

Molecular systematics and taxonomic revision of the Ihering's Antwren complex (*Myrmotherula iheringi*: *Thamnophilidae*), with description of a new species from southwestern Amazonia

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Ihering's Antwren (*Myrmotherula*⁸ *iheringi*) belongs to a morphologically conservative group of antbirds (i.e., the *Myrmotherula* “gray antwren assemblage” *sensu* Hackett and Rosenberg 1990) and is endemic to southwestern Amazonia where it occurs in Bolivia, Brazil, and Peru (Zimmer and Isler 2003). Currently, two parapatric subspecies are recognized in the polytypic *M. iheringi* based primarily on differences in female plumage patterns (Todd, 1927): *M. i. iheringi* Sneath, 1914, distributed in the Madeira–Tapajós interfluvium in the Brazilian states of Amazonas, Pará, and Rondônia; and *M. i. heteroptera* Todd, 1927, which occurs west of the Madeira and south of the Amazon rivers in the state of Amazonas, and the departments of Pando in Bolivia and Madre de Dios in Peru (Zimmer and Isler 2003). In July, 1996, during the avifaunal aspect of a Rapid Ecological Evaluation (REA) of the Serra do Divisor National Park in Acre, Brazil, conducted by the non-governmental organization “S.O.S. Amazônia” in Rio Branco and the Museu Paraense Emílio Goeldi (MPEG) in Belém, and largely funded by The Nature Conservancy International (TNC), BMW made the first recordings of *M. i. heteroptera* and collected an adult male, the first modern specimen of the taxon. He subsequently recorded multiple other individuals in the Serra do Divisor, on the left bank of the middle Rio Madeira in Amazonas state, and also along the right bank of the lower rio Javari where he and LFS collected two additional specimens of *M. i. heteroptera*; later on, in March 2006, AA obtained five additional specimens and recordings of *M. i. heteroptera* at the “Reserva de Desenvolvimento Sustentável Cujubim” in Amazonas state. The loudsong of *M. i. heteroptera* from these regions was well differentiated from that of individuals which AA, BMW, EG, and MPDS had recorded in the more southerly portion of that taxon's supposed range in eastern Acre and southeastern Peru, and from the vocalizations of *M. i. iheringi* which BMW recorded at the type locality and numerous points across the Madeira–Tapajós interfluvium. More recently, the morphological diagnoses of *M. iheringi* subspecies has been questioned (Zimmer and Isler 2003), underscoring the need of a modern, multi-character taxonomic revision of the *M. iheringi* complex. New molecular, morphological and vocal data presented herein show that the current taxonomy of *M. iheringi* does not reflect its evolutionary history. Molecular analyses recovered three main reciprocally monophyletic clades (Fig. 1) also diagnosed by distinct loudsong note structures (Fig. 2) and female plumage patterns, which correspond to a monophyletic *M. i. iheringi* and a paraphyletic *M. i. heteroptera* (Fig. 3). We show that these three clades are better treated as separate species and propose to name one of them, formerly treated as a part of the subspecies *M. i. heteroptera*, as:

Myrmotherula oreni

Bamboo Antwren

choquinha-do-bambu (Portuguese)



Holotype.— MPEG 61342, skin, adult female, skull 100% ossified, ovary 6×4 mm, collected in bamboo forest on 12 November 2006 by E. Guilherme and M. P. D. Santos at km 11 of “Ramal Jarinal”, Transacrea highway (AC-090), Rio Branco, Acre, Brazil (09°54'02,1"S/68°28'32,1"W); prepared by José Nilton da Silva Santa-Brígida under field number UFAC 798. Tissue samples deposited at MPEG under field number UFAC 798. Hologenotype (Chakrabarty 2010) sequences of the mitochondrial gene NADH subunit 2 (1,015 bp) deposited in GenBank (accession number KC495708).

