fewer vocal characters may suffice. The identification of multiple vocal characters as a point of reference, as opposed to individual characters (e.g. note shape) or vocalization types (e.g. the loudsong), allows for greater latitude in the diagnosis. A focus on the number of characters is appropriate given the possibility that the role and importance of vocalization types in species' repertoires may differ across groups of taxa. The methodology and results may also have application in the study of other avian groups in which vocalizations are innate, especially the suboscines. *Received 16 September 1997, accepted 2 February 1998.*

THE CONSISTENT DEFINITION OF SPECIES is a necessary foundation for systematic, zoogeographic, ecological, and conservation research. The Neotropics are home to more species of birds than any other region and support the most diverse ecosystems on earth (see Stotz et al. 1996). Among Neotropical birds, recent studies (Robbins and Ridgely 1992, Willis 1992, Prum 1994, Whitney et al. 1995, Bierregaard et al. 1997, Isler et al. 1997, Krabbe and Schulenberg 1997, Zimmer 1997) exemplify a growing concern that many taxa presently considered subspecies are more appropriately recognized at the species level. Additionally, undescribed but diagnosable populations are known to exist (Fjeldså and Krabbe 1990, Whitney 1994, Brumfield and Remsen 1996). One of the numerically most important families of Neotropical birds is the Thamnophilidae (sensu AOU 1997), repre-sented by 35 to 50 sympatric species in Amazonian forest localities. As with other Neotropical birds, their current ranking into species and subspecies was established by Hellmayr (Cory and Hellmayr 1924), Zimmer (1931 and subsequent papers), and more recent authors solely on assumptions of the significance of differences and similarities in plumage and external measurements. Furthermore, as Mayr (1982) noted, "every isolated 'species' was . . . scrutinized for the possibility that it was simply a geographic representative of some other species, in which case it was reduced to the rank of subspecies." The resulting judgments were unavoidably inconsistent and sometimes highly arbitrary.

Since these decisions were made, and especially over the past 20 years, knowledge of Neotropical birds has been augmented greatly. New specimens clarify our understanding of morphological variation and distribution. Molecular evidence regarding genetic variation

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among thamnophilid populations also is beginning to emerge (Capparella 1987, Hackett and Rosenberg 1990, Hackett 1993, Bates 1995, Brumfield and Capparella 1996). Thanks to a growing body of new information from the field, we now have the opportunity to consider vocalizations, behavior, and ecology together with morphology and patterns of distribution in assessing taxonomic rank and systematic relationships. Of all the newly emerging data sets complementing the study of specimens, that of vocalizations is the most complete. We now have in hand an inventory of nearly 9,000 recordings of thamnophilid antbirds, contributed by many field workers.

The use of vocalizations in avian systematics studies has been reviewed by Becker (1982) and Payne (1986). One potential problem with the use of vocal characters as a guide to species relationships is the possible effect of song learning. In this respect, it is important to distinguish between oscines, among which several elements of song learning have been documented, and suboscines, among which there is no evidence of song learning (Kroodsma and Konishi 1991). Experimental evidence that vocalizations are innate in one family of suboscines, the Tyrannidae, is substantial and convincing (Kroodsma 1984, 1985, 1989). In addition, neurological evidence indicates that a motor pathway in the anterior brain is essential for song learning (Brenowitz and Kroodsma 1996), and that the cell clusters that control song production in oscine forebrains are absent in at least one tyrannid studied (Kroodsma and Konishi 1991). Evidence for the lack of vocal learning in suboscines is supplemented by a finding of geographic congruence between genetic and vocal differentiation of a tyrannid complex (Johnson 1980, Johnson and Marten 1988) and by field observations, prominent among which are studies demonstrating the lack of geographic variation in tyrannid songs (e.g. Lanyon 1978).

The lack of within-taxon geographic variation in vocalizations is as evident in the Thamnophilidae (Whitney et al. pers. obs.) as in the Tyrannidae. E. S. Morton (in Kroodsma 1984) hand-reared a Barred Antshrike (Thamnophilus doliatus) from seven days of age whose fledgling calls were similar and adult song identical by ear to those of birds in nature. Furthermore, vocal differences among antbirds appear to ac-

company findings of large genetic distances. For example, large molecular distances found in the Black-faced Antbird (Myrmoborus myotherinus) across the Amazon River just east of the Rio Napo (Capparella 1987) are being corroborated by vocalizations (Isler et al. unpubl. data). In a related suboscine family, the Rhinocryptidae, genetically differentiated populations in the genus Scytalopus have distinctive songs even though the taxa are barely distinguishable morphologically (Arctander and Fjeldså 1994).

The greater diversity of syringeal morphology in suboscines, as compared with oscines, has been suggested to result from natural or sexual selection on suboscine vocalizations (Prum 1992). Our principal understanding of the particular vocalizations that serve in the process of antbird pair formation comes from a study by Morton (1996), who experimentally removed mates of Dusky Antbirds (Cercomacra tyrannina). Morton and his colleagues found that the survivors delivered what Morton has termed a "courtship song." In the case of females, the songs differed substantially from those delivered by paired females, and they incorporated elements of the male song. However, vocal characters employed in this paper (e.g. note shape, pace) do not appear to differ appreciably between the courtship songs and the loudsongs of paired individuals (Morton 1996: figure 14.1).

Thus, based on available evidence, we assume that vocalizations in thamnophilid antbirds are innate, have an important role in the maintenance of species integrity, and can serve as characters by which populations can be diagnosed. To date, however, taxonomic studies have lacked a consistent methodology for employing vocal characters in assessing species limits in antbirds and other suboscines, especially for allopatric populations. Here, we present such a methodology through analysis of songs and calls of eight syntopic pairs of congeneric species of antbirds.

METHODS

SELECTION OF SUBJECTS

Criteria for selecting species and study areas.—We reviewed all thamnophilid antbirds systematically to identify the congeneric pairs of syntopic species that looked and sounded most alike. To be considered

syntopic, pairs had to live in sufficiently close proximity to hear each other's vocalizations and thus potentially interbreed, regardless of whether their microhabitats differed. We sought pairs whose plumage was not highly differentiated on the premise that if congeners look at least superficially alike, their vocalizations are likely to be important in species recognition (Stein 1963, Lanyon 1978). Of these morphologically similar pairs, we gave priority to those that resembled one another vocally, seeking pairs that were likely to be closely related. Eight pairs (including the same pair from two regions) of antbirds were selected that best met these criteria and for which we had sufficient recordings. Recordings were selected from as small a region of sympatry as possible to obtain approximately 10 recordings of each species. Confining our sample to a restricted region allowed us to minimize anomalies introduced by unstudied geographic variation. We employed all available recordings within the designated regions. Recording locations are identified in the Appendix. Unless stated otherwise, observations of syntopy were derived from personal experience. The eight pairs and regions are listed below.

