



## Species limits in antbirds (Aves: Passeriformes: Thamnophilidae): an evaluation of *Frederickena unduligera* (Undulated Antshrike) based on vocalizations

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### Abstract

The Undulated Antshrike, *Frederickena unduligera*, a resident of lowland humid forests of western Amazonia, is somewhat poorly known as a result of its low population density and retiring habits. In recent years, vocalizations of *F. unduligera* have been recorded sufficiently to permit geographic analysis. Vocalizations supply valuable measures of species limits for antbirds, whose vocalizations are thought not to be learned. Based on vocalizations, we found that populations of the Undulated Antshrike are more appropriately considered as two biological species. Three populations considered subspecies of *F. unduligera* await further evaluation pending the acquisition of additional vocal recordings, specimens, and tissue for genetic analysis.

**Key words:** speciation, Neotropics, *Frederickena*, systematics, vocalizations, Thamnophilidae

### Introduction

The Undulated Antshrike, *Frederickena unduligera* (Pelzeln 1869), was considered a monotypic species until Zimmer (1944) compared plumages of a small series of specimens. Zimmer described three new subspecies, primarily on the basis of female plumage characters, an arrangement which has been followed ever since (e.g., Peters 1951). *Frederickena unduligera* is a low density species throughout its range, restricted to large tracts of terra firme forest where it favors isolated patches of dense forest undergrowth, especially light-gap tangles around tree falls and stream edges (Zimmer and Isler 2003) and thick, impenetrable palm (often *Lepidocaryum tenue* and occasionally *Leopoldinia pulchra*) undergrowth in sandy and poorly drained forest spaces (pers. obs. and M. Cohn-Haft, pers. comm.). Specimens of *F. unduligera* are rare in collections, the birds vocalize relatively less frequently than do most other antshrikes, and consequently its geographic range is poorly known. *F. u. unduligera* is known only from the right bank of the upper and middle Rio Negro in Amazonas, Brazil; *F. u. fulva* has been thought to be restricted to south-central Colombia near the base of the Andes, eastern Ecuador, and northeastern Peru north of the Rio Amazonas and Rio Marañón (but see below); *F. u. diversa* is said to occur from the south bank of the Rio Amazonas in Peru south to southeastern Peru, extreme southwestern Brazil, and northwestern Bolivia; and *F. u. pallida* occupies the Purus-Madeira interfluvium in Amazonas, Brazil (Fig. 1).

Vocalizations of the Thamnophilidae appear not to be learned, to be an important isolating mechanism in the family, and consequently, to provide a “yardstick” (*sensu* Mayr and Ashlock 1991) for estimating

reproductive isolation and species status under the Biological Species Concept (BSC) (Isler *et al.* 1998, Johnson *et al.* 1999, Baptista and Kroodsmas 2001, Helbig *et al.* 2002, Isler *et al.* 2005, Renssen 2005). Recently obtained recordings of vocalizations provide a more rigorous basis than was heretofore available for reassessing species limits in the complex. That analysis is the objective of this paper.

## Methods

Recordings of vocalizations were compiled from the Macaulay Library (ML, Cornell Laboratory of Ornithology, Ithaca) and from unarchived contributions in the inventory maintained by the Islers (see Appendix). A total of 85 recordings was examined. We reviewed every recording to identify the number and sex of individuals vocalizing and to label every vocalization as either loudsong (following Willis 1967) or call. Calls were not classified further because of the paucity of recordings and of information regarding the context in which they were given.

RAVEN, version 1.2 (Bioacoustics Research Program, Cornell Laboratory of Ornithology) was used to make a spectrogram of every vocalization type delivered by each individual of either sex on every recording. All clearly delineated spectrograms were examined visually for character states (e.g., differences in note shape) that might distinguish one population from the others. Spectrograms shown in figures were selected to express centrality in measurements (e.g., the mean number of notes in loudsongs) and typicality in note shape and were made by exporting RAVEN files into CANVAS, version 9.0.4 (ACD systems, Victoria, British Columbia).

