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RESEARCH ARTICLE

A new species of antbird (Passeriformes: Thamnophilidae) from the Cordillera Azul, San Martín, Peru

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ABSTRACT

We describe a distinctive new species of antbird (Passeriformes: Thamnophilidae) from humid montane forest (1,340–1,670 m above sea level) of the Cordillera Azul, San Martín Region, Peru. Plumage, voice, and molecular evidence distinguish this species from its sister taxon *Myrmoderus ferrugineus* (Ferruginous-backed Antbird), which is found in lowland Amazonian rainforests of the Guiana Shield and Madeira-Tapajós interfluvium. The new species is presently known only from one ridge in the Cordillera Azul, and therefore we recommend further fieldwork to better estimate its distribution and population size.

Keywords: *Myrmeciza*, *Myrmoderus*, new species, outlying ridges, taxonomy

Una nueva especie de hormiguero (Passeriformes: Thamnophilidae) de la Cordillera Azul, San Martín, Perú

RESUMEN

Describimos una nueva y distintiva especie de hormiguero (Passeriformes: Thamnophilidae) de los bosques montañosos húmedos (1,340–1,670 metros sobre el nivel del mar) de la Cordillera Azul, región de San Martín, Perú. El plumaje, la voz, y la evidencia molecular distinguen a esta especie de su taxón hermano *Myrmoderus ferrugineus* (Hormiguero Lomirrufo), el cual se encuentra en los bosques tropicales amazónicos de llanura del Escudo Guayanés y el interfluvio Madeira-Tapajós. A esta nueva especie se le conoce en la actualidad únicamente de una cresta de la Cordillera Azul, y por lo tanto, recomendamos mayor investigación de campo para poder estimar mejor su distribución y el tamaño de su población.

Palabras clave: cadenas montañosas aisladas, *Myrmeciza*, *Myrmoderus*, nueva especie, taxonomía

INTRODUCTION

Antbirds in the genus *Myrmoderus* Ridgway, 1909 (*sensu* Remsen et al. 2017) are found in the Atlantic rainforests of eastern Brazil (White-bibbed Antbird [*M. loricatus* Lichtenstein, 1823], Squamate Antbird [*M. squamosus* Pelzeln, 1868], and Scalloped Antbird [*M. ruficauda* Wied, 1831]) and the Amazonian rainforests of the Guiana Shield and Madeira-Tapajós interfluvium (Ferruginous-backed Antbird [*M. ferrugineus* Müller, 1776]). With no representative known in western Amazonian South America, it is with some surprise that we report the discovery of a new species in this genus from the foothills of the Peruvian Andes. The new antbird inhabits forests surrounding the small coffee-

growing town of Flor de Café (7.398°S, 76.299°W), previously called “Plataforma,” at 1,600 m above sea level [a.s.l.] in the western Cordillera Azul. This town has become a destination for ornithologists and birdwatchers since Todd Mark and Walter Vargas discovered an easily accessible population of Scarlet-banded Barbets (*Capito wallacei* O’Neill et al., 2000) there in May 2011 (T. Mark personal communication). This barbet species was first discovered in 1996 during an ornithological expedition to a remote and uninhabited part of the eastern Cordillera Azul (O’Neill et al. 2000).

In July 2016, J.R.B. visited Flor de Café, and on July 9, while birding in undisturbed, humid montane forest near the town at an elevation of ~1,570 m a.s.l., he heard a

rattling alarm call of an antbird. Playback of similar antbird calls did not result in any direct response but may have excited the bird, which sang from the vicinity of the initial alarm call. After making an audio recording of the song on his HTC One M8 cell phone, J.R.B. used playback to obtain views of a ground-walking antbird that did not match any known species. The following day, as J.R.B. was preparing to leave Flor de Café to request help in documenting his find, A.E.M., D.F.L., F.A., and J.F. serendipitously arrived. Joining efforts through July 13, we documented this new species with further voice recordings, photos, video, and the collection of voucher specimens. A.E.M. remained through July 20, further documenting the species around Flor de Café at elevations of 1,390–1,670 m a.s.l. In September and October 2016, O.J., D.F.L., Emil Bautista, and Walter Vargas visited a nearby area, accessed from the town of Selva Andina (7.398°S, 76.230°W), and documented the new species at 1,340 m a.s.l.

Plumage, morphometrics, voice, behavior, and genetic evidence point to a close relationship between *Myrmoderus ferrugineus* and the new species. There are numerous characters unique to these 2 taxa, yet they are also closely allied to the other 3 members of the genus (*M. loricator*, *M. squamosus*, and *M. ruficauda*). For this reason, we recognize *Myrmoderus* as the appropriate genus for the new species, which we name

***Myrmoderus eowilsoni*, species novum**

Cordillera Azul Antbird

Hormiguero de la Cordillera Azul (Spanish)

Holotype

Study skin, Centro de Ornitología y Biodiversidad (CORBIDI) AV-12381; tissue, Louisiana State University Museum of Natural Science (LSUMZ) B-93477; adult male; 2.5 km west-northwest of Flor de Café, Cordillera Azul, San Martín Region, Peru (7.390°S, 76.320°W; Figure 1); elevation 1,570 m a.s.l.; collected July 12, 2016; prepared by A.E.M., original catalog number 193; audio-recorded by A.E.M., D.F.L., F.A., and J.F. (Macaulay Library of Natural Sounds [ML], Cornell Laboratory of Ornithology, Ithaca, New York, USA; audio: ML 46435931, ML 224879, ML 224880); GenBank sequences KY849953 (ND2) and KY849952 (ND3).

Diagnosis

We assign *Myrmoderus eowilsoni* to the genus *Myrmoderus* on the basis of its combination of black ear coverts, extensively rufous brown plumage, and blackish wing coverts with broad white or buff tips (see Isler et al. 2013). Additional characters shared with *M. ferrugineus* include bluish bare orbital skin, gray feet and tarsi, lack of white interscapular patch, and terrestrial walking behavior. Despite these similarities, it is readily distinguishable from

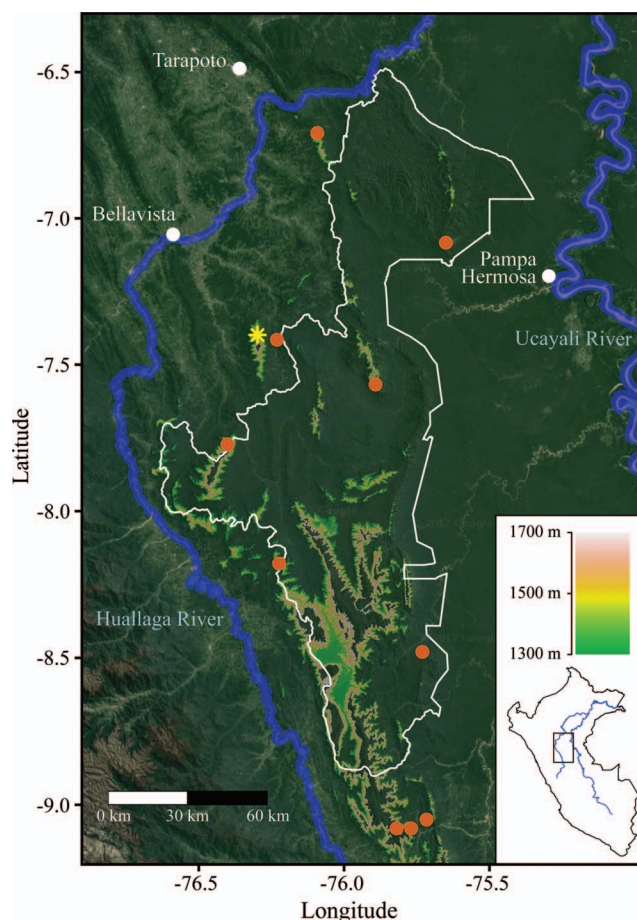


FIGURE 1. Map of the Cordillera Azul showing the type locality, which is also the only known locality, of *Myrmoderus eowilsoni* (yellow star) in relation to other surveyed sites on ridges of the Cordillera Azul (orange circles; O'Neill et al. 2000, Alverson et al. 2001, Merkord et al. 2009, J. Bates personal communication, T. Mark personal communication, LSUMZ field expeditions). The white line represents the boundary of the Cordillera Azul National Park. Areas east of the Huallaga River between 1,300 and 1,700 m a.s.l. are shaded to emphasize potential areas of occurrence of *M. eowilsoni*. Inset map shows the location of the Cordillera Azul in Peru.

M. ferrugineus by (1) crown and nape color, (2) supercilium color, (3) extent of bare orbital skin, (4) belly color, (5) breast color (females), and (6) song (Figures 2 and 3). Compared to *M. ferrugineus*, the new species has a colder brown crown and nape, a gray rather than white supercilium, and less extensive bluish bare orbital skin. The belly of *M. eowilsoni* is black (males) or dark brown (females), whereas both sexes of *M. ferrugineus* show substantial white in this area. Additionally, females of *M. eowilsoni* have a rufous breast, whereas females of *M. ferrugineus* have a black breast (Figure 2A). The song differs substantially from *M. ferrugineus* by having fewer notes and a slower pace.