Thamnophilus doliatus/T. palliatus.—Although they mostly replace one another in a checkerboard pattern, T. A. Parker III (pers. comm.) noted *T. doliatus* and *T. palliatus* in syntopy at Perseverancia (northern Santa Cruz, Bolivia), and S. Herzog (pers. comm.) found both species in the Rio Masicuri valley (southwestern Santa Cruz). Their habitat preferences differed, but Parker found the two species within hearing distance, and Herzog felt that *T. doliatus* and *T. palliatus* undoubtedly come within hearing distance. Recordings were from Santa Cruz and La Paz, Bolivia, and Rondônia, Brazil.

Thamnophilus schistaceus/T. murinus.—These species are sympatric over a large region of western Amazonia. Despite possible habitat differences, voices of the two species are often heard together. Recordings used were from the region of the Rio Napo and Rio Tigre in northern Peru and eastern Ecuador.

Dysithamnus mentalis/D. stictothorax.—These species overlap in southeastern Brazil and are often observed in the same mixed-species flocks. Recordings were taken from the entire region of sympatry.

Myrmotherula brachyura/M. obscura.—These species are sympatric throughout the range of *M. obscura* in western Amazonia. Vocalizations of the two species are frequently heard together, and habitat differences between them are unclear. All recordings came from the vicinity of Quebrada Sucusari on the left bank of the Rio Napo in Loreto, Peru.

Myrmotherula surinamensis/M. cherriei.—These species are syntopic in Amazonas, Venezuela (Zimmer and Hilty 1997), and northern Peru (Alvarez 1994) where both species have been found in the same location although not at the same time of year

(B. Whitney pers. obs.). Two named *M. surinamensis* subspecies (*surinamensis* and *multostriata*) are involved. Consequently, *M. cherriei* vocalizations were compared separately with those of both subspecies. A paucity of recordings from known regions of syntopy required that we use all available recordings of *M. s. surinamensis* and *M. cherriei* and a geographically balanced sample from the entire range of *M. s. multostriata*.

Myrmoborus leucophrys/M. myotherinus.— These species are sympatric over a large region. In general, *M. leucophrys* inhabits river-edge and seasonally flooded forest, and *M. myotherinus* terra firme forest, but the two are often found together at ecotones. The recordings in our sample were from southeastern Peru, northwestern Bolivia, and Acre, Brazil.

Hypocnemis cantator/H. hypoxantha.—These species often occur in syntopy in western Amazonia and to the east in the region between the Rio Tapajós and Rio Xingu in central Brazil. We examined recordings from both regions. The sample from Region 1 was confined to the area around the mouth of the Rio Napo, north of the Rio Amazonas, Loreto, Peru (*H. c. saturata* and *H. h. hypoxantha*). In Region 2, the *H. hypoxantha* (*H. h. ochraceiventer*) sample was drawn from the area east of the Rio Tapajós from Santarém to the vicinity of Rurópolis, Pará, Brazil. To obtain a sufficient sample of *H. cantator* (*H. c. striata*), this area was extended (east of the Rio Tapajós) south to the Rio Cristalino, extreme northern Mato Grosso.

VOCALIZATION ANALYSIS PROCEDURES

We assumed that all vocalization types are relevant, that birds hear sounds in the same frequency range as do humans, and that birds have an ability to discriminate among differences in frequency and time intervals, the principal variables expressed in spectrograms (Dooling 1982). Series of notes delivered loudly by thamnophilid antbirds, usually throughout the year in the equatorial region, were termed loudsongs (following Willis 1967) to distinguish them from other vocalizations that fit the general definition of songs. Recordings were obtained from archives and individuals listed in the Appendix. We initially viewed every recording in its entirety as a real-time spectrogram on a Uniscan II (Multigon Industries) to identify the number and sex of individuals vocalizing and to label each vocalization as to type. At the initial viewing, we screened recordings for the following: (1) recordings that were unmeasurable because of "over-recording" (gain set too high) or because the signal was too faint; (2) rerecording of an individual (which would have distorted the sample size); (3) erroneous documentation (e.g. identification of sex appeared to be incorrect); and (4) premature termination of a multinote vocalization, as can happen when a bird is startled.

Following the screening procedure, we used Canary 1.2 (Bioacoustics Research Program, Cornell Laboratory of Ornithology) to obtain measurements and descriptive data from each recording. The default settings of Canary were maintained except that the display style employed was smooth rather than boxy, and overlap was set at 96.88% in preparing spectrograms for figures. Brightness and contrast settings were adjusted for each recording to match recording levels. Most recordings included repetitions of the same vocalization type by the same individual. We typically measured the first three repetitions and every third one thereafter. Measurements for each repetition were entered as one record in an Access (Microsoft Corporation) database application. Ranges, means, and standard deviations were calculated in the database for each individual and for species. Spectrograms chosen for figures reflected central tendencies in key vocal characteristics. Information entered for individual records included sex and whether the recording was made after playback. Because of possible differences between sexes (Ratcliffe and Otter 1996), measurements were initially sorted for each type of vocalization by sex, and records were aggregated only if no significant sexual differences were identified. Some antbirds are rarely identifiable to sex, in which case it was necessary to use all recordings regardless of sex. Finally, we analyzed at least one well-documented recording (if available) of an individual vocalizing naturally and after playback to determine whether vocalizations differed between these two circumstances.

VOCAL CHARACTERS STUDIED

We studied a standard set of vocal characters and measures. Characters were defined to reflect independent features of vocalizations. Typically, multiple measures were taken that reflected the same character. If two or more overlapping measures were diagnosable, we employed the one that appeared to be most reflective of the character.

Number of notes.—A note was defined as an unbroken trace on a spectrogram, including associated overtones.

Duration of vocalization.—Duration was measured in seconds, expressed to the nearest hundredth, from the beginning of the first note to the end of the last note.

Pace.—Pace was defined as the number of notes per second. Overall pace was computed by counting the number of notes and measuring the duration from the beginning of the first note to the beginning of the last note. We also divided lengthier vocalizations into three or five (depending on complexity) approximately time-equivalent sections and computed the pace for each section.

Change in pace.—To obtain measures of how the pace of a lengthy vocalization changed (e.g. speeded up or slowed down), we calculated ratios between the pace of sections as defined above. We also compared the duration of representative notes and internote intervals that followed them. For example, we divided the duration of the second note and the following interval by the duration of the second-from-last note and interval.