In visual examination, it became clear that some loudsong vocal characters included in other studies (e.g., change in pace of notes) did not differ diagnostically across populations, and vocal characters of loudsongs employed in this study were limited to: (1) number of notes, (2) overall duration, (3) overall pace (notes/s), (4) note shape, (5) duration of middle note, (6) duration of interval following middle note, (7) highest frequency of second, middle, and penultimate notes, (8) lowest frequency of second, middle, and penultimate notes, (9) bandwidth (frequency range) of the second, middle, and penultimate notes, and (10) change in highest frequency. These characters appeared independent from one another in that variation in one character could occur without resulting in a different outcome for another character. Given the possibility, however, that some characters might be linked by common ancestry, we required pairs of measurements expressing diagnostic character states to have correlation coefficients  $< 0.80$ , an arbitrary level but one that, in our experience, falls well below that of obviously correlated vocal measures.

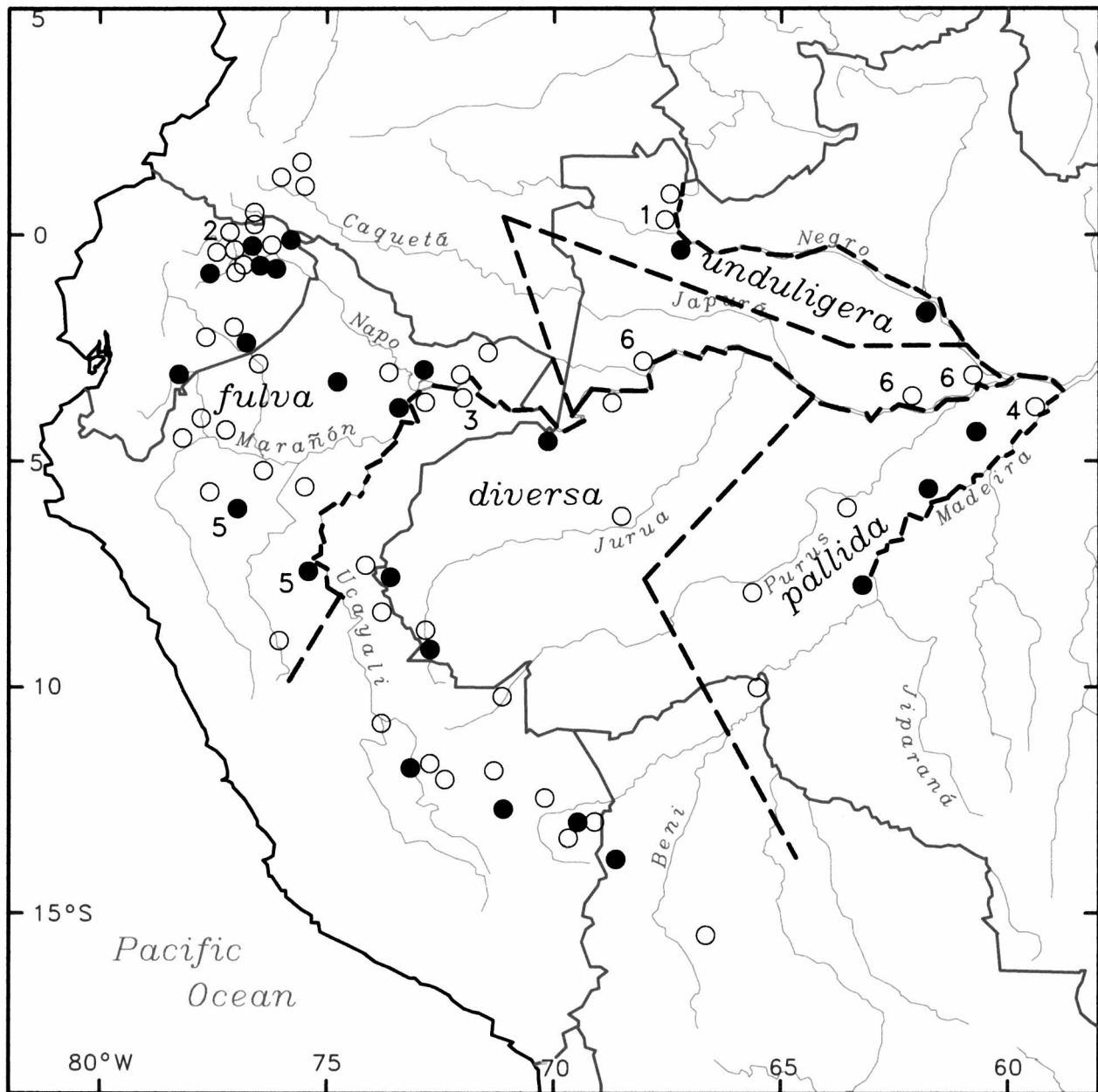
Measurements were made of all loudsong recordings of individuals of *pallida* and *unduligera* but were restricted to geographically representative samples of individuals of *fulva* and *diversa*. Sample sizes reflect number of individuals, not number of vocalizations measured. Quantitative measures were obtained from spectrograms projected on a 43 cm screen using default settings of Raven 1.2 (Charif *et al.* 2004), except that the display was set to smooth, overlap was adjusted from 50% to 93.7% depending on recording quality, and contrast was adjusted according to recording intensity with care taken to retain all elements of the vocalization. Cursor measurements were typically at scales of 0.12 sec/cm and 1.5 kHz/cm. All available calls were examined visually to identify differences in note shape. Diagnostic differences had to be discrete, non-overlapping character states that have the potential for unambiguous signal recognition (Isler *et al.* 1998, 1999). Ranges of samples of continuous variables could not overlap, and the likelihood that ranges would not overlap with larger sample sizes was estimated by requiring the means ( $\xi$ ) and standard deviations (SD) of the population with the smaller set of measurements (a) and the population with the larger set of measurements (b) to meet the test:

$$\xi_a + t_i SD_a \leq \xi_b - t_i SD_b$$

where  $t_i$  = the  $t$ -score at the 97.5 percentile of the  $t$  distribution for  $n - 1$  degrees of freedom.

A similar test could not be used for ratios, which are not distributed normally. Therefore, a non-parametric bootstrap simulation was used to examine statistical significance. We compared the difference between the

means (DBM) for the two taxa being analyzed and two groups of generated data of the same sample sizes. The method generated 10,000 sample population pairs, with replacement, and compared the DBM of the two compared species to the distribution of DBMs of the simulated populations. The result was distributed normally, and significance assigned according to the rules of this distribution.



**FIGURE 1.** Geographic ranges. Locations documented by specimens, vocal recordings, or published sight records are assigned to geographic sectors (Isler 1997) and are identified by open circles. Circles in sectors in which loudsong recordings were available are filled in solidly. Except where they follow rivers, dotted lines that separate taxa are symbolic because actual geographic limits are unknown. Circles numbered 1 through 4 are type localities. 1 = *Frederickena u. unduligera*. 2 = *F. fulva*. 3 = *F. u. diversa*. 4 = *F. u. pallida*. Circles numbered 5 identify sites south of the Río Marañón in which loudsongs having the characteristics of *F. fulva* were recorded (see text). Circles numbered 6 denote sites where populations remain to be identified by vocal recordings (see text). Nomenclature follows recommendations of this paper.

We assessed taxonomic status based on vocal distinctions. We recommend species status for populations that differed sufficiently in their vocalizations to meet guidelines developed in studies of sympatric species

(Isler *et al.* 1998). In general, vocal differences are considered to be of a scale reflective of species status under the BSC if the analysis revealed three or more diagnostic characters. For brevity, we use current subspecies names to refer to the four named populations. As an adjunct to the vocal analysis, we examined specimens at the Louisiana State University Museum of Natural Science and the Carnegie Museum of Natural History and compared plumage and mensural characteristics to subspecies descriptions by Zimmer (1944) of specimens in the American Museum of Natural History.

## Results

Vocalizations were categorized as either loudsongs or calls. *Loudsongs* (following Willis 1967) were consistently patterned multiple-note vocalizations that were often repeated at regular intervals. *Calls* were single notes, continuous tracings on spectrograms.