FIGURE 2. Ventral (A) and lateral (B) views of both species of *Myrmoderus*. Left to right: male *M. eowilsoni* (CORBIDI 12381; holotype), female *M. eowilsoni* (CORBIDI 12380; mate of holotype), male *M. ferrugineus* (LSUMZ 178458), and female *M. ferrugineus* (LSUMZ 178456). Scale bars = 5 cm.

Description of Holotype

Capitalized color names are based on Ridgway (1912), and alphanumeric color codes in parentheses refer to Munsell (no date). Crown and nape Warm Sepia (10YR3/4) with feather tips edged slightly darker, imparting a faintly scaled appearance. Forehead and lores black. Back Brussels Brown (5YR3/6) tending toward Amber Brown (5YR4/8) on upper scapulars and upper mantle. Two mantle feathers have a small amount of white fringing toward the vane bases, suggesting a rudimentary interscapular patch, but otherwise mantle feather bases are variably dark gray to blackish. Rump and uppertail coverts Brussels Brown (5YR3/6). Dorsal side of tail Bone Brown (7.5YR2/2) tending toward Fuscous-Black (slightly darker than 10YR2/2) at tip with outer vanes fringed Brussels Brown (5YR3/6). Ventral side of tail uniformly Fuscous (10YR2/2). Undertail coverts Brussels Brown (5YR3/6). Chin, throat, auriculars, breast, sides, upper flanks, and belly black. Lower belly color blending toward Raw Umber (10YR3/4) on vent and lower flanks. Supercilium Light Gull Gray (N6.75), beginning above anterior edge of eye and extending to and broadening at nape. Lesser coverts black with narrow white tips, becoming entirely white on leading edge of wing. Greater and median secondary coverts black, broadly tipped Warm Buff (7.5YR8/8) to Ochraceous-Buff (7.5YR6/8), forming 2 obvious wing bars. Primary coverts black, narrowly tipped Warm Buff (7.5YR8/8). Underwing coverts blackish, greater coverts tipped white. Primaries and secondaries Fuscous-Black (slightly darker than 10YR2/2) fringed with Brussels Brown (5YR3/6). Tertiaries Fuscous (10YR2/2) with diffuse black subterminal spot on secondaries 7 and 8 and diffusely tipped with Cinnamon (5YR5/8) on outer vane. Soft-part colors recorded at the

time of collection: irides dark brown, skin of orbit blue-gray, feet and tarsi dark gray, mandible blue-gray, and maxilla blackish with blue-gray tomium. Measurements are provided in Table 1; no molt or fat, stomach contained insect parts, left testis 4.5×2 mm.

Paratypes

There are 7 paratypes of *M. eowilsoni*. Six were collected near Flor de Café between July 12 and 19, 2016 (CORBIDI 12380, 12382, 12383; LSUMZ 190882, 190883, 190884), and one was collected 6 km southeast of Flor de Café on September 30, 2016 (LSUMZ 190885). Data from field labels and morphometric data for all specimens of *M. eowilsoni* are shown in Table 1. Female plumage differs strikingly from that of males in the following characters: throat and malar white with fine black tips, more extensively black toward chin; breast and sides between Xanthine Orange (5YR6/10) and Amber Brown (5YR4/8); center of belly Dark Gull Gray (N4.25) blending to Raw Umber (10YR3/4) on the surrounding belly and through the flanks and vent. All individuals of both sexes show an area of paler Amber Brown (5YR4/8) on the upper mantle and scapulars, but to varying degrees of intensity and extent. The tips of the lesser coverts are slightly variable in color, with 2 females (LSUMZ 190882 and 190884) showing buffy tips and all other individuals showing exclusively white tips. The wing bars formed by the tips of the median coverts are also slightly variable in color, with some individuals tending toward white. The amount of Raw Umber (10YR3/4) on the belly is variable among females, being largely replaced by gray on one individual (CORBIDI 12380). A male and a female in formative plumage (LSUMZ 190883 and 190884), aged on the basis of molt limits in the rectrices and between the greater secondary and greater primary coverts and by the presence of bursa; like adults in definitive plumage, except that the young female has a nearly pure white throat and chin with greatly reduced scaling.

Etymology

We name *Myrmoderus eowilsoni* in honor of Dr. Edward Osborne Wilson to recognize his tremendous devotion to conservation and his patronage of the Rainforest Trust, which strives to protect the most imperiled species and habitats in the Neotropics and across the globe. We select the English name to draw attention to the little known but biogeographically important and biodiverse mountain range that contains the type locality of the species.

REMARKS

Phylogenetic Relationships

To assess the evolutionary relationships within *Myrmoderus*, we estimated a phylogeny based on sequence data