Frequency.—To provide a measure of the overall frequency, we used the peak frequency measurement of Canary, which is the frequency at the point of highest amplitude (Charif et al. 1995).

Change in frequency.—Using sections defined for pace measurements, we obtained peak frequencies within each section of long vocalizations. These were examined for consistent differences in pattern, such as increase in the frequency of the vocalization of one species and decrease in frequency of the other. If possible, given the structure of the notes, we also manipulated the Canary screen cursors to ascertain change of frequency of individual notes (obtaining the frequency of each, for example, at the peak of the note).

Amplitude.—The point in time of highest amplitude ("peak time," as defined by Canary) was expressed as a percentage of total duration of the vocalization. Raw amplitude was not compared because there is no way to calibrate the recording levels set by recordists nor the attenuating effects of the recording environment.

Change in amplitude.—Using sections defined for pace measurements, we obtained "Average Intensity" (as calculated by Canary) for each section of lengthy vocalizations. We compared these to ascertain whether there were consistent differences in pattern, such as when one species consistently became louder and the other's vocalization declined in amplitude.

Note structure and tonality.—Individual notes were measured for duration and examined visually for distinctions in note shape (e.g. upslurred or hill-shaped) and tonality. Measures of tonality (Baptista 1996) included the presence or absence of: (1) "noise," (2) overtones, and (3) minute frequency modulations. "Noise" was defined as a random mixture of audio frequencies that made a note sound dissonant. Overtones appeared as separate and simultaneous traces on a spectrogram, one above the other. Because overtones may be generated by recording equipment, consistency in the entire set of spectrograms was required. Frequency modulated notes produced a spectrogram trace looking like a "zigzag" sewing machine stitch and sounded warbled or harsh. To be considered frequency-modulated, a note had to exhibit a clear pattern of regularly spaced modulation at an analysis resolution setting of 349.70 Hz filter bandwidth in Canary. This filter bandwidth permitted obvious frequency modulations to be observed clearly, while rejecting spurious modulations.

Change in note structure and tonality.—We looked for consistent patterns of change in the foregoing measures of note structure and tonality. Examples of measures were the point in a series when simple notes become frequency modulated, or when down-slurred notes become hill-shaped.

Syntax.—Syntax was defined as the order in which notes were arranged, including distinctive notes such as doublets or the final "barks" of some antbird loudsongs. Measures of syntax were qualitative or quantitative depending on circumstances.

CRITERIA FOR ESTABLISHING DIAGNOSABILITY

In comparing two populations, measures were said to differ diagnosably only when they distinguished every vocalization with certainty. This meant that with regard to continuous variables, such as note duration, ranges of measurements obtained for the two populations could not overlap. In order to give equal weight to individuals, means were computed for the sample of vocalizations for each individual and became the sample points from which ranges, means, and standard deviations were computed. Differences in discrete variables determined visually, such as note shape, were considered diagnosable only when the character could be used unequivocally to identify every spectrogram to species. If it was possible that vocalizations would be indistinguishable with small modifications, such as in note structure, diagnosability was rejected.

When the range of observed variation of continuous variables did not overlap, the measures (except for pace ratios, which are not normally distributed) had to meet a second criterion. Namely, means ($\bar{x}$) and standard deviations (SD) of the population with the smaller set of measurements (*a*) and the population with the larger set of measurements (*b*) had to meet the requirement:

$$\bar{x}_a + t_a \, SD_a \leq \bar{x}_b - t_b \, SD_b, \qquad (1)$$

where t_i = the *t*-score at the 97.5 percentile of the *t* distribution for $n - 1$ degrees of freedom. The *t* distribution was used to take into account sampling effect for sample sizes of less than 30. This criterion provided a test of whether overlap was likely to be found if samples had been larger. This method is substantially more discriminating than the familiar *t*-test because it uses the SD of the sample points, not the much smaller SD of the population mean.

RESULTS

Qualitative differences resulting from analyses of the eight syntopic pairs are exemplified in sound spectrograms. Quantitative data are expressed in ranges, means, and standard deviations, where appropriate, for characters that

yielded diagnostic differences. Full data sets are available from the authors. It is important to recall that the diagnoses relate to specific geographic regions (as defined above) and may not be relevant to other populations. Two results generally apply. First, diagnostic characters did not vary significantly before and after playback. The principal outcome of playback was shortened time between loudsong repetitions, a character not employed in the analysis because it was so variable. Second, individual variation within populations was expressed primarily in the number of notes and duration of loudsongs. However, as seen in the ranges and standard deviations in the diagnoses, some individual variation existed in nearly all quantitative measures.

Thamnophilus doliatus/T. palliatus.—Three characters distinguished the loudsongs (Fig. 1A, B): (1) note structure (initial notes were downslurred for *doliatus* and hill-shaped for *palliatus*); (2) change in note structure (setting aside the long downslurred end note, notes of *doliatus* changed shape, whereas those of *palliatus* were similar throughout); and (3) change in pace (notes of *palliatus* became shorter and therefore accelerated more rapidly). Change in pace of the loudsong was measured as the ratio of the duration of the second note and interval divided by the next-to-last note and interval. Corresponding ratios for *T. doliatus* (41 vocalizations from 13 individuals) ranged from 1.62 to 2.05, whereas those for *T. palliatus* (37 vocalizations from 11 individuals) ranged from 2.58 to 3.66. Recordings of calls from the study region were insufficient for analysis.