Loudsongs of all populations (Fig. 2) consisted of clear, evenly spaced whistles that initially grew louder but otherwise were relatively constant in intensity. The shape of the notes differed, however, between *fulva* and the remaining populations. Notes of *fulva* were upslurred whereas notes of the other populations were rounded into an inverted U, a difference that was readily audible to the human ear. In addition, the pace (notes/s) of *fulva* loudsongs was significantly slower ( $\xi = 2.89$ ,  $SD = 0.30$ , range = 2.46–3.49,  $n = 11$ ) than that of the other three populations combined ( $\xi = 4.27$ ,  $SD = 0.46$ , range = 3.49–4.93,  $n = 16$ ). Finally, as measured by dividing the highest frequency of the penultimate note by the highest frequency of the middle note, notes of the second half of loudsongs of *fulva* maintained near constant frequency ( $\xi = 0.99$ ,  $SD = 0.02$ , range = 0.97–1.03,  $n = 11$ ) whereas those of other populations rose in frequency ( $\xi = 1.09$ ,  $SD = 0.03$ , range = 1.03–1.14,  $n = 16$ ). As apparent in Figure 1, terminal notes of *diversa* loudsongs typically displayed a wider bandwidth than those of *pallida* and *unduligera*, but differences did not meet our standards for diagnosability.

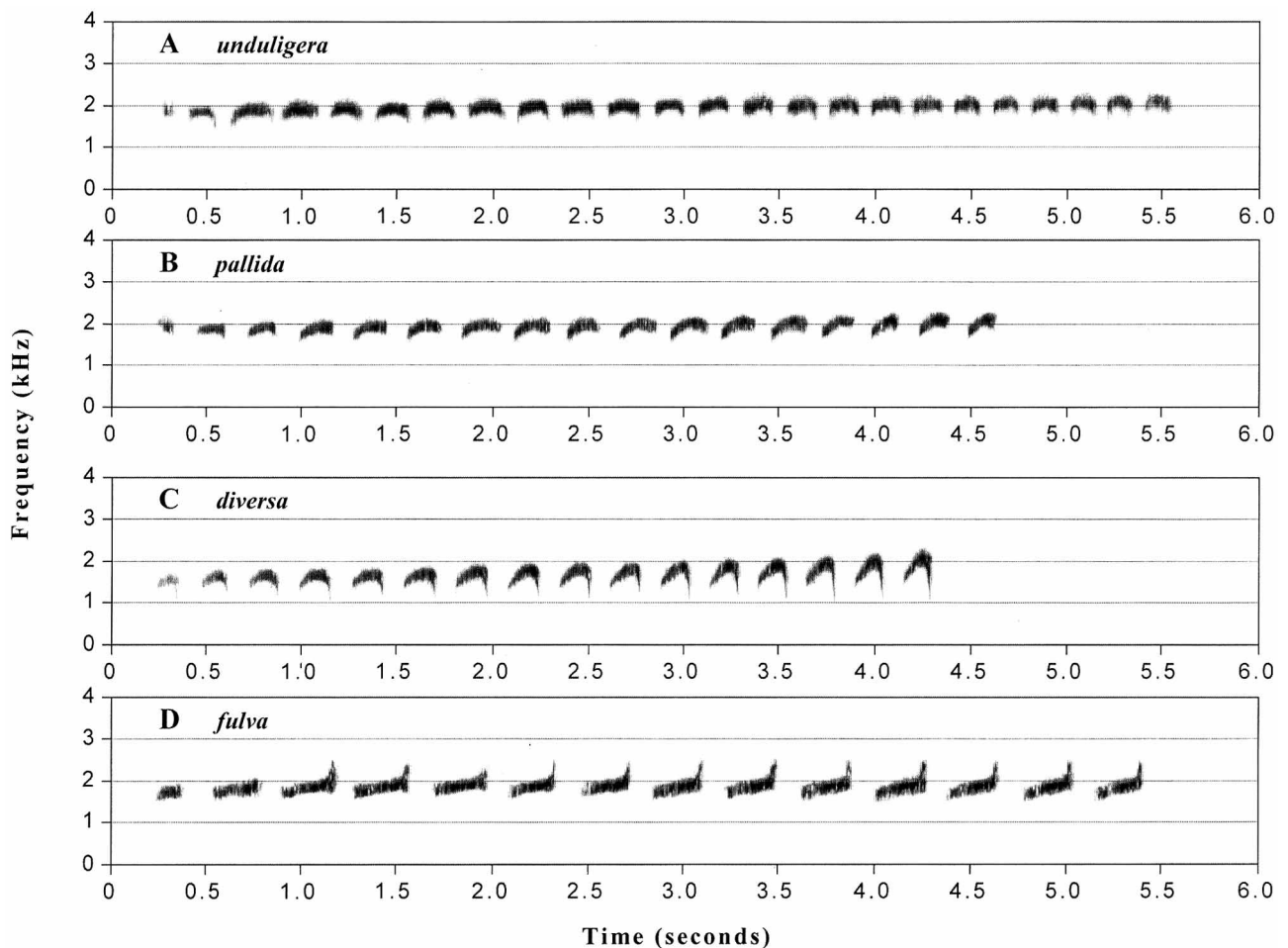
An adequate inventory of recordings of calls was available only for *fulva*. Three types of *fulva* calls were identified (Fig. 3). Whistles ( $N = 5$ ) began with a sharp upscale element and were relative long in duration (0.65–1.3 s) while dropping sharply in frequency (peaks ~3500–4000 Hz dropping to 1500–2000 Hz, once to 2500). A second type of call was part descending whistle, part snarl ( $N = 6$ ). The whistle segment included an abrupt upscale element at the start and a sharp frequency drop like the straight whistle but then dropped even more sharply to become a snarl that was usually relatively flat in pitch. The third type of call ( $N = 4$ ) began with the abrupt upscale element but immediately became a snarl that typically dropped and then flattened in frequency.