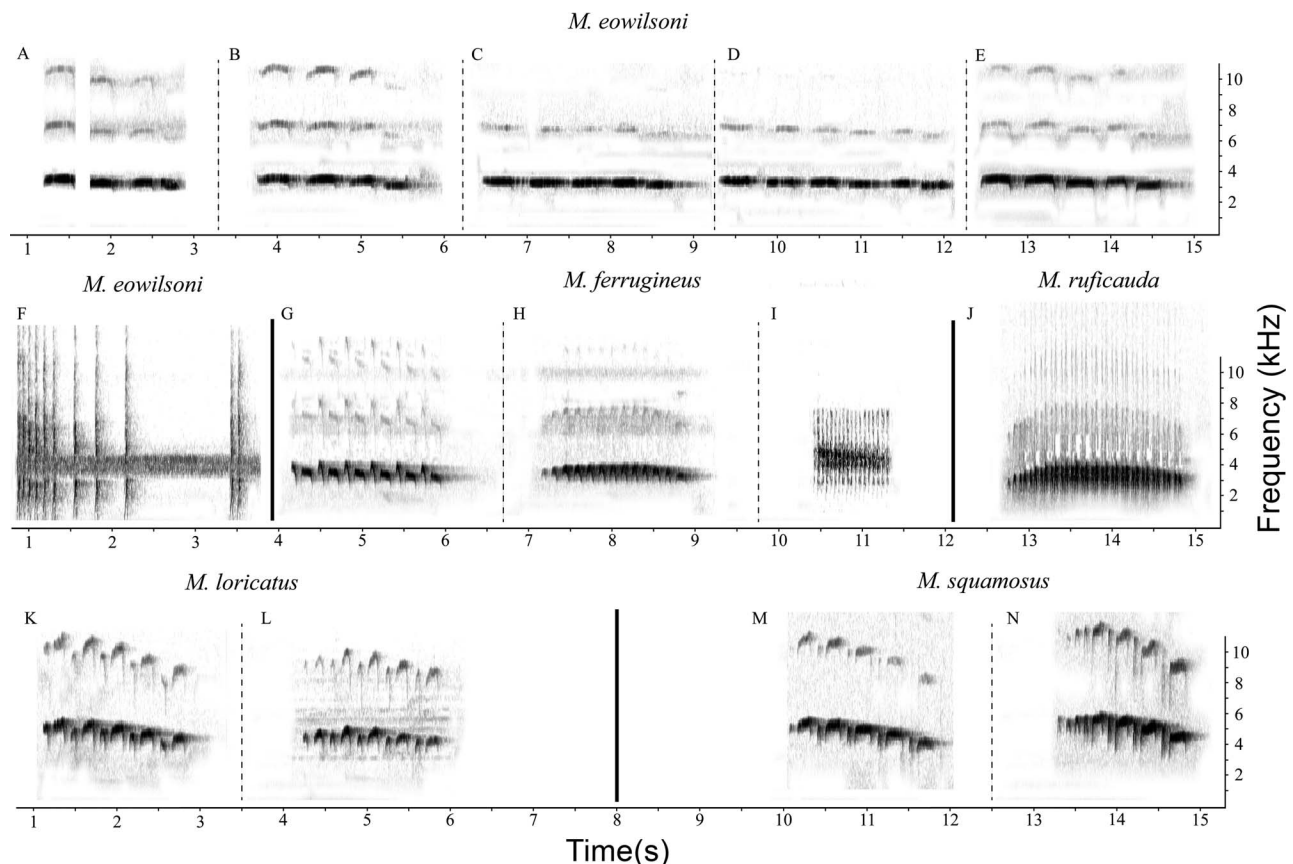


FIGURE 3. Sonograms of representative vocalizations of *Myrmoderus* species. Recordings are available at Macaulay Library (ML), Xeno-canto.org (XC), or Isler and Whitney (2002), with the exception of Macedo recordings, which are in the collection of the recordist and used here with permission. Specimen number, recordist, date and location recorded, and archival catalog number follow in parentheses, as available. (A) Song of holotype male *M. eowilsoni* (CORBIDI 12381; D.F.L.; July 12, 2017; ML224880). (B) Song of female *M. eowilsoni* (CORBIDI 12380; mate of holotype; D.F.L.; July 12, 2017; ML224880). (C, D) Variation among songs of female *M. eowilsoni* (D.F.L.; July 13, 2017; ML224882). (E) Song of female *M. eowilsoni* (LSUMZ 190882; D.F.L.; July 12, 2017; ML224881). (F) Chatter call of *M. eowilsoni* with insect noise between 3 and 5 kHz (CORBIDI 12380 or 12381; D.F.L.; July 12, 2017; ML224880). (G) Song of male *M. ferrugineus* (B. Whitney; Isler and Whitney 2002). (H) Song of female *M. ferrugineus* (B. Whitney; Isler and Whitney 2002). (I) Chatter call of *M. ferrugineus* (D.F.L.; March 13, 2011; Suriname, Palumeu; XC74997). (J) Song of male *M. ruficauda* (T. Parker III; Isler and Whitney 2002). (K) Song of male *M. loricatus* (G. Macedo field recording no. 0327; November 30, 2014; Brazil, Rio de Janeiro, Estrada do Contorno). (L) Song of female *M. loricatus* (G. Macedo field recording no. 0328; November 30, 2014; Brazil, Rio de Janeiro, Estrada do Contorno). (M) Song of male *M. squamosus* (G. Macedo field recording no. 0469; September 3, 2015; Brazil, São Paulo, Paranapiacaba). (N) Song of female *M. squamosus* (G. Macedo field recording no. 0469; September 3, 2015; Brazil, São Paulo, Paranapiacaba).

from all taxa in the genus, using 2 or 3 individuals of each taxon except *M. r. ruficauda*, for which we had genetic data from only one individual (Appendix Table 3). We obtained sequences of 2 mitochondrial genes, *NADH dehydrogenase subunit 2* (ND2; 1,041 base pairs) and *NADH dehydrogenase subunit 3* (ND3; 351 base pairs) from 11 individuals sequenced previously by Bravo (2012). To augment this dataset, we generated new sequences from 2 individuals of *M. eowilsoni* and 2 individuals of *M. ferrugineus* Todd, 1927. For these 4 individuals, we extracted total DNA from 25 mg of pectoral muscle using a Qiagen DNEasy kit using the manufacturer's protocol and performed polymerase chain reactions (PCR) for ND2

and ND3 following the protocol of Bravo (2012). PCR product was purified and sequenced at Eton Biosciences (Durham, North Carolina, USA) or the LSU Genomics Facility (Baton Rouge, Louisiana, USA). Four outgroup taxa from the Bravo (2012) dataset were used to root the tree: Barred Antshrike (*Thamnophilus doliatus* Linnaeus, 1764), Spotted Antbird (*Hylophylax naevioides* Lafresnaye, 1847), White-bellied Antbird (*Myrmeciza longipes* Swainson, 1825), and White-plumed Antbird (*Pithys albifrons* Linnaeus, 1766). All sequence data are deposited in GenBank (Appendix Table 3).

Each new sequence was cleaned manually and assembled into contigs in Geneious 10.1.3 (Kearse et al. 2012).

TABLE 1. Measurements from *Myrmoderus eowilsoni* specimens ($n = 8$).

| Sex | Catalog number ^a | Tissue number | Preparator number | Date collected | Macaulay Library numbers | Elevation where collected (m a.s.l.) | Wing-span (mm) | Weight (g) | Tail length (mm) | Wing length (mm) | Bill length exposed (mm) | Bill length from nares (mm) | Bill width (mm) | Bill depth (mm) | Tarsus length (mm) | Bursa (mm) | Skull ossification (%) |
|---------------------|-----------------------------|---------------|-------------------|--------------------|--------------------------|--------------------------------------|----------------|------------|------------------|------------------|--------------------------|-----------------------------|-----------------|-----------------|--------------------|------------|------------------------|
| Female | CORBIDI 12380 | B-93476 | AEM 192 | July 12, 2016 | 46435931, 224879, 224880 | 1,570 | 217 | 29.0 | 57 | 68.7 | 17.3 | 10.8 | 6.2 | 5.4 | 28.8 | None | 100 |
| Male ^b | CORBIDI 12381 | B-93477 | AEM 193 | July 12, 2016 | 46435931, 224879, 224880 | 1,570 | NA | 27.2 | 62 | 72.8 | 18.7 | 11.2 | 7.8 | 5.8 | 27.3 | None | 100 |
| Female | LSUMZ 190882 | B-93478 | DFL 2683 | July 12, 2016 | 224881 | 1,490 | NA | 27.5 | 66 | 68.4 | 18.5 | 11.0 | 6.7 | 5.9 | 27.8 | None | 100 |
| Male ^c | LSUMZ 190883 | B-93479 | DFL 2684 | July 12, 2016 | 224881 | 1,490 | 228 | 27.3 | 62 | 66.0 | 17.6 | 11.2 | 6.6 | 5.4 | 27.4 | 3 × 2 | 100 |
| Female ^c | LSUMZ 190884 | B-93482 | AEM 195 | July 18, 2016 | 46041311 | 1,510 | 225 | 27.6 | 67 | 68.0 | 16.7 | 11.0 | 6.6 | 5.7 | 28.0 | 3.5 × 2.5 | 100 |
| Female | CORBIDI 12382 | B-93483 | AEM 196 | July 19, 2016 | 46046081 | 1,390 | 215 | 28.7 | 60 | 65.4 | 17.1 | 10.7 | 7.2 | 5.4 | 27.7 | None | 100 |
| Male | CORBIDI 12383 | B-93484 | AEM 197 | July 19, 2016 | 46045061 | 1,390 | 220 | 24.7 | 61 | 69.1 | 16.8 | 10.9 | 6.4 | 5.9 | 26.6 | None | 100 |
| Male | LSUMZ 190885 | B-72699 | OJ 569 | September 30, 2016 | 51252971, 51253111 | 1,340 | 217 | 27.2 | 62 | 70.1 | 18.1 | 11.1 | 6.9 | 5.5 | 25.8 | None | 100 |

^a Abbreviations: CORBIDI = Centro de Ornithología y Biodiversidad; LSUMZ = Louisiana State University Museum of Natural Science.^b Holotype.^c Formative plumage.**TABLE 2.** Morphometric data from all *Myrmoderus* taxa ($n = 105$). Mean values are given, followed by 2 standard deviations, with sample sizes in parentheses.

| Trait | <i>M. eowilsoni</i> | <i>M. f. ferrugineus</i> | <i>M. f. elutus</i> | <i>M. r. ruficauda</i> | <i>M. r. soror</i> | <i>M. loricatus</i> | <i>M. squamosus</i> |
|------------------------|------------------------|--------------------------|------------------------|------------------------|------------------------|-------------------------|-------------------------|
| Weight (g) | 27.4 ± 2.6 ($n = 8$) | 25.5 ± 3.8 ($n = 36$) | NA | NA | NA | NA | NA |
| Wing chord (mm) | 68.6 ± 4.6 ($n = 8$) | 63.6 ± 3.3 ($n = 36$) | 64.6 ± 3.3 ($n = 5$) | 63.9 ± 1.6 ($n = 9$) | 66.6 ± 7.9 ($n = 5$) | 59.8 ± 4.6 ($n = 13$) | 59.1 ± 2.6 ($n = 28$) |
| Tail length (mm) | 62.1 ± 6.4 ($n = 8$) | 54.9 ± 4.9 ($n = 36$) | 54.6 ± 3.6 ($n = 5$) | 51.7 ± 4.1 ($n = 9$) | 52.4 ± 1.8 ($n = 5$) | 65.2 ± 8.0 ($n = 13$) | 64.5 ± 6.3 ($n = 28$) |
| Wing:tail ratio | 1.1 ± 0.1 ($n = 8$) | 1.2 ± 0.1 ($n = 36$) | 1.2 ± 0.1 ($n = 5$) | 1.2 ± 0.1 ($n = 9$) | 1.3 ± 0.1 ($n = 5$) | 0.9 ± 0.1 ($n = 13$) | 0.9 ± 0.1 ($n = 28$) |
| Tarsus (mm) | 27.4 ± 1.8 ($n = 8$) | 26.2 ± 2.1 ($n = 36$) | 26.2 ± 1.2 ($n = 5$) | 23.8 ± 1.0 ($n = 9$) | 23.6 ± 2.0 ($n = 5$) | 25.6 ± 1.8 ($n = 12$) | 26.7 ± 2.2 ($n = 28$) |
| Exposed culmen (mm) | 17.6 ± 1.5 ($n = 8$) | 19.1 ± 2.3 ($n = 35$) | 18.4 ± 1.4 ($n = 5$) | 16.2 ± 1.6 ($n = 9$) | 16.3 ± 1.0 ($n = 5$) | 14.9 ± 2.0 ($n = 13$) | 13.6 ± 1.2 ($n = 27$) |
| Nares to bill tip (mm) | 11.0 ± 0.4 ($n = 8$) | 12.1 ± 1.6 ($n = 35$) | 11.6 ± 0.6 ($n = 5$) | 10.6 ± 0.9 ($n = 9$) | 10.3 ± 1.1 ($n = 5$) | 9.2 ± 0.9 ($n = 13$) | 8.5 ± 0.8 ($n = 27$) |
| Bill width (mm) | 6.8 ± 1.0 ($n = 8$) | 6.6 ± 1.0 ($n = 36$) | 6.5 ± 1.5 ($n = 5$) | 5.9 ± 0.4 ($n = 9$) | 5.6 ± 0.8 ($n = 5$) | 5.3 ± 0.8 ($n = 12$) | 5.0 ± 1.1 ($n = 27$) |
| Bill depth (mm) | 5.6 ± 0.5 ($n = 8$) | 5.3 ± 1.1 ($n = 36$) | 5.0 ± 0.4 ($n = 5$) | 5.2 ± 1.0 ($n = 9$) | 5.3 ± 1.4 ($n = 5$) | 4.4 ± 0.7 ($n = 13$) | 4.2 ± 0.7 ($n = 27$) |