Thamnophilus schistaceus/T. murinus.—Loudsongs (Fig. 1C, E) were distinguished only by change in note structure; notes of *T. schistaceus* (46 vocalizations from 13 individuals) retained the same basic shape and typically dropped in frequency at the end, whereas those of *T. murinus* (47 vocalizations from 21 individuals) became more upslurred as the song progressed. The "caw" calls (Fig. 1D, F) differed in two characters: (1) duration (call of *murinus* was abrupt); and (2) note structure (call of *schistaceus* was flat and slightly downslurred, whereas that of *murinus* was hill-shaped). The mean duration of the "caw" call was 0.44 ± SD of 0.03 s (range 0.40 to 0.49) for *T. schistaceus* (41 vocalizations from 13 individuals) and 0.13 ±
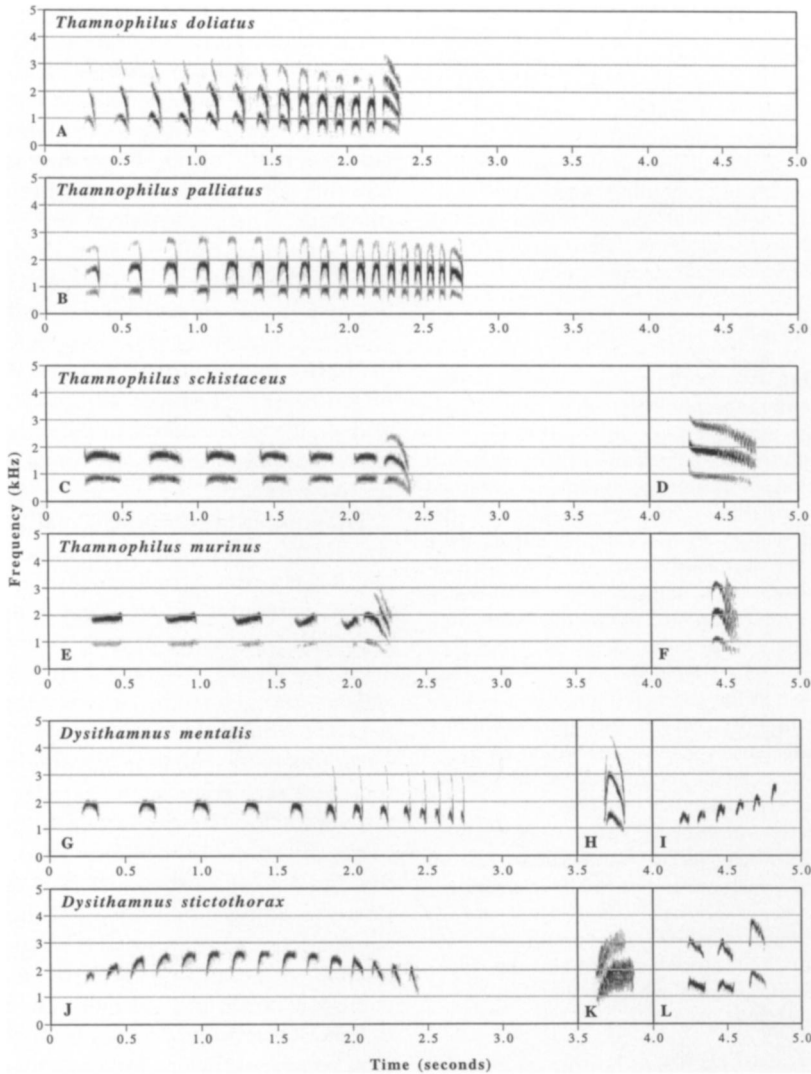
FIG. 1.   Sound spectrograms of antbird species. (A) *Thamnophilus doliatus* loudsong, Santa Cruz, Bolivia. (B) *T. palliatus* loudsong, Santa Cruz. (C) *T. schistaceus* loudsong, Napo, Ecuador, and (D) "caw" call, Loreto, Peru. (E) *T. murinus* loudsong, Loreto, and (F) "caw" call, Loreto. (G) *Dysithamnus mentalis* loudsong, Rio de Janeiro, Brazil, (H) short call, São Paulo, Brazil, and (I) multisyllabic call, Rio de Janeiro. (J) *D. stictothorax* loudsong, Rio de Janeiro, (K) short call, Espírito Santo, Brazil, and (L) multisyllabic call, Rio de Janeiro.

0.03 s (range 0.09 to 0.16) for *T. murinus* (15 vocalizations from 4 individuals).

Dysithamnus mentalis/D. stictothorax.— Three characters distinguished the loudsongs (Fig. 1G, J): (1) pace (the initial sections of *mentalis* loudsongs were slower); (2) change in pace (loudsongs of *mentalis* accelerated in pace throughout, whereas those of *stictothorax* maintained a steady pace, accelerating slightly only through the final 0.5 s); and (3) change in frequency (peaks of notes decreased slightly throughout the song of *mentalis* but increased and then decreased in *stictothorax*). To measure pace and change in pace, vocalizations were divided into five sections. The mean value of the pace of the first section was 2.83 ± 0.25 notes/s (range 2.47 to 3.36) for *D. mentalis* (40 vocalizations from 12 individuals) and 6.27 ± 0.63 notes/s (range 5.19 to 7.91) for *D. stictothorax* (77 vocalizations from 26 individuals). When
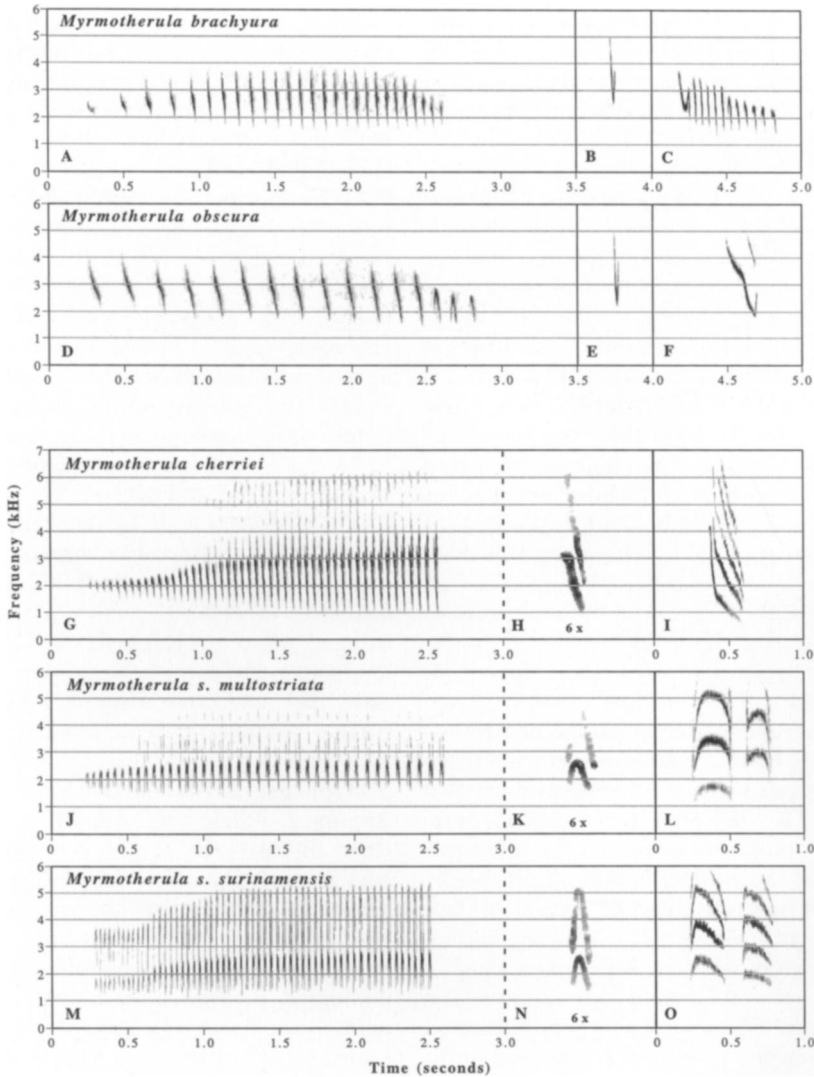
FIG. 2.   Sound spectrograms of antbirds. (A) *Myrmotherula brachyura* loudsong, (B) abrupt call, and (C) stereotyped trill, all from Loreto, Peru. (D) *M. obscura* loudsong, (E) abrupt call, and (F) downslurred call, all from Loreto. (G) *M. cherriei* loudsong, (H) with lengthened note, Amazonas, Venezuela, and (I) downslurred call, Amazonas, Venezuela. (J) *M. surinamensis multostriata* loudsong, (K) with lengthened note, Santa Cruz, Bolivia, and (L) hill-shaped call, Amazonas, Brazil. (M) *M. s. surinamensis* loudsong, (N) with lengthened note, Suriname, and (O) hill-shaped call, Amazonas, Venezuela.