Few recordings of calls were available for the other populations (Fig. 3). Although these calls showed a similarity to those of *fulva* in consisting of descending whistles and snarls, differences among them suggested that, with larger samples, calls of *diversa*, *pallida*, and *unduligera* might be distinct from *fulva* and possibly from one another.

Recorded calls were available for only one individual of nominate *unduligera*. This snarl lacked the introductory element found in calls of *fulva*; one example appeared to be two parted.

Three apparently different calls were recorded from four individuals of *pallida*. The frequency shift in the *pallida* whistle ( $N = 2$ ) was flatter than those of *fulva* (peaks descending ~3700 to 3000 Hz) and the initial upscale element was longer and more clearly audible than that of *fulva*. Whistles from another location lacked any initial upscale element, were short (0.45 s), flat, and at a lower frequency (2600 to 2300 Hz). Finally, a perfectly flat (3200 Hz), short (0.3 s) whistle dropped into a short snarl.

We had recordings of calls of only two individuals of *diversa*. They differed from one another and from calls recorded for *fulva*. The first was a slightly descending (~3700 to 3200 Hz) whistle dropping to snarl. The whistle showed some suggestion of an initial upscale element, and the snarl portion sometimes started at a lower frequency (2000 Hz), appearing as a disconnected element. The second was a snarl lacking an introductory element. The initial portion of this snarl had a wide band width but the emphasis was at ~2500–2000 Hz; the frequency dropped sharply and became flat, similar to the snarl recorded for the nominate form.



**FIGURE 2.** Loudsongs of *Frederickena unduligera* and *F. fulva*. (A) *F. u. unduligera* São Gabriel da Cachoeira, Amazonas, Brazil (R. Parrini ISL-MISC.007:49). (B) *F. u. pallida* Tupana Lodge, Amazonas, Brazil (A. Whittaker ISL-AW.020:33). (C) *F. u. diversa* Reserva Natural Palmari, Amazonas, Brazil (B. Whitney ISL-BMW.209:38). (D) *F. fulva* Yuturi Lodge, Napo, Ecuador (N. Krabbe ISL-NK.006:06).