The 2 loci were aligned separately in MUSCLE (Edgar 2004) from within Geneious using default values and then concatenated. Using PartitionFinder 2 (Lanfear et al. 2017) to compare DNA substitution models available in RAxML 8 (Stamatakis 2014) in a corrected Akaike's Information Criterion (AIC_c) framework gave a 3-partition scheme that pertained to the first, second, and third codon positions and an overall GTR+I+G model of DNA substitution. We used these settings to conduct a maximum-likelihood analysis in RAxML 8.2.10 (Stamatakis 2014) and selected the tree with the best likelihood score from 100 independent tree searches. Statistical support for the topology of this tree was then computed with the automatic majority-rule convergence criterion in RAxML 8.2.10 (Stamatakis 2014), resulting in 800 bootstrap replicates (Felsenstein 1985) and a final majority-rule consensus tree (Figure 4). When selecting among the substitution models available in MrBayes 3.2.6 (Ronquist et al. 2012), PartitionFinder 2 (Lanfear et al. 2017) gave the same partition scheme as for the maximum-likelihood analysis, but with substitution models of GTR+G, HKY+I, and GTR+I for the first, second, and third codon positions, respectively. We used these partitions and substitution models to perform the Bayesian analysis, comprising 4 independent runs of 4 MCMC chains, a chain temperature of 1.75, sampling for 20 million generations, a sampling frequency of 1,000, and a burn-in of 20%. We set a variable substitution-rate prior, an exponential alpha of 0.05, and a flat Dirichlet prior on the exchangeability parameters and base frequencies. Results from our Bayesian analyses were visualized in Tracer 1.6.0 (Rambaut et al. 2014) to assess convergence and stationarity. All runs reached convergence, and the average standard deviation of split frequencies from MrBayes 3.2.6 (Ronquist et al. 2012) was 0.002. Topologies of the maximum-likelihood and Bayesian trees are identical, so we report the maximum-likelihood tree with nodal support values from both methods (Figure 4).

We recovered *M. eowilsoni* as sister to *M. ferrugineus* with high support in all analyses (Figure 4). *Myrmoderus eowilsoni* has an uncorrected pairwise genetic distance of 8.4% in ND2 and 8.7% in ND3 from *M. f. ferrugineus* (found north of the Amazon River), and 9.2% in ND2 and 7.6% in ND3 from *M. f. elutus* (found south of the Amazon River). These distances are high when compared to those between other antbird sister-species, even within the same genus (*M. loricatus* and *M. squamosus*: ND2 uncorrected pairwise distance of 4.5%). *Myrmoderus f. elutus* has an uncorrected pairwise distance of 3.6% in ND2 and 4.3% in ND3 from *M. f. ferrugineus*, although it differs only slightly in plumage (Todd 1927) and voice (average 5.7 notes second⁻¹ in *M. f. elutus*, *n* = 5 individuals vs. average 7.0 notes second⁻¹ in *M. f. ferrugineus*, *n* = 20 individuals).

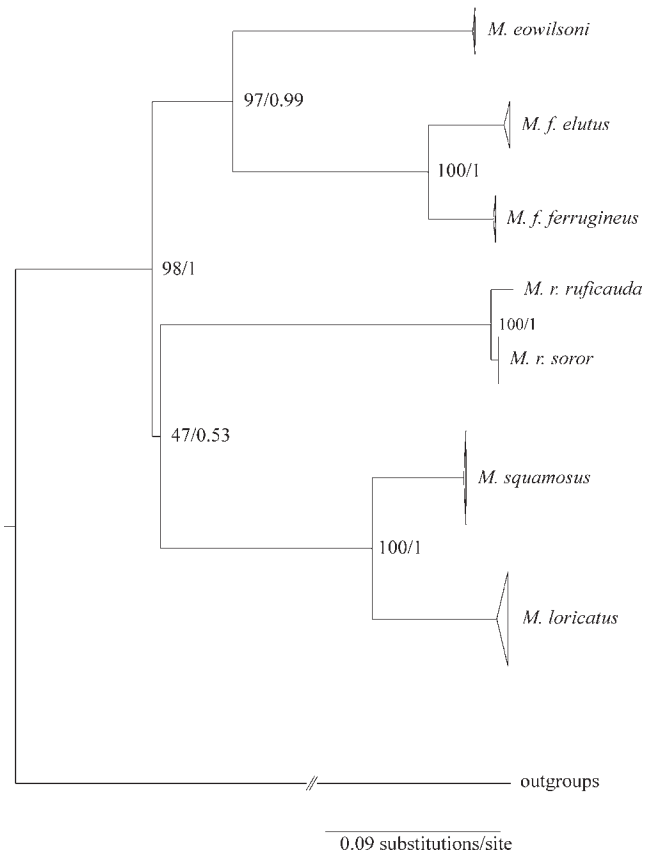


FIGURE 4. Phylogeny of the genus *Myrmoderus* estimated from a concatenated ND2–ND3 dataset (1,392 bp) using a maximum-likelihood analysis. The Bayesian analysis produced a tree that was topologically identical. Nodal support values are the likelihood bootstrap values and Bayesian posterior probabilities, respectively.

Isler et al. (2013) presented a taxonomic revision of the highly polyphyletic *Myrmeciza* antbirds in which they resurrected the genus *Myrmoderus* (Ridgway 1909) for *M. loricatus*, *M. squamosus*, *M. ruficauda*, and *M. ferrugineus*. Although *Myrmoderus* (*sensu* Isler et al. 2013) formed a clade supported by molecular, morphological, and some behavioral data, taxonomic relationships within this clade were unclear except for the sister relationship of *M. loricatus* and *M. squamosus*. With the discovery of *M. eowilsoni*, the sister relationship of this new species and *M. ferrugineus* becomes clear. The placement of *M. ruficauda* remains uncertain in our analyses, because of low support values on the subtending node. It was placed, however, as sister to *M. loricatus*–*M. squamosus* in all analyses (Figure 4). Adding nuclear loci to the mitochondrial DNA dataset would likely increase confidence in our placement of *M. ruficauda* (Maddison 1997), but we note that plumage, behavior, and vocalizations are all consistent with the genetically inferred relationships in this study.

Taxonomy

Myrmoderus eowilsoni and *M. ferrugineus* share several distinctive morphological traits, including bluish bare orbital skin, gray feet and tarsi, and white leading edges to the inner bend of the wing (proximal to the wrist), and lack the white interscapular patch shown by other species of *Myrmoderus*. Conversely, the other members of *Myrmoderus*, including the type of the genus (*M. loricatus*), have pink legs and feet and obvious white interscapular patches, the latter of which are regularly used in visual signaling in the forest understory (D. F. Lane personal observation). *Myrmoderus eowilsoni* and *M. ferrugineus* differ behaviorally from the other *Myrmoderus* by walking rather than hopping as a means of locomotion over the ground (Zimmer and Isler 2003; B. Whitney personal communication). Furthermore, *M. eowilsoni* and *M. ferrugineus* exhibit strong sexual dimorphism in song, whereas the 3 other *Myrmoderus* do not (B. Whitney personal communication; Figure 3). Todd (1927) noted morphometrics, extensively bare orbital skin, plumage coloration, and dark feet to justify the creation of a monotypic genus, *Myrmedestes*, for *Myrmoderus ferrugineus*. However, the name *Myrmedestes* Todd, 1927 fell into disuse when this genus was subsumed into a broadly conceived *Myrmeciza* Gray, 1841 by multiple authorities (Zimmer 1932, Peters 1951, Meyer de Schauensee 1970), prior to separation of *Myrmoderus* by Isler et al. (2013). We consider it appropriate, given the sister relationship of *Myrmoderus ferrugineus* and *M. eowilsoni* and the presence of numerous morphological and behavioral synapomorphies, to recognize *Myrmedestes* as a subgenus in *Myrmoderus* to include these 2 species.