the pace of first section was divided by the pace of the fifth section in order to obtain a measure of change in pace, ratios of 0.21 to 0.43 were obtained for *D. mentalis* and 0.61 to 0.93 for *D. stictothorax*. Short calls (Fig. 1H, K) differed in note structure and tonality; those of *D. mentalis* (4 individuals) were hill-shaped and clear, whereas those of *D. stictothorax* (13 individuals) were upslurred or flat and frequency modulated.

Multisyllabic calls (Fig. 1I, L) also appeared to differ, but sample sizes were inadequate for inclusion in the analysis.

Myrmotherula brachyura/M. obscura.— Three characters distinguished the loudsongs (Fig. 2A, D): (1) pace (the *brachyura* loudsong was faster); (2) change of pace (the *obscura* loudsong speeded up more); and (3) note shape (central notes of *brachyura* loudsongs were

short and sharply downslurred sounding un-
musical to the human ear, whereas those of *ob-
scura* were longer and less steeply downslur-
red, having a more musical quality). The mean
value of the overall pace of loudsong for *M.
brachyura* (21 vocalizations from 11 individu-
als) was 11.34 ± 0.74 (range 10.04 to 12.39) and
for *M. obscura* (41 vocalizations from 19 indi-
viduals) was 6.11 ± 0.58 (range 5.21 to 7.05).
Dividing loudsongs into fifths to obtain a mea-
sure of the change of pace, the range of ratios
of the pace of the first section divided by the
pace of the fourth section was 0.40 to 0.52 for
M. brachyura and 0.55 to 0.77 for *M. obscura*. The
abrupt call (Fig. 2B, E) of the two species ap-
peared to be identical. The stereotyped trill of
M. brachyura (Fig. 2C) has not been recorded for
M. obscura from any region, and its presence or
absence was considered a character. However,
we did not employ the lack of the downslurred
call of *M. obscura* (Fig. 2F) in the repertoire of
M. brachyura as a character because a similar
call appears to occur in other populations of *M.
brachyura* and will require further study.

Myrmotherula surinamensis/M. cherriei.—
The loudsong of *M. cherriei* differed from those
of both subspecies of *M. surinamensis* in two
characters (Fig. 2G, H, J, K, M, N): (1) note
shape (notes of *cherriei* were sharply downslur-
red, whereas those of *surinamensis* subspecies
were abrupt chevrons); and (2) change of pace
(loudsongs of *cherriei* were evenly paced,
whereas those of *M. s. surinamensis* and *M. s.
multostriata* slowed in pace throughout). The
change in pace of the loudsong was measured
as the ratio of the pace of the first section di-
vided by the pace of the third section (vocali-
zations divided into three sections). Corre-
sponding values for *M. cherriei* (54 vocaliza-
tions from 15 individuals) ranged from 0.91 to
1.11, whereas those for *M. s. multostriata* (57 vo-
calizations from 19 individuals) ranged from
1.23 to 1.53, and those for *M. s. surinamensis* (24
vocalizations from 11 individuals) ranged from
1.16 to 1.50.

Short calls (Fig. 2I, L, O) differed in note
shape; the short call of *M. cherriei* (14 individ-
uals) was downslurred, whereas those of *M. s.
multostriata* (34 individuals) and *M. s. surina-
mensis* (25 individuals) were hill-shaped. Fi-
nally, the repertoires of *M. s. surinamensis* (19
recordings) and *M. s. multostriata* (89 record-
ings) included a stereotyped call (not illustrat-

ed) that was absent from the repertoire of *M.
cherriei* (28 recordings). Additional characters
that distinguish *M. cherriei* from only one of the
two *M. surinamensis* subspecies are omitted
from this summary but will be described in a
subsequent analysis.

**Myrmoborus leucophrys/M. myotheri-
nus.—**Three characters distinguished the loud-
songs of males (Fig. 3A, B, C, D): (1) number of
notes (loudsong of *leucophrys* contained more
notes); (2) pace (*leucophrys* loudsongs were fast-
er-paced); and (3) note shape (notes were di-
agnostically longer in the *myotherinus* loud-
song). The corresponding mean number of
notes in the loudsong was 45.4 ± 6.4 (range 28
to 54) for *M. leucophrys* (39 vocalizations from
14 individuals) and 10.7 ± 1.6 (range 8.0 to
13.4) for *M. myotherinus* (50 vocalizations from
11 individuals). The mean overall pace of loud-
songs was 10.47 ± 0.94 for *M. leucophrys* (range
8.73 to 11.93) and 3.15 ± 0.33 for *M. myotherinus*
(range 2.68 to 3.74). Females delivered shorter
loudsongs, but sample sizes were insufficient.
Calls did not differ diagnosably but deserve
further comparative study when larger sam-
ples are available.

**Hypocnemis cantator/H. hypoxantha from
Region 1.—**Male loudsongs (Fig. 3E, G) dif-
fered in three characters: (1) change of pace
(the second half of *cantator* loudsong became
slower as notes become longer, whereas that of
hypoxantha was more evenly paced); (2) note
shape (initial notes downslurred in *cantator* and
upslurred in *hypoxantha*); and (3) change in
note shape (notes changed shape throughout
loudsong of *cantator* and, after initial notes, *hy-
poxantha* notes maintained same shape).
Change in pace of the loudsong was measured
as the ratio of the duration of the middle note
divided by the duration of the next-to-last note.
Corresponding values for *H. cantator* (39 vocal-
izations from 9 individuals) ranged from 0.60
to 0.73, whereas those for *H. hypoxantha* (44 vo-
calizations from 9 individuals) ranged from
0.87 to 0.99. Female songs also seemed to differ,
but sample sizes were inadequate for analysis.