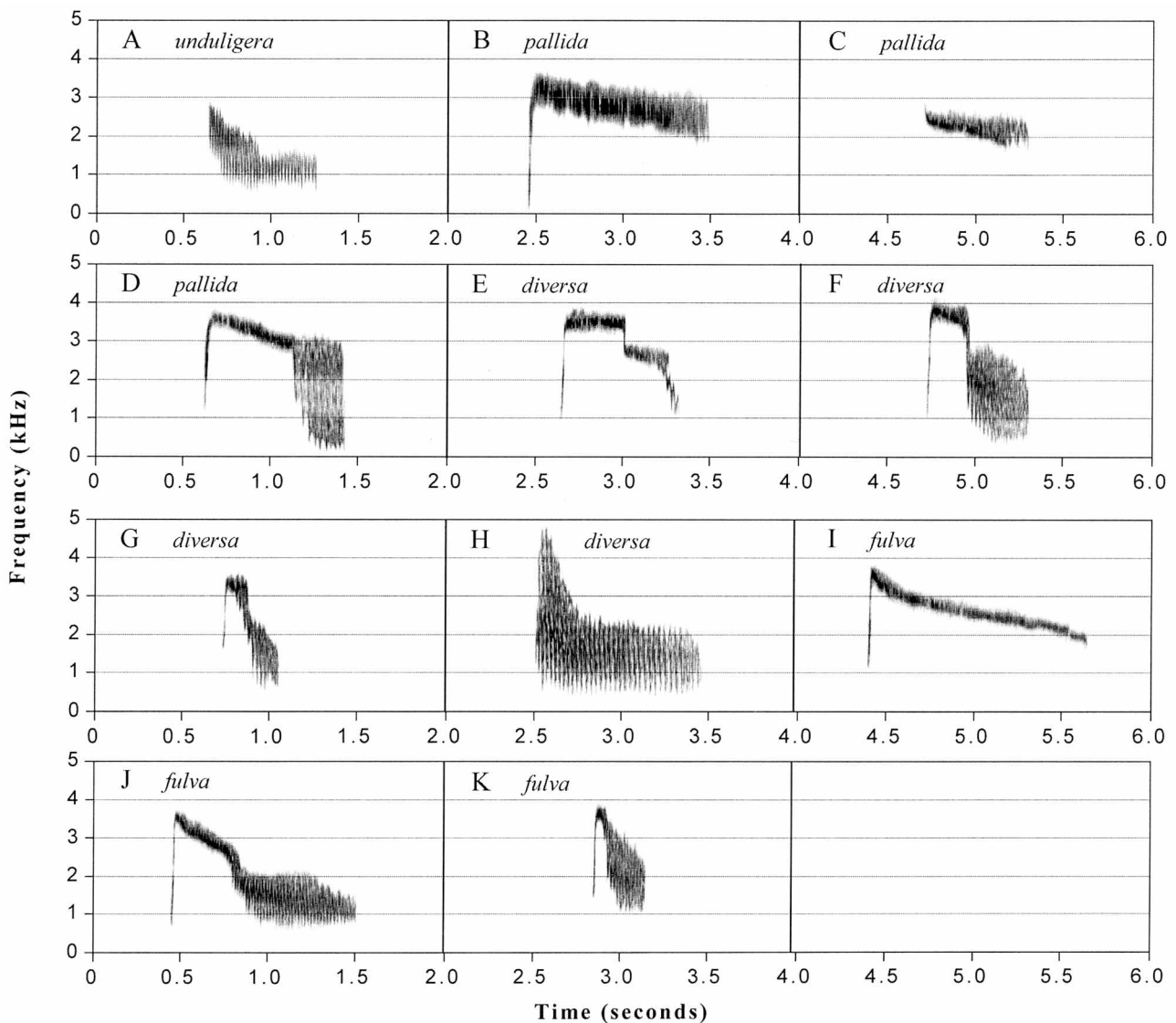
As noted in the Introduction, relatively few specimens of *Frederickena unduligera* are available in collections. Examination of female specimens (on which subspecies definitions were primarily based) at two museums containing a substantial portion of the specimens available in the United States did not provide additional insights. In general, as described by Zimmer (1944), specimens of *fulva* were most reddish-brown (fulvous) and heavily barred and those of *pallida* palest and least barred, but an unusual amount of plumage variation was found among individuals in female plumage, even among those collected at the same location. Data were unavailable to indicate whether this variation was age related, and it is possible that some specimens sexed as female might have been subadult males. Of particular interest were two female specimens in the Carnegie Museum from Manacapuru and Tonantins which lie in a region of uncertain affinity (see Fig. 1). Neither specimen clearly had the plumage characteristics of *fulva* or *unduligera*, and the more fulvous-backed and heavily barred specimen came from the eastern locality, Manacapuru, contrary to what one might expect if there were clinality in plumage coloration towards *fulva*.