Morphological Diagnosability

We took standard morphological measurements from 105 specimens representing all recognized taxa in the genus *Myrmoderus* (Appendix Table 4). For consistency, O.J. took all measurements. Measurement protocols followed Baldwin et al. (1931; their figure numbers follow the measurements) for tail length (fig. 120), wing chord (fig. 100), tarsus (fig. 136), exposed culmen (fig. 3), bill tip to nares (fig. 8), bill width at base (fig. 13), and bill depth at base (fig. 10; Table 2).

To evaluate the morphological data, we performed a principal component analysis with the PCA function in Scikit-learn (Pedregosa et al. 2011) using all specimens for which we had complete morphological data ($n = 101$). The first 2 principal components explained 91.4% of the variation in our dataset and clustered the species into 2 non-overlapping groups: one containing *M. loricatus* and *M. squamosus* and the other containing *M. eowilsoni*, both subspecies of *M. ferrugineus* (*M. f. ferrugineus* and *M. f. elutus*), and both subspecies of *M. ruficauda* (*M. r. ruficauda* and *M. r. soror* Pinto, 1940) (Figure 5). Despite

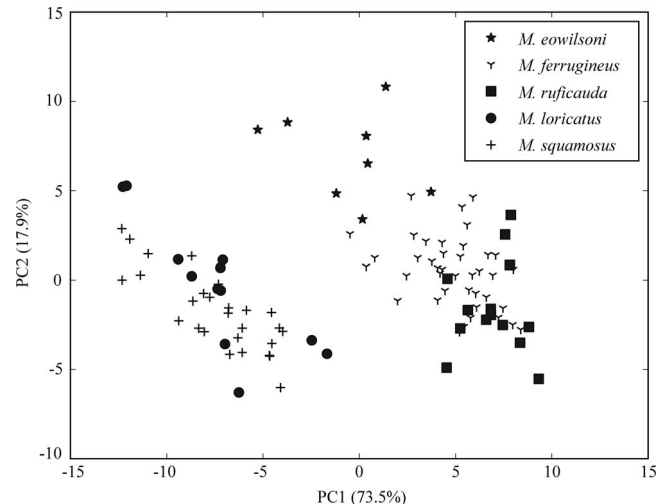


FIGURE 5. The first 2 principal components (PC1 and PC2) of 7 morphometric variables from all species of *Myrmoderus*. The loadings for PC1 and PC2 accounted for 73.5% and 17.9% of the variation in the dataset, respectively.

this overlap between *M. ferrugineus* and *M. ruficauda* in morphological measurements, the genetic data suggest that *M. ruficauda* is allied with *M. loricatus* and *M. squamosus* (Figure 4). In addition, *M. ruficauda* has pink legs and feet, a white interscapular patch, and hopping locomotory behavior, which all suggest a closer relationship to *M. loricatus* and *M. squamosus*.

Vocalizations

Songs of both male and female *M. eowilsoni* are distinguished from those of other members of the Thamnophilidae by a combination of a clear whistled quality, few notes, and a simple pattern. Compared to songs of *M. ferrugineus*, those of *M. eowilsoni* consist of fewer notes (2–6 vs. 8–14) that are delivered more slowly (average 2 notes second⁻¹ vs. average 7 notes second⁻¹; Figure 3). The male song seems quite stereotyped, but with some minor variation, particularly in pitch. Males sing 4 whistled notes given as 2 couplets (songs of 2 or 3 notes heard rarely), usually with the first note highest in pitch, the second lower in pitch, the third of similar or slightly higher pitch, and the final note lowest in pitch (Figure 3A). Although it is distinctive to the ear, the song of male *M. eowilsoni* can be likened to the slowed-down terminal 2 couplets of the song of male *M. ferrugineus*. The song of female *M. eowilsoni* shows wider variation within and among individuals in pitch and number of notes (3–6) than in the male, and the female song is delivered more slowly and often with a raspier quality (Figure 3B–3E). The call (Figure 3F) is generally a sputtering series of notes similar to that of *M. ferrugineus* (Figure 3I), but it is delivered at a slower pace and occasionally consists of only

single or doubled notes. The songs of *M. ferrugineus* (Figure 3G, 3H), *M. loricatus* (Figure 3K, 3L), and *M. squamosus* (Figure 3M, 3N) are similar to one another in also being composed of couplets that generally descend, but differ from that of *M. eowilsoni* in having more notes. By contrast, the dry, rattled song of *M. ruficauda* (Figure 3J) is immediately distinguishable from that of the other members of the genus. The songs of *M. eowilsoni* and *M. ferrugineus* are sexually dimorphic (i.e. female songs differ consistently from those of males in pattern, note number, and note shape), whereas the songs of the other 3 *Myrmoderus* are not (B. Whitney personal communication; Figure 3).

Distribution

Myrmoderus eowilsoni is known currently only from the Flor de Café ridge around the type locality, between 1,340 and 1,670 m a.s.l. (Figure 1). This distribution encompasses just 15 km² (minimum convex polygon of known localities), although extrapolating the range to include habitat from 1,300 to 1,700 m a.s.l. on the same ridge increases the distribution to ~78 km². We believe it is very likely that this species is found on additional ridges within the Cordillera Azul, and it should be looked for farther afield, perhaps as far as the Cordillera El Sira. Multiple previous ornithological surveys in the Cordillera Azul since the 1990s did not detect *M. eowilsoni*, yet there are ~2,480 km² of habitat between 1,300 and 1,700 m a.s.l. in the Cordillera Azul that may be suitable for this species, most of which are within the Parque Nacional Cordillera Azul (Figure 1). With knowledge of the elevational distribution and habitat requirements of the new species, as well as song playback, we believe that efforts to revisit previously surveyed localities within the Cordillera Azul are warranted in addition to exploring new localities.

Habitat, Ecology, and Behavior

Myrmoderus eowilsoni appears to be restricted to tall, montane, evergreen forest with intact understory characterized by small trees (diameter at breast height about 5–10 cm) and ferns, many moss-covered logs, and extensive dead leaf matter on the ground. We did not observe any individuals in second growth, edge, or tree-fall gap habitats, although in a few cases we could hear individuals singing from within 10 m of large plantations of sun-grown coffee. Most sightings occurred on or near level ridge tops, although this may have been biased by a lack of trails in steeper terrain. We did encounter a few individuals up to ~200 m downslope of ridgeline trails. Despite conducting extensive playback (at intervals of <100 m) along trails through forested habitats around Flor de Café from 900 to 1,850 m a.s.l., we did not detect the species below 1,340 or above 1,670 m a.s.l. Both members of the pair defend their territory, and most of our observations were of pairs

responding to playback of the song together, typically walking or occasionally flying toward the source of playback, and singing for as much as an hour after playback ceased. Only one female (CORBIDI 93483) had an enlarged ovary suggestive of breeding activity. Aside from the initial detection by J.R.B., we detected the species only after playback, and it seemed largely silent under natural conditions. We note, however, that we were generally not near known territories at dawn or dusk, when unprovoked singing would be most likely. Alternatively, unsolicited singing may be seasonal; other species of *Myrmoderus* can become quieter in the dry season, and their period of maximum singing is typically early in the morning between about 0630 and 0700 hours (B. Whitney personal communication). We observed *M. eowilsoni* only within 1 m of the ground, and individuals typically moved by short, low flights and by walking slowly along the ground. Walking involved deliberate steps accompanied by a jerking, dove-like head bob, with the tail held straight out behind. As with many terrestrial walking antbirds, antthrushes, and tapaculos, *M. eowilsoni* often hopped onto fallen logs or low branches in response to playback. We noted few instances of tail movements, mostly when an agitated individual was perched off the ground and responding to playback, when it would give occasional tail-raising flicks, bringing the tail slightly above horizontal from a position well below horizontal. Brief foraging observations consisted of birds picking through leaf litter to search for arthropod prey, and preserved stomach contents of specimens (CORBIDI 12380, 12381; LSUMZ 190882, 190883, 190884) contain arthropod parts.

When surveying for the species with playback, we located several adjacent territories along a ridgetop trail, which helped us estimate territory lengths of roughly 300–500 m. We revisited territories on consecutive days, and playback did not always elicit a response; this suggests that the pair may have been far enough away as to be out of earshot and that territories are quite large. We tentatively estimate a maximum territory size of 0.25 km², by squaring our estimate of the longest territory length.

Conservation

Myrmoderus eowilsoni is presently known only from the ridge of Flor de Café, yet little fieldwork has been conducted within the nearby Parque Nacional Cordillera Azul, one of the largest national parks in the country with an area of >13,500 km². Future surveys should target localities within this national park, which contains ~1,940 km² of area between 1,300 and 1,700 m a.s.l. that may be appropriate habitat for *M. eowilsoni* (Figure 1). Habitat alteration, primarily clear-cutting, around Flor de Café is extensive and ongoing. Sun coffee plantations, the primary agricultural land use there, do not provide habitat for *M. eowilsoni* or other forest species. Nevertheless, we found

M. eowilsoni to be fairly common in forest fragments around the type locality, and these fragments seem to maintain a remarkably intact avifauna, at least for the time being. Human colonists from other parts of Peru are rapidly clearing forest in the area and may soon eliminate much of the remaining forest around Flor de Café. Therefore, confirming the presence of *M. eowilsoni* in the national park is a high priority. Considering the proximity of extensive protected habitat within the national park, we are optimistic that the species will be found to be a common resident in other parts of the mountain range, and we hope that this discovery spurs further conservation and research in this unique region.