Diagnosis: Morphology.— Alphanumeric color designations determined through direct comparison with Smithe (1975). Phenotypically, as other taxa currently grouped under *M. iheringi*, the new species can be assigned to the “gray antwren assemblage” (*sensu* Hackett and Rosenberg 1990) of the genus *Myrmotherula* (*Thamnophilidae*) along with *M. axillaris*, *M. schisticolor*, *M. sunensis*, *M. minor*, *M. fluminensis*, *M. behni*, *M. grisea*, *M. unicolor*, *M. snowi*, *M. longipennis*, *M. urosticta*, and *M. menetriesii* based on the males' predominantly gray plumage (Zimmer and Isler 2003), even though unpublished molecular data indicate this

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⁸ Genus *Myrmotherula* 8: 577.

grouping as not monophyletic (Bravo, pers. comm.). However, both its plumages and its vocalizations clearly place it with the *M. iheringi* complex. Adult females of the new taxon are readily differentiated from female *M. iheringi iheringi* and *M. i. heteroptera* by the combination of a pale horn (color 92) eyering, forehead and conspicuous superciliary, and the sides of neck, throat, and belly solid yellow ocher (color 123C); it is further distinguished from *heteroptera* by more purely gray (medium plumbeous; color 87) upper parts and jet black wing-coverts with white terminal dots. Males of the new taxon and those of nominate *iheringi* and *heteroptera* are not mutually diagnosed by any plumage or morphometric characters. **Voice.**— The loudsong is immediately distinguished in spectrographic analysis from those of *iheringi* and *heteroptera* by the structure of the notes (Fig. 2; see also below). **Genetic divergence.**— Separated from its close relatives *iheringi* and *heteroptera* by approximately 1.8 and 5.1% sequence divergence, respectively, in the mitochondrial genes cytochrome *b* and NADH subunit 2 (Fig. 1).

Distribution.— *Myrmotherula oreni* occurs in the eastern part of the Brazilian state of Acre (BMW recordings 1997 [see SI]; Guilherme and Santos 2009, Aleixo and Guilherme 2010, Guilherme 2012), and the departments of Pando in Bolivia (Schulenberg *et al.* 2000, Flores and Martínez 2007) and Madre de Dios, Cuzco, Ucayali, and Puno in Peru (Schulenberg *et al.* 2007; Fig. 3; see SI). Thus, as also verified for a second recently described species (Rufous Twistwing *Chnipodectes superrufus*; Lane *et al.* 2007, Tobias *et al.* 2008), the distribution of the new taxon described herein coincides with that of bamboo-dominated forests in southwestern Amazonia (Nelson 1994).

Description of holotype.— See color illustration. Alphanumeric color designations determined through direct comparison with Smithe (1975). Crown, nape, and mantle through uppertail coverts medium plumbeous (color 87). Forehead and superciliary pale horn (color 92), contrasting strongly with the plumbeous upperparts. Sides of neck, cheeks, flanks, and belly solid yellow ocher (color 123C). Throat and breast slightly lighter than remaining underparts and with a distinct chamois (123D) color. Primaries and secondaries medium plumbeous, outer vanes of primaries edged with blackish, inner vanes narrowly edged whitish. Wing-coverts solid jet black with white terminal dots; underwing coverts white. Tail worn, with medium plumbeous rectrices presenting central and terminal blackish areas. **Soft parts in life:** Iris gray; maxilla black and mandible bluish-gray; tarsi and feet bluish-gray. **Measurements of holotype:** Wing length: 46.6 mm; tail length: 34.8 mm; tarsus length: 16.7 mm; bill length from anterior edge of nares: 8.5 mm; bill width at anterior edge of nares: 3.3 mm; bill depth at anterior edge of nares 3.2 mm; body mass 8 g.

Etymology.— The new taxon is named after our colleague David C. Oren who, among many other contributions to Amazonian ornithology, inaugurated the modern ornithological exploration of the Brazilian state of Acre, which resulted in a new species description (Whitney *et al.* 2004), several range extensions and new country records (Whittaker and Oren 1999), and the inspiration of a new generation of resident ornithologists (Guilherme 2012). The common names Bamboo Antwren (English) and “choquinha-do-bambu” (Portuguese) refer to the frequent

association of the new species with bamboo-dominated forests in southwestern Amazonia (Fig. 4).