## Discussion

On the basis of the vocal analysis described above, in combination with morphological distinctions described by Zimmer (1944), we recommend that the *Frederickena unduligera* complex be considered as two biological species, as follows:

*Frederickena unduligera* (Pelzeln) Undulated Antshrike  
*Frederickena fulva* Zimmer Fulvous Antshrike

Differences in pattern and quality of loudsongs of *F. fulva* and *F. unduligera* were first noted by Parker *et al.* (1991) who urged further investigation. Diagnostic loudsong distinctions in note shape, overall pace of notes, and change in frequency provide three independent vocal characters, consistent with the extent of vocal differentiation documented for closely related sympatric species of thamnophilid antbirds (Isler *et al.* 1998). The more fulvous plumage coloration and more extensive barring of females of *F. fulva* as compared with females of *F. unduligera* were described by Zimmer (1944). The English name of Fulvous Antshrike for *F. fulva* refers to the female plumage, which is appropriate in this species group and in a family in which differences among species are often more pronounced in females than in males (Hellmayr 1929).



**FIGURE 3.** Calls of *Frederickena unduligera* and *F. fulva*. (A) *F. u. unduligera* snarl. Parque Nacional de Jaú, Amazonas, Brazil (S. Borges ISL-AW.020:29). (B–D) *F. u. pallida*. (B) whistle. Tupana Lodge, Amazonas, Brazil (A. Whittaker ISL-AW.020:28). (C) short whistle. Igarapé Santa Maria, Amazonas, Brazil (B. Whitney ISL-BMW.184:55). (D) whistle-snarl. Tupana Lodge, Amazonas, Brazil (A. Whittaker ISL-AW.020:21). (E–H) *F. u. diversa*. (E) whistle. Parque Nacional da Serra do Divisor, Acre, Brazil (B. Whitney ISL-BMW. 126:07). (F) whistle-snarl. same recording. (G) snarl. same recording. (H) rattle. same location (B. Whitney ISL-BMW. 126:04). (I–K) *F. fulva*. (I) whistle. Kapawi Lodge, Pastaza, Peru (B. Whitney ISL-BMW.157:08). (J) whistle-snarl. same recording. (K) snarl. same location (B. Whitney ISL-BMW.153:08).

Loudsongs recorded in northern Peru at 15 km NE of Jirillo, San Martín (06°03'S, 76°44'W), and 84 km WNW of Contamana on the Río Cushabatay, Loreto (07°09'S, 75°44'W), displayed vocal characteristics typical of *F. fulva*. These extend the range of *F. fulva* south of the Río Marañón and west of the Río Ucayali (Fig. 1). North of the Amazon River, the eastern limits of the geographic range of *F. fulva* and the western limits of *F. u. unduligera* are unclear. Specimens have been collected along the north bank of the Amazon (Solimões) at Tonantins (Carnegie Museum), Codajás (Swedish Museum of Natural History), and Manacapuru (Carnegie Museum) (west to east in Fig. 1), but no vocal recordings from the region are available.

Confirmation of the validity and clarification of the geographic limits of named subspecies (*diversa* and *pallida*) of *F. unduligera* was not possible with available materials. Their reconsideration requires additional specimens, ideally including tissue, and vocal recordings from throughout the range of *F. unduligera* to investigate possibilities of clinality and introgression. As noted above, the limited available specimen information presents a confusing picture, and the same holds for vocal data. For example, a single recording of an adult male from just south of Humaitá, Amazonas, Brazil, might have been expected to align well with those of *pallida* from lower in the Madeira/Purús interfluvium, but it appears to be closer to recordings of *diversa*. Further vocal recording should place an emphasis on obtaining recordings of calls. The existing, limited sample of recordings suggests the possibility that calls differ diagnostically among populations. In one sympatric pair of *Hypocnemis* antbirds, calls were shown to differ whereas loudsongs were indistinguishable (Isler *et al.* 2007).