We here make a preliminary estimate of the population size of the species. Based on a territory size ranging from 0.066 km² (territory size reported for *M. ferrugineus* by Johnson et al. 2011) to 0.25 km² (our maximum estimate), 2 birds territory⁻¹, territories in only 45.2% of appropriate habitat (taken from mean estimate for occupancy of *M. ferrugineus* by Stouffer 2007), and an area of 1,940 km² between 1,300 and 1,700 m a.s.l., the predicted population size within the national park is 7,000–27,000 individuals. If we include ridges of the Cordillera Azul found outside the park (including the Flor de Café ridge) but within the latitudinal range of the park, the area between 1,300 and 1,700 m a.s.l. increases to ~2,480 km², and the predicted population size is 9,000–34,000 individuals. These estimates of population size are crude and highly preliminary because of a large number of assumptions, but they nonetheless serve as a starting point for assessment of the actual population size. Flor de Café lies on the leeward side of the Cordillera Azul, and we suspect that the lower elevational limit of *M. eowilsoni* is locally maintained by drier habitats as one descends toward the rain shadow of the Huallaga valley. In more windward and humid regions of the Cordillera Azul, appropriate habitat may extend considerably lower in elevation, perhaps as low as ~900 m. Survey work is urgently needed to determine the full distribution of *M. eowilsoni*, to assess territory size and occupancy, and to improve estimates of population size. Because most of the estimated distribution of *M. eowilsoni* lies within the Parque Nacional Cordillera Azul, we do not expect this species to face extensive habitat loss. Despite the restricted distribution and habitat loss in the immediate vicinity of the type locality, we consider an IUCN Red List status of “Data Deficient” as most appropriate until the distribution and population trends can be further evaluated.

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Ethics statement: Specimen collecting and export permits were provided by the Servicio Nacional Forestal y de Fauna Silvestre (SERFOR) under the following permits: Resolución no. 203-2015 SERFOR-DGGSPFFS, Resolución no. 222-2015 SERFOR-DGGSPFFS, Permiso no. 003104 SERFOR, and Permiso no. 003105 SERFOR. All specimen collection was done under Louisiana State University’s Institutional Animal Care and Use Committee protocol no. 15-036.

Author contributions: J.R.B. made the initial discovery. A.E.M., O.J., D.F.L., J.R.B., F.A., and J.F. collected data. A.E.M., O.J., and D.F.L. collected and prepared specimens and analyzed the data. A.E.M. and O.J. wrote the paper.

Data deposits: All genetic data are deposited in GenBank (see Appendix Table 3 for accession numbers). Sequences alignments and phylogenetic trees are available at TreeBASE (<http://purl.org/phylo/treebase/phylovs/study/TB2:S21548>).

Nomenclature: The nomenclature in this paper has been reviewed by the Working Group on Avian Nomenclature of the International Ornithologists’ Union. *Myrmoderus eowilsoni* was registered on ZooBank and it received the following LSID: urn:lsid:zoobank.org:act:A05E5983-E5BC-4189-99C7-AC9E813D1E1C

LITERATURE CITED

- Alverson, W. S., L. O. Rodríguez, and D. K. Moskovits (2001). Perú: Biabo Cordillera Azul. Rapid Biological Inventories 2. The Field Museum, Chicago, IL, USA.
- Baldwin, S. P., H. C. Oberholser, and L. G. Worley (1931). Measurements of birds. Scientific Publications of the Cleveland Museum of Natural History 2.
- Bravo, G. A. (2012). Phenotypic and niche evolution in the antbirds (Aves, Thamnophilidae). Ph.D. dissertation, Louisiana State University, Baton Rouge, LA, USA.
- Edgar, R. C. (2004). MUSCLE: Multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Research* 32:1792–1797.

Felsenstein, J. (1985). Confidence limits on phylogenies: An approach using the bootstrap. *Evolution* 39:783–791.

Isler, M. L., G. A. Bravo, and R. T. Brumfield (2013). Taxonomic revision of *Myrmeciza* (Aves: Passeriformes: Thamnophilidae) into 12 genera based on phylogenetic, morphological, behavioral, and ecological data. *Zootaxa* 3717:469–497.

Isler, P. R., and B. M. Whitney (2002). Songs of the Antbirds [CD]. Macaulay Library of Natural Sounds, Ithaca, NY, USA.

Johnson, E. I., P. C. Stouffer, and C. F. Vargas (2011). Diversity, biomass, and trophic structure of a central Amazonian rainforest bird community. *Revista Brasileira de Ornitologia* 19:1–16.

Kearse, M., R. Moir, A. Wilson, S. Stones-Havas, M. Cheung, S. Sturrock, S. Buxton, A. Cooper, S. Markowitz, C. Duran, T. Thierer, et al. (2012). Geneious Basic: An integrated and extendable desktop software platform for the organization and analysis of sequence data. *Bioinformatics* 28:1647–1649.

Lanfear, R., P. B. Frandsen, A. M. Wright, T. Senfeld, and B. Calcott (2017). PartitionFinder 2: New methods for selecting partitioned models of evolution for molecular and morphological phylogenetic analyses. *Molecular Biology and Evolution* 34: 772–773.

Maddison, W. P. (1997). Gene trees in species trees. *Systematic Biology* 46:523–536.

Merkord, C. L., T. Mark, D. Susanibar, A. Johnson, and C. C. Witt (2009). Avifaunal survey of the Rio Chipaota Valley in the Cordillera Azul region, San Martín, Peru. *Ornitología Neotropical* 20:535–552.

Meyer de Schauensee, R. (1970). *A Guide to the Birds of South America*. Livingston, Wynnewood, PA, USA.

Munsell, A. (No date). *Munsell Book of Color, Glossy Collection*. Gretag Macbeth, New Windsor, NY, USA.

O'Neill, J. P., D. F. Lane, A. W. Kratter, A. P. Capparella, and C. F. Joo (2000). A striking new species of barbet (Capitoninae: *Capito*) from the eastern Andes of Peru. *The Auk* 117:569–577.

Pedregosa, F., G. Varoquaux, A. Gramfort, V. Michel, B. Thirion, O. Grisel, M. Blondel, P. Prettenhofer, R. Weiss, V. Dubourg, J. Vanderplas, et al. (2011). Scikit-learn: Machine learning in Python. *Journal of Machine Learning Research* 12:2825–2830.

Peters, J. L. (1951). *Check-list of Birds of the World*, vol. 7. Museum of Comparative Zoology, Cambridge, MA, USA.

Rambaut, A., M. A. Suchard, D. Xie, and A. J. Drummond (2014). Tracer 1.6. <http://tree.bio.ed.ac.uk/software/tracer/>

Remsen, J. V., Jr., J. I. Areta, C. D. Cadena, S. Claramunt, A. Jaramillo, J. F. Pacheco, J. Pérez-Emán, M. B. Robbins, F. G. Stiles, D. F. Stotz, and K. J. Zimmer (2017). A classification of the bird species of South America. American Ornithologists' Union. <http://www.museum.lsu.edu/~Remsen/SACCBaseline.htm>

Ridgway, R. (1909). New genera, species and subspecies of Formicariidae, Furnariidae, and Dendrocolaptidae. *Proceedings of the Biological Society of Washington* 22:69–74.

Ridgway, R. (1912). *Color Standards and Color Nomenclature*. Published by the author, Washington, DC, USA.

Ronquist, F., M. Teslenko, P. van der Mark, D. L. Ayres, A. Darling, S. Höhna, B. Larget, L. Liu, M. A. Suchard, and J. P. Huelsenbeck (2012). MrBayes 3.2: Efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology* 61:539–542.

Stamatakis, A. (2014). RAxML version 8: A tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics* 30:1312–1313.

Stouffer, P. C. (2007). Density, territory size, and long-term spatial dynamics of a guild of terrestrial insectivorous birds near Manaus, Brazil. *The Auk* 124:291–306.

Todd, W. E. C. (1927). New gnateaters and antbirds from tropical America, with a revision of the genus *Myrmeciza* and its allies. *Proceedings of the Biological Society of Washington* 40:149–178.

Zimmer, J. T. (1932). Studies of Peruvian birds. VI. The formicarian genera *Myrmoborus* and *Myrmeciza* in Peru. *American Museum Novitates* 545:1–24.

Zimmer, K. J. and M. L. Isler. (2003). Family Thamnophilidae (typical antbirds). In *Handbook of Birds of the World*, vol. 8: Broadbills to Tapaculos (J. del Hoyo, A. Elliott, and D. A. Christie, Editors). Lynx Edicions, Barcelona, Spain.