Calls of both *H. cantator* (10 vocalizations
from 6 individuals) and *H. hypoxantha* (24 vo-
calizations from 3 individuals) included three
(sometimes one, two, or four) notes. Three-note
calls (Fig. 3F, H) differed in: (1) pace (*cantator*
delivered notes more slowly); (2) pattern of fre-
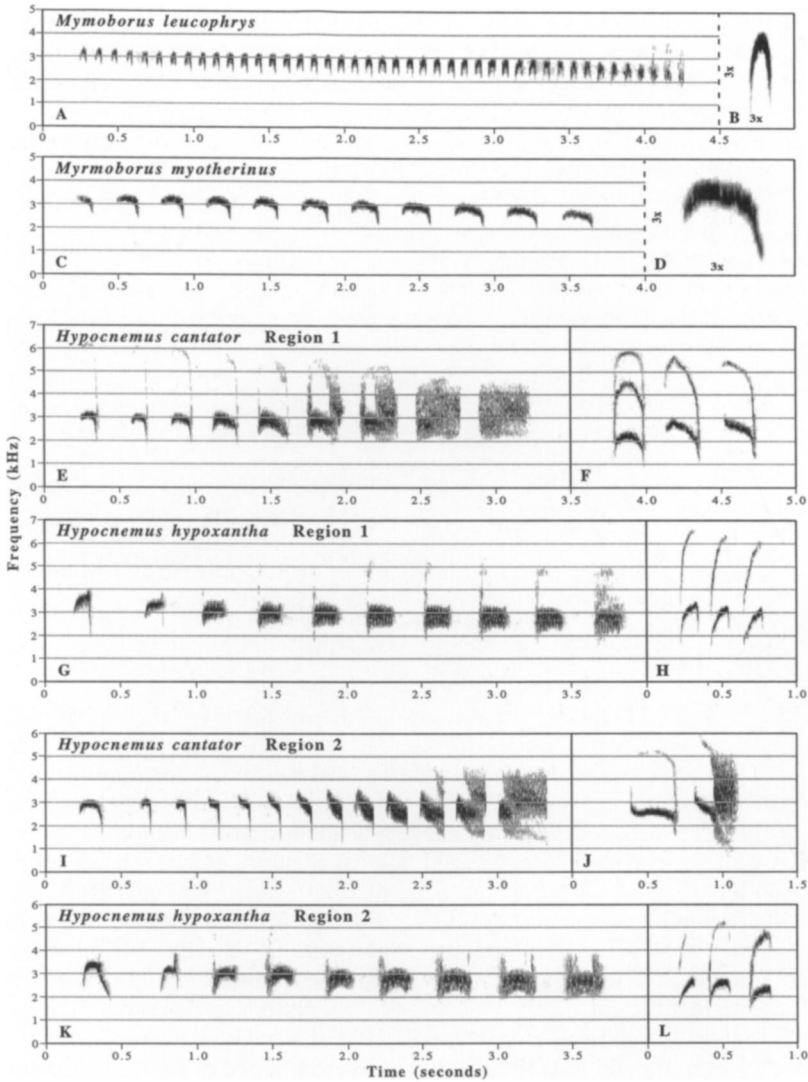quency change (the peak of each note became

FIG. 3. Sound spectrograms of antbird species. (A) *Myrmoborus leucophrys* loudsong, (B) with magnified note, Pando, Bolivia. (C) *M. myotherinus* loudsong, (D) with magnified note, Madre de Dios, Peru. (E) *Hypocnemis cantator* Region 1 loudsong, and (F) three-note call, both from Loreto, Peru. (G) *H. hypoxantha* Region 1 loudsong, and (H) three-note call, both from Loreto. (I) *H. cantator* Region 2 loudsong, and (J) two-note call, both from Pará, Brazil. (K) *H. hypoxantha* Region 2 loudsong, and (L) three-note call, both from Pará.

higher in *cantator* and lower in *hypoxantha*); (3) note shape (downslurred in *cantator*, upslurred in *hypoxantha*); and (4) change in note shape (notes became more downslurred in *cantator* but remained uniform in *hypoxantha*). The mean overall pace of the three-note call was 2.74 ± 0.18 (range 2.41 to 2.89) for *H. cantator* and 4.44 ± 0.16 (range 4.26 to 4.58) for *H. hypoxantha*. Other calls were not analyzed because of small sample sizes.

Hypocnemis cantator/H. hypoxantha from Region 2.—Diagnostic differences in male loudsongs (Fig. 3I, K) were found in: (1) pace (faster in *cantator*); (2) change of pace (*cantator* accelerated greatly at first and only decelerated slightly at the end, whereas *hypoxantha* accelerated slightly at first but then decelerated slightly throughout); (3) note structure (sharply downslurred in *cantator* except for first note, upslurred or flat in *hypoxantha*); and (4) change

TABLE 1. Summary of diagnostic vocal characters for pairs of thamnophilid antwrens.

Species	Loudsongs[a]						Calls[a]					
	NN	PA	CP	CF	NS	CN	DV	PA	CF	NS	CN	PAC
Thamnophilus doliatus / T. palliatus			X		X	X	Data insufficient					
Thamnophilus schistaceus / T. murinus						X	X		X			
Dysithamnus mentalis / D. stictothorax		X	X	X	?[b]				X			
Myrmotherula brachyura / M. obscura		X	X		X							X
Myrmotherula cherriei / M. surinamensis			X		X					X		X
Myrmoborus leucophrys / M. myotherinus	X	X			X							
Hypocnemis cantator / H. hypoxantha Region 1			X		X	X	X	X	X	X		
Hypocnemis cantator / H. hypoxantha Region 2		X	X		X	X	Data insufficient					

[a] NN = Number of notes; PA = Pace; CP = Change in pace; CF = Change in frequency; NS = Note structure / tonality; CN = Change in note structure / tonality; DV = Duration of vocalization; PAC = Presence / absence of a call.

[b] Possible, but uncertain (see text).

in note structure (in *cantator*, notes changed shape throughout and became strongly frequency modulated late in the song, whereas in *hypoxantha*, after initial notes, notes remained uniform and became frequency modulated early in the song). The mean value of the overall pace of the loudsong was 5.96 ± 0.52 (range 5.14 to 6.54) for *H. cantator* (25 vocalizations from 8 individuals) and 2.42 ± 0.29 (range 1.73 to 2.76) for *H. hypoxantha* (32 vocalizations from 9 individuals). Loudsongs were divided into five sections, and change of pace was measured as the ratio of the first section divided by the middle section. Corresponding values ranged from 2.53 to 3.48 for *H. cantator* and 0.81 to 1.41 for *H. hypoxantha*. Female loudsongs (not illustrated) and recorded calls (Fig. 3J, L) also differed but were not included in the analysis because samples were insufficient.