*Frederickena fulva* and *F. unduligera* are low-density species that appear to be indicators of high-quality lowland forest (Zimmer and Isler 2003). This attribute, combined with the results of our analysis, indicates that independently evolving populations are geographically restricted and suggests that their continued conservation depends on the maintenance of multiple large protected areas in western Amazonia.

## Acknowledgments

The analysis was made possible by the contributions of the recordists listed in the Appendix. We are grateful to M. Cohn-Haft for providing field observations. We appreciate the continuing support of the Macaulay Library, Cornell Laboratory of Ornithology (G. Budney), J. V. Remsen, Jr., an anonymous reviewer, and editor R. T. Chesser made helpful suggestions for improving the manuscript.

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## Appendix. Recordings examined

The following list identifies recordings used in the study by taxon, country, state or department, recording location, and recordist. Nomenclature follows recommendations of this paper. Allocation of recordings to subspecies of *F. unduligera* follow current assumptions of geographic limits (e.g., Zimmer and Isler 2003). Numbers following the recordist name identify the number of cuts per recordist per location. Acronyms for recording archives: ML = Macaulay Library, Cornell Laboratory of Ornithology, Ithaca; ISL = recordings not yet archived in an institutional collection but that have been copied into the inventory maintained by MLI and PRI. Many of these unarchived recordings either are in the process of being archived or will eventually be archived by the recordists.

*Frederickena u. unduligera*: (2 recordings; 2 localities). Brazil: Amazonas: Parque Nacional de Jaú (Borges 1 ISL), right bank Rio Negro opposite São Gabriel da Cachoeira (Parrini 1 ISL).

*Frederickena unduligera pallida*: (15 recordings; 3 localities). Brazil: Amazonas: 40 km S Humaitá (Whitney 2 ISL), Igarapé Santa Maria (Whitney 2 ISL), Tupana Lodge (Whittaker 9 ISL, Zimmer 2 ISL).

*Frederickena unduligera diversa*: (14 recordings; 8 localities). Brazil: Acre: Boca de Tejo on left bank R. Juruá (Whittaker 1 ISL), Parque Nacional da Serra do Divisor (Whitney 5 ISL), Amazonas: Barro Vermelha on left bank R. Juruá (Whittaker 1 ISL), Reserva Natural Palmarí (Whitney 1 ISL). Bolivia; La Paz: Alto Madidi (Parker 1 ISL). Peru: Cusco: Camisea (Christian 1 ISL), Madre de Dios: Explorer's Inn (Parker 3 ISL), Pantiacolla Lodge (Lambert 1 ISL).

*Frederickena fulva*: (54 recordings, 17 localities). Ecuador: Morona-Santiago: Santiago (Robbins 3 ML), Napo: Coca (J. Rowlett 1 ISL), Lagoa Añangu (Krabbe 2 ISL), La Selva Lodge (Behrstock 1 ISL, Krabbe 2 ISL, Michael 1 ISL, G. Rosenberg 1 ISL, R. Rowlett 1 ISL), Maxus Road (Krabbe 3 ISL, Zimmer 1 ISL), Sacha Lodge (Arvin 1 ISL), Tiputini Biodiversity Station (Arvin 1 ISL, Zimmer 7 ISL), Volcán Sumaco (Whitney 2 ISL), Yuturi Lodge (Krabbe 1 ISL), Pastaza: Kapawi Lodge (Whitney 2 ISL), Sucumbios: Cuyabeno (J. Rowlett 1 ISL, Whitney 2 ISL). Peru: Loreto: El Dorado (Whitney 2 ISL), El Tigre (Alvarez 3 ISL), Intuto (Alvarez 2 ISL), Quebrada Sucusari (Parker 2 ML, J. Rowlett 1 ISL, Whitney 8 ISL), Rio Cushabatay, 84 km WNW Contamana (Lane 1 ISL), San Martín: Jirillo (Valqui 1 ISL).