APPENDIX

Specimen and Tissue Samples Used for Phylogenetic and Morphometric Analyses

APPENDIX TABLE 3. Individuals sampled for mitochondrial phylogeny, including outgroup taxa.

| Taxon | GenBank accession numbers ^a | Tissue catalog number ^b | Locality | Latitude | Longitude |
|--|--|------------------------------------|---|----------|-----------|
| <i>Myrmoderus eowilsoni</i> ^c | KY849953, KY849952 | LSUMZ B-93477 | Peru: San Martín; 2.5 km WNW Flor de Café | 7.39°S | 76.32°W |
| | KY849951, KY849950 | LSUMZ B-93476 | Peru: San Martín; 2.5 km WNW Flor de Café | 7.39°S | 76.32°W |
| <i>Myrmoderus f. ferrugineus</i> | HM637280, HM637145 | LSUMZ B-55285 | Suriname: Sipaliwini; 78 km S Apura | 4.48°N | 57.04°W |
| <i>Myrmoderus f. elutus</i> | KY849954, KY849937 | LSUMZ B-20403 | Brazil: Amazonas; ~80 km N Manaus | 2.37°S | 60.04°W |
| | KY849936, KY849935 | MZUSP 96106 | Brazil: Amazonas; left bank of Rio Sucunduri | 5.28°S | 59.7°W |
| <i>Myrmoderus r. ruficauda</i> | KY849934, KY849933 | LSUMZ B-86315 | Brazil: Amazonas; Rio Sucunduri | 6.77°S | 59.09°W |
| | KY849943, NA | LGEMA 1527 | Brazil: Bahia; Ribeirão do Largo, Fazenda Boa Esperança | 15.42°S | 40.63°W |
| <i>Myrmoderus r. soror</i> | KY849945, KY849944 | FMNH 392445 | Brazil: Pernambuco; Serra do Espelho | 8.7°S | 35.83°W |
| | KY849947, KY849946 | FMNH 399262 | Brazil: Alagoas; Ibateguara | 8.98°S | 35.87°W |

APPENDIX TABLE 3. Continued.

| Taxon | GenBank accession numbers ^a | Tissue catalog number ^b | Locality | Latitude | Longitude |
|---|--|------------------------------------|---|----------|-----------|
| <i>Myrmoderus loricatus</i> | KY849940, KY849939 | MZUSP 85430 | Brazil: Minas Gerais; Mina da Alegria, Mariana | 20.38°S | 43.42°W |
| | KY849942, KY849941 | MZUSP 85433 | Brazil: Minas Gerais; Mina da Alegria, Mariana | 20.38°S | 43.42°W |
| | KC715502, KY849938 | LGEMA 13014 | Brazil: Rio de Janeiro; PN Serra dos Órgãos (Teresópolis) | 22.43°S | 42.99°W |
| <i>Myrmoderus squamosus</i> | HM637281, HM637146 | LSUMZ B-16940 | Brazil: São Paulo; Salesópolis | 23.53°S | 45.85°W |
| | KC715574, KY849948 | LGEMA 1526 | Brazil: São Paulo; Biritiba Mirim | 23.56°S | 46.05°W |
| | KC715576, KY849949 | MZUSP 81159 | Brazil: São Paulo; E. E. Bananal | 22.81°S | 44.37°W |
| <i>Thamnophilus doliatus</i> ^d | EF030296, EF030234 | UWBM 71559 | Bolivia: Santa Cruz; Provincia de Cordillero, Abapo | 18.9°S | 63.4°W |
| <i>Hylophylax naevioides</i> ^d | EF640019, EF640086 | LSUMZ B-2230 | Panama: Darien; ~6 km NW Cana on E slope Cerro Pirre | 7.8°N | 77.72°W |
| <i>Myrmeciza longipes</i> ^d | HM637279, HM637144 | LSUMZ B-46533 | Panama: Panama; ~7 km SE Pacora | 9.04°N | 79.25°W |
| <i>Pithys albifrons</i> ^d | EF640047, EF640114 | FMNH 391430 | Brazil: Amapá; Fazenda Itapoã | 2.07°N | 50.93°W |

^a For ND2 and ND3, respectively.^b Abbreviations: FMNH = Field Museum of Natural History; LGEMA = Laboratório de Genética e Evolução Molecular de Aves, São Paulo; LSUMZ = Louisiana State University Museum of Natural Science; MZUSP = Museum of Zoology of the University of São Paulo; and UWBM = University of Washington Burke Museum.^c Holotype.^d Outgroup.**APPENDIX TABLE 4.** Specimens used for morphometric analyses ($n = 105$; measurement data are shown in Table 2).

| Species | Catalog number ^a | Locality | Latitude | Longitude |
|----------------------------------|-----------------------------|---|----------|-----------|
| <i>Myrmoderus eowilsoni</i> | CORBIDI 12380 | Peru: San Martín; 2.5 km WNW Flor de Café | 7.39°S | 76.32°W |
| | CORBIDI 12381 | Peru: San Martín; 2.5 km WNW Flor de Café | 7.39°S | 76.32°W |
| | CORBIDI 12382 | Peru: San Martín; 1.6 km NE Flor de Café | 7.39°S | 76.29°W |
| | CORBIDI 12383 | Peru: San Martín; 1.6 km NE Flor de Café | 7.39°S | 76.29°W |
| | LSUMZ 190882 | Peru: San Martín; 2.5 km WNW Flor de Café | 7.39°S | 76.32°W |
| | LSUMZ 190883 | Peru: San Martín; 2.5 km WNW Flor de Café | 7.39°S | 76.32°W |
| | LSUMZ 190884 | Peru: San Martín; 2.5 km WNW Flor de Café | 7.39°S | 76.32°W |
| | LSUMZ 190885 | Peru: San Martín; 6 km SE Flor de Café | 7.43°S | 76.25°W |
| <i>Myrmoderus f. ferrugineus</i> | FMNH 108377 | Guyana: Essequibo River, Rockstone | 5.98°N | 58.55°W |
| | FMNH 108378 | Guyana: Essequibo River, Rockstone | 5.98°N | 58.55°W |
| | FMNH 120247 | Guyana: Corentyne, Itabu Creek head | 1.55°N | 58.17°W |
| | FMNH 120248 | Guyana: Corentyne, Itabu Creek head | 1.55°N | 58.17°W |
| | FMNH 120249 | Guyana: Corentyne, Itabu Creek head | 1.55°N | 58.17°W |
| | FMNH 264476 | Suriname: Wilhelmina Mountains, West River | 3.43°N | 56.75°W |
| | FMNH 264477 | Suriname: Wilhelmina Mountains, West River | 3.43°N | 56.75°W |
| | FMNH 295737 | Brazil: Amapá; mun. Macapá, Rio Amaparí | 1.6°N | 52.49°W |
| | FMNH 295738 | Brazil: Amapá; mun. Macapá, Rio Amaparí | 1.6°N | 52.49°W |
| | FMNH 373073 | Guyana: Essequibo; between Tapakuma and Pomeroon rivers | 7.24°N | 58.72°W |
| | FMNH 56900 | Guyana: Mazaruni-Potaro, Bartica Grove | 6.41°N | 58.63°W |
| | KU 88819 ^b | Guyana: Iwokrama Reserve; ~41 km SW Kurupukari | 4.34°N | 58.85°W |
| | KU 89038 | Guyana: North West district, Baramita | 7.35°N | 60.48°W |
| | KU 90840 | Guyana: Parabara savanna | 2.16°N | 59.3°W |
| | LSUMZ 178456 | Suriname: Sipaliwini; ~70 km SE Apura | 4.66°N | 56.76°W |
| | LSUMZ 178457 ^b | Suriname: Sipaliwini; ~70 km SE Apura | 4.66°N | 56.76°W |
| | LSUMZ 178458 | Suriname: Sipaliwini; ~70 km SE Apura | 4.66°N | 56.76°W |
| | LSUMZ 67334 | Brazil: Amapá; alto Rio Araguari | 1.52°N | 52.02°W |
| | LSUMZ 67335 | Brazil: Amapá, Estrada de Ferro Amapá | 0.67°N | 51.83°W |
| | LSUMZ 67336 | Brazil: Amapá, Estrada de Ferro Amapá | 0.67°N | 51.83°W |
| | LSUMZ 67337 | Brazil: Amapá, Fóz do Rio Falcino | 0.93°N | 51.58°W |
| | USNM 147368 | Guyana: Mazaruni-Potaro, Bartica Grove | 6.41°N | 58.63°W |
| | USNM 147369 | Guyana: Mazaruni-Potaro, Bartica Grove | 6.41°N | 58.63°W |

APPENDIX TABLE 4. Continued.