Summary of findings.—A compilation of results across the eight pairs (Table 1) illustrated several regularities. First, all pairs were distinguished by at least three vocal characters. Three pairs were diagnosable by three characters, four pairs by four characters, and one pair by seven characters. Second, loudsongs of all pairs can be diagnosed by at least one character. Note structure / tonality (or change in such) was almost always diagnostic. In the only exception, the pair of *Dysithamnus* species, diagnosable differences in note structure were judged possible but uncertain. Other recurring loudsong characters were pace and change in pace, for which six pairs differed. Third, calls of five of the six pairs for which we had sufficient data differed in at least one character. In two pairs, more characters distinguished calls than loudsongs. Finally, every pair was distin-

guished by at least two of the following characters: loudsong pace, change in loudsong pace, loudsong note structure / tonality, change in loudsong note structure / tonality, and call note structure / tonality.

DISCUSSION AND CONCLUSIONS

At least three vocal characters distinguished each syntopic congeneric pair, which provides a consistent basis for identifying distinct antbird taxa that almost certainly are species by any definition. If such vocal differences in allopatric populations coincide with diagnosable distinctions in nonvocal characters (e.g. morphological or molecular), we believe that the populations should be considered species. However, three diagnosable differences in vocal characters, as defined herein, should be considered a point of reference, not a requirement, in setting species limits in thamnophilid antbirds. For taxa that are highly differentiated in nonvocal characters, or for parapatric taxa, fewer than three diagnosable vocal characters might be considered an appropriate threshold for species recognition. Finally, although thamnophilid species typically exhibit vocal differences, a vocal point of reference does not preclude that allopatric populations that differ strongly in molecular and morphological characters, but without any diagnosable vocal distinctions, may be worthy of species designation.

When employing vocalizations in setting antbird species limits, a three-character point of reference minimizes the possibility of a Type II error in which populations not appropriately designated as species are erroneously consid-

ered species. On the other hand, a reasonable argument can be made that some or all of the pairs of species that we studied could have been differentiated by a number of speciation events and may have diverged vocally beyond that necessary to maintain species integrity, thereby leading to Type I errors of rejecting species status for populations that should be considered species. The possibility that we have recommended an overly conservative threshold will be monitored carefully as we continue to study thamnophilid populations and compare vocal analyses with results of molecular studies.

We selected three vocal characters as a point of reference because we considered this number to be the most rigorous and yet the most encompassing of possible guidelines based on the findings of our study. We did not focus on particular vocal types (such as loudsong) because the role and importance of homologous vocalization types may prove to vary across different groups of species. In particular, calls as well as loudsongs appear to be involved in territory defense and species recognition in antbirds. Nor did we believe that a point of reference should focus on specific characters, such as note structure or pace, because it appears likely that different characters are significant in vocalizations of different clades. To others who contemplate using vocalizations in systematic studies of the Thamnophilidae, we suggest a thorough analysis of all the characters described herein. Although five vocal characters dominated our results, some characters (e.g. frequency) that were of no value in distinguishing syntopic species may prove informative in studies of antbird phylogeny above the species level.

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APPENDIX. Recordings of thamnophilid antbird vocalizations examined. The following list identifies re-
cordings used in the study by taxon, state or department, and recording location. Recordist names aid in
identifying the recording as well as providing credit. Numbers following the recordist name identify the
number of cuts per recordist per location. Acronyms for recording archives: BLS = British Library of
Sounds, London; FSM = Florida State Museum Sound Archive, Gainesville; and 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. Many of these
unarchived recordings are in the process of being archived or eventually will be archived by the recordists.

Thamnophilus doliatus BOLIVIA: La Paz: Miguillas (S. Herzog 1, ISL). Santa Cruz: Curuyuqui (T. Parker 1,
ISL), Perforación (T. Parker 2, ISL), Perseverancia (T. Parker 1, ISL), Rio Tucuvaca (T. Schulenberg 1, ISL),
Serranía de Huanchaca region (T. Parker 3, ISL; B. Whitney 3, ISL).

Thamnophilus palliatus BRAZIL: Rondônia: Cachoeira Nazaré (T. Schulenberg 1, LNS). BOLIVIA: La Paz: Ser-
ranía Bellavista (T. Parker 1, LNS). Santa Cruz: Amboro (T. Parker 2, ISL), Loma Larga (S. Herzog 1, ISL),
Perseverancia (T. Parker 5, ISL), Samaipata (T. Parker 2, LNS).

Thamnophilus schistaceus ECUADOR: Napo: La Selva Lodge (R. Behrstock 3, ISL; G. Budney 1, LNS; G. Ro-
senberg 1, ISL; B. Whitney 1, ISL), Limoncocha (B. Coffey 2, ISL). PERU: Loreto: Intuto (J. Alvarez 2, ISL),
Libertad (T. Parker 1, LNS), Quebrada Sucusari (P. Isler 2, LNS; T. Parker 4, LNS), Quebrada Yanamono (G.
Budney/T. Parker, 1 LNS).

Thamnophilus murinus ECUADOR: Napo: La Selva Lodge (G. Budney 1, LNS). PERU: Loreto: Libertad (T.
Parker 1, LNS), Intuto (J. Alvarez 3, ISL), Quebrada Sucusari (G. Rosenberg 1, ISL; M. Isler 1, LNS; P. Isler
1, LNS; T. Parker 5, LNS).

Dysithamnus mentalis BRAZIL: Espírito Santo: Santa Teresa (P. Isler 1, LNS; T. Parker 2, LNS; R. Ward 1, LNS;
K. Zimmer 1, ISL). Rio de Janeiro: P. N. do Itatiaia (B. Whitney 3, ISL; K. Zimmer 1, ISL). Rio Grande do
Sul: Garruchos (W. Belton 1, LNS), Santo Cristo (W. Belton 2, LNS), São Borja (W. Belton 1, LNS). São Paulo:
Boracéia (D. Snow 2, BLS), Fazenda Berareorico (R. Behrstock 1, ISL), P. E. Carlos Botelho (B. Whitney 2,
ISL); Ubatuba (T. Parker 2, ISL).