| Species | Catalog number ^a | Locality | Latitude | Longitude |
|----------------------------------|-----------------------------|---|----------|-----------|
| <i>Myrmoderus f. ferrugineus</i> | USNM 514992 | Brazil: Amapá, Serra do Navio Amapá | 0.98°N | 52.05°W |
| | USNM 514993 | Brazil: Amapá, Serra do Navio Amapá | 0.98°N | 52.05°W |
| | USNM 515594 | Brazil: Amapá, Serra do Navio Amapá | 0.98°N | 52.05°W |
| | USNM 586395 | Guyana: North West district, Baramita | 7.35°N | 60.48°W |
| | USNM 625221 | Guyana: North side Acari Mountains | 1.38°N | 58.93°W |
| | USNM 625526 | Guyana: upper Essequibo River | 1.58°N | 58.63°W |
| | USNM 625527 | Guyana: upper Essequibo River | 1.58°N | 58.63°W |
| | USNM 627058 | Guyana: Courantyne River, 8 km S Siparuta | 5.17°N | 57.29°W |
| | USNM 637017 | Guyana: Upper Takutu, upper Rewa River | 3.45°N | 58.58°W |
| | USNM 637075 | Guyana: Upper Takutu, upper Rewa River | 3.45°N | 58.58°W |
| | USNM 84093 | Guyana: Demerara | 6.77°N | 58.15°W |
| | USNM 90584 | Guyana: Demerara | 6.77°N | 58.15°W |
| | USNM 92006 | Guyana: Demerara | 6.77°N | 58.15°W |
| | USNM 92016 | Guyana: Demerara | 6.77°N | 58.15°W |
| <i>Myrmoderus f. elutus</i> | FMNH 254862 | Brazil: Pará; Villa Braga | 4.42°S | 56.29°W |
| | LACM 31977 | Brazil: Pará; Rio Tapajós, Urucurituba | 3.8°S | 55.53°W |
| | LACM 31978 | Brazil: Pará; Rio Tapajós, Urucurituba | 3.8°S | 55.53°W |
| | LACM 31979 | Brazil: Pará; Rio Tapajós, Urucurituba | 3.8°S | 55.53°W |
| | LACM 31980 | Brazil: Pará; Rio Tapajós, Urucurituba | 3.8°S | 55.53°W |
| <i>Myrmoderus r. ruficauda</i> | LSUMZ 113498 | Brazil: Espírito Santo, Lagoa Juparanã | 19.27°S | 40.11°W |
| | LACM 28048 | Brazil: Espírito Santo, Pau Gigante | 19.83°S | 40.37°W |
| | LACM 28049 | Brazil: Espírito Santo, Pau Gigante | 19.83°S | 40.37°W |
| | LACM 28050 | Brazil: Espírito Santo, Pau Gigante | 19.83°S | 40.37°W |
| | USNM 368286 | Brazil: Espírito Santo, Mun. Santa Cruz | NA | NA |
| | USNM 368287 | Brazil: Espírito Santo, Mun. Colatina, Linhares | 19.4°S | 40.07°W |
| | USNM 368288 | Brazil: Espírito Santo, Mun. Colatina, Linhares | 19.4°S | 40.07°W |
| | USNM 368289 | Brazil: Espírito Santo, Mun. Colatina, Linhares | 19.4°S | 40.07°W |
| | USNM 44799 | Brazil: Bahia | NA | NA |
| | FMNH 311031 | Brazil: Alagoas, Usina Sinimbu | 9.92°S | 36.13°W |
| <i>Myrmoderus r. soror</i> | LACM 26938 | Brazil: Alagoas, Usina Sinimbu | 9.92°S | 36.13°W |
| | LACM 26939 | Brazil: Alagoas, Usina Sinimbu | 9.92°S | 36.13°W |
| | LACM 26940 | Brazil: Alagoas, Usina Sinimbu | 9.92°S | 36.13°W |
| | LACM 26941 | Brazil: Alagoas, Usina Sinimbu | 9.92°S | 36.13°W |
| | FMNH 311032 | Brazil: Rio de Janeiro, Parque Nacional do Itatiaia | 22.44°S | 44.61°W |
| <i>Myrmoderus loricatus</i> | FMNH 311033 | Brazil: Rio de Janeiro, Miguel Pereira | 22.45°S | 43.37°W |
| | LACM 27950 | Brazil: Rio de Janeiro, Terezopolis, Fazenda Boa Fe | 22.36°S | 42.93°W |
| | LACM 66626 | Brazil: Rio de Janeiro, Parque Nacional do Itatiaia | 22.44°S | 44.61°W |
| | LACM 74070 | Brazil: Rio de Janeiro, Terezopolis, Fazenda Boa Fe | 22.36°S | 42.93°W |
| | LACM 74071 | Brazil: Rio de Janeiro, Miguel Pereira | 22.45°S | 43.37°W |
| | LSUMZ 113499 | Brazil: Bahia, Itirussú | 13.53°S | 40.15°W |
| | USNM 14441 ^b | South America: unknown locality | NA | NA |
| | USNM 32856 | Brazil: unknown locality | NA | NA |
| | USNM 42613 | South America: unknown locality | NA | NA |
| | USNM 525966 | South America: unknown locality | NA | NA |
| | USNM 84094 | Brazil: Bahia | NA | NA |
| | USNM 84095 | Brazil: Bahia | NA | NA |
| | FMNH 258114 | Brazil: São Paulo, Trapandé, Pasto Grande | 25.07°S | 47.93°W |
| | FMNH 265197 | Brazil: São Paulo, Rio Ipiranga, Boa Vista | 24.37°S | 47.83°W |
| <i>Myrmoderus squamosus</i> | FMNH 265198 | Brazil: São Paulo, Rio Juquiá, Pousinho | 24.37°S | 47.55°W |
| | FMNH 265199 | Brazil: São Paulo, Rio Ipiranga, Laranja Azeda | 24.32°S | 47.85°W |
| | FMNH 265200 | Brazil: São Paulo, Rio Ipiranga, Laranja Azeda | 24.32°S | 47.85°W |
| | FMNH 265201 | Brazil: São Paulo, Barra do Rio Juquiá | 24.37°S | 47.82°W |
| | FMNH 344536 | Brazil: São Paulo, Barra do Icapara | 24.67°S | 47.42°W |
| | FMNH 344537 | Brazil: São Paulo, Barra do Icapara | 24.67°S | 47.42°W |
| | FMNH 344538 | Brazil: São Paulo, Barra do Icapara | 24.67°S | 47.42°W |
| | FMNH 344539 | Brazil: São Paulo, Barra do Icapara | 24.67°S | 47.42°W |
| | FMNH 344540 | Brazil: São Paulo, Barra do Icapara | 24.67°S | 47.42°W |
| | FMNH 344541 | Brazil: São Paulo, Estação Engenheiro Ferraz | 23.98°S | 46.6°W |
| | FMNH 344542 | Brazil: São Paulo, Barra do Icapara | 24.67°S | 47.42°W |

APPENDIX TABLE 4. Continued.

| Species | Catalog number ^a | Locality | Latitude | Longitude |
|-----------------------------|-----------------------------|---|----------|-----------|
| <i>Myrmoderus squamosus</i> | FMNH 344543 | Brazil: São Paulo, Costão dos Engenhos | 24.67°S | 47.5°W |
| | FMNH 344544 | Brazil: São Paulo, Costão dos Engenhos | 24.67°S | 47.5°W |
| | FMNH 50741 | Brazil: São Paulo, Fazenda Cajoa | 22.95°S | 49.98°W |
| | FMNH 56960 | Brazil: São Paulo, Victoria | 22.78°S | 48.4°W |
| | FMNH 73615 | Brazil: Santa Catarina, Joinville | 26.3°S | 48.83°W |
| | FMNH 73616 | Brazil: Santa Catarina, Joinville | 26.3°S | 48.83°W |
| | FMNH 73617 ^b | Brazil: Santa Catarina, Joinville | 26.3°S | 48.83°W |
| | KU 67585 | Brazil: São Paulo, Salesopolis, Casa Grande | 23.54°S | 45.85°W |
| | LSUMZ 52763 | Brazil: São Paulo, Salesopolis, Casa Grande | 23.54°S | 45.85°W |
| | LSUMZ 65179 | Brazil: São Paulo, Salesopolis, Casa Grande | 23.54°S | 45.85°W |
| | LSUMZ 68029 | Brazil: São Paulo, Salesopolis, Casa Grande | 23.54°S | 45.85°W |
| | LSUMZ 68030 | Brazil: São Paulo, Salesopolis, Casa Grande | 23.54°S | 45.85°W |
| | LSUMZ 68259 | Brazil: São Paulo, Salesopolis, Casa Grande | 23.54°S | 45.85°W |
| | USNM 108244 | Brazil: Santa Catarina | NA | NA |
| | USNM 177730 | Brazil: Iguape | NA | NA |

^a Abbreviations: LSUMZ = Louisiana State University Museum of Natural Science; CORBIDI = Centro de Ornitología y Biodiversidad; FMNH = Field Museum of Natural History; USNM = National Museum of Natural History, Smithsonian Institution; KU = University of Kansas Biodiversity Institute; and LACM = Natural History Museum of Los Angeles County.

^b Excluded from PCA because of incomplete data.