Dysithamnus stictothorax BRAZIL: Bahia: Boa Nova (B. Whitney 1, ISL). Espírito Santo: Santa Teresa (T. Parker
2, LNS; B. Whitney 1, ISL; K. Zimmer 1, ISL). Rio de Janeiro: Floresta da Tijuca (T. Parker 2, ISL), Parati (B.
Whitney 1, ISL), P. E. Desengano (B. Whitney 1, ISL), P. N. do Itatiaia (R. Behrstock 1, ISL; K. Zimmer 2,
ISL). São Paulo: Ubatuba (T. Parker 2, ISL; K. Zimmer 1, ISL).

Myrmotherula brachyura PERU: Loreto: vicinity of Quebrada Sucusari (T. Parker 5, LNS; B. Whitney 7, ISL).

Myrmotherula obscura PERU: Loreto: vicinity of Quebrada Sucusari (T. Parker 4, LNS; G. Rosenberg 2, ISL; B.
Whitney 8, ISL).

Myrmotherula s. surinamensis BRAZIL: Amapá: Serra do Navio (J. F. Pacheco 1, ISL; A. Whittaker 2, ISL). SU-
RINAME: Raleigh Vallen/Voltz Berg (T. Davis 2, LNS; B. Whitney 6, ISL). VENEZUELA: Bolívar: Cam-
pamento Rio Grande/El Palmar (R. Behrstock 1, ISL; P. Schwartz 1, LNS; D. Stejskal 1, ISL; B. Whitney 1,
ISL), Rio Caura Forest Reserve (D. Stejskal 2, ISL), Rio Cuyuni/La Escalera (B. Whitney 2, ISL). Amazonas:
Junglaven Camp, Rio Ventuari (K. Zimmer 1, ISL).

Myrmotherula s. multostriata BOLIVIA: Pando: Ingavi (T. Parker 2, ISL). Santa Cruz: Serranía de Huanchaca
region (T. Parker 3, ISL; B. Whitney 4, ISL). BRAZIL: Amazonas: P. N. de Jaú (M. Cohn-Haft 1, ISL), Rio
Javarí (B. Whitney 1, ISL). Rondônia: Fazenda Rancho Grande (K. Zimmer 2, ISL). Pará: Itapoama (B. Whit-
ney 1, ISL), Reserva Ind. Kayapó (B. Whitney 2, ISL), Rio Cupari (B. Whitney 3, ISL), Rurópolis (P. Isler 2,
LNS), Serra dos Carajas (B. Whitney 4, ISL). Mato Grosso: Rio Cristalino (B. Whitney 2, ISL; K. Zimmer 2,
ISL). ECUADOR: Sucumbios: Cuyabeno Reserve (B. Whitney 1, ISL). PERU: Loreto: Intuto (J. Alvarez 2,
ISL), Liborio (B. Whitney 1, ISL), Nueva York (J. Alvarez 1, ISL), P. N. Pacaya-Samiria (A. Begazo 1, ISL),
Quebrada Sucusari (P. Isler 2, LNS; T. Parker 1, LNS), Yarapa Reserve (D. Michael 3, ISL). Madre de Dios:
Cocha Salvador (R. Behrstock 1, ISL; B. Whitney 1, ISL), Manu Lodge (L. Kibler 2, LNS; B. Whitney 1, ISL),
Explorer's Inn (A. van den Berg 2, LNS).

Myrmotherula cherriei BRAZIL: Amazonas: Arquipélago das Anavilhanas (B. Whitney 1, ISL), P. N. de Jaú (J.
F. Pacheco 3, ISL; A. Whittaker 1, ISL). COLOMBIA: Guainía: Puerto Inírida (P. Kaestner 2, ISL). PERU:
Loreto: Intuto region (J. Alvarez 5, ISL; B. Whitney 1, ISL). VENEZUELA: Amazonas: Puerto Ayacucho
(K. Zimmer 1, ISL), Junglaven Camp, Rio Ventuari (R. Behrstock 1, ISL; K. Zimmer 6, ISL).

Myrmoborus leucophrys BOLIVIA: Cochabamba: Sajta (S. Mayer 1, ISL). El Beni: Chimanes (T. Parker 1, ISL),
Riberalta (S. Mayer 2, ISL). Pando: Cobija (T. Parker 2, ISL). PERU: Cuzco: Amazonia Lodge (R. Behrstock
1, ISL). Madre de Dios: Ccolpa de Guacamayos (K. Zimmer 3, ISL), Explorer's Inn (M. Isler 2, LNS; T. Parker
12, LNS). Ucayali: Abujao (T. Meyer 1, ISL).

APPENDIX. Continued.

Myrmoborus myotherinus BOLIVIA: Cochabamba: Sajta (S. Mayer 1, ISL). El Beni: Serranía de Pilón (T. Parker 1, LNS). La Paz: Rio Tuichi (B. Whitney 3, ISL). BRAZIL: Acre: Boca de Tejo (A. Whittaker 1, ISL), Porangaba (A. Whittaker 1, ISL), P. N. Serra do Divisor (B. Whitney 2, ISL), Seringal Ocidente (A. Whittaker 1, ISL). PERU: Madre de Dios: Ccolpa de Guacamayos (K. Zimmer 2, ISL), Explorer's Inn (B. Coffey 1, ISL; M. Isler 1, LNS; T. Parker 4, LNS), P. N. Manu (R. Behrstock 1, ISL). Puno: Cerros de Távara (T. Parker 2, ISL). Ucayali: Abujao (T. Meyer 1, ISL).

Hypocnemis cantator (Region 1) PERU: Loreto: Quebrada Oran (B. Whitney 2, ISL), Quebrada Sucusari (G. Budney/T. Parker 2, LNS; M. Isler 3, LNS; T. Parker 3, LNS; G. Rosenberg 1, ISL; B. Whitney 2, ISL), Quebrada Yanamono (J. Rowlett 1, ISL).

Hypocnemis hypoxantha (Region 1) PERU: Loreto: Quebrada Sucusari (G. Budney/T. Parker 2, LNS; M. Isler 1, LNS; P. Isler 2, LNS; T. Parker 4, LNS; B. Whitney 5, ISL).

Hypocnemis cantator (Region 2) BRAZIL: Mato Grosso: Rio Cristalino (B. Whitney 1, ISL; K. Zimmer 4, ISL). Pará: Itapoama (B. Whitney 1, ISL), Rurópolis (P. Isler 2, LNS).

Hypocnemis hypoxantha (Region 2) BRAZIL: Pará: Aveiro (B. Whitney 1, ISL), Itapoama (B. Whitney 4, ISL), Mirituba (B. Whitney 1, ISL), Rurópolis (M. Isler 2, LNS; P. Isler 2, LNS).