REMARKS

Type series.— The allotype of *Myrmotherula oreni* is MPEG 61344, skin, male, testes 2×2 mm, collected in bamboo forest on 14 November 2006 by E. Guilherme and M. P. D. Santos at the type locality and prepared by M. Santa-Brigida under field number UFAC 818. Tissue samples deposited at MPEG under field number UFAC 818. Mitochondrial genes cytochrome *b* and NADH subunit 2 sequences deposited in GenBank (KC495695 and KC495709). Paratypes of *M. oreni* are the following four specimens: MPEG 61343: skin, adult female, skull 100% ossified, ovary 6×4 mm, collected in bamboo forest on 14 November 2006 by E. Guilherme and M. P. D. Santos at the type locality and prepared by M. Santa-Brigida under field number UFAC 819. Tissue samples deposited at MPEG under field number UFAC 819. Mitochondrial genes cytochrome *b* and NADH subunit 2 sequences deposited in GenBank (KC495696 and KC495710). MUSM 16174: skin, adult male, netted in the dense bamboo understory of river-edge forest on 23 May 1992 at Colpa de Guacamayos, Rio Tambopata, depto. Madre de Dios, Peru; prepped by A. W. Kratter under field number #472. Tissue samples deposited at LSUMZ under tissue catalog # 21213. Mitochondrial genes cytochrome *b* and NADH subunit 2 sequences deposited in GenBank (KC495700 and HM449844). AMNH 824069: skin, adult male, netted in tangled forest in elevated terrain, ca. 1 km away from the Manu river on 21 October 1976 at Cocha Cashu Biological Station, Manu National Park, depto. Madre de Dios, Peru (11°55'S; 77°18'W); prepped by J. W. Fitzpatrick under field number #76-115. LSUMZ 157128: skin, adult male, skull 100% ossified, testes 2×1 mm, netted in the dense bamboo understory of river-edge forest on 28 May 1992 at Colpa de Guacamayos, Rio Tambopata, depto. Madre de Dios, Peru (12°50'S, 69°30'W); prepped by A. W. Kratter under field number #488. **Variation in the type series:** The type series includes six specimens: four males and two females. Besides a strong sexual dimorphism, little variation is present in the type series as evidenced by morphometric, plumage, and molecular characters. The lone female paratype is essentially identical to the holotype.

Ecology and behavior.— *Myrmotherula oreni* appears to be frequently associated with bamboo thickets, as indicated by specimen labels (FMNH 321976, LSUMZ 157128, MPEG 61342 - 44) and publications, even though it may also occur away from bamboo, especially in areas where the latter is not present (Parker 1982, Kratter 1997, Schulenberg *et al.* 2007, Aleixo and Guilherme 2010). BMW recorded *M. oreni* accompanying understory mixed-species flocks away from bamboo in large forest fragments in eastern Acre, and discovered through interviews with local people that bamboo in that region had flowered and died in its normal life-cycle “several years earlier”; searches in the leaf litter revealed small shoots of new bamboo in abundance. He suspects that *Myrmotherula oreni* and some other “bamboo specialists” in southwestern Amazonia, such as *Chnipodectes superrufus* (tape-recorded by BMW and J. L. Rowlett away from bamboo at Cocha Juarez in the buffer zone of Manu National Park, Peru in July 1992) and *Celeus spectabilis* (Rufous-headed Woodpecker, BMW recordings away from bamboo in Acre July 1997), maintain established territories during the transitory, post-flowering “absence stage” in the life-cycle of *Guadua* and perhaps some other bamboos. *Myrmotherula oreni* has been reported both in the mature stage of transitional forest, where bamboo tends to be more common, and in upland *terra-firme* forest (Robinson and Terborgh 1997, Aleixo and Guilherme 2010); in both vegetation types, it occupies the understory where pairs forage regularly at dead-leaf clusters in close association with mixed-species flocks (Parker 1982, Rosenberg 1997, Schulenberg *et al.* 2007). BMW has observed *M. oreni* and also *M. iheringi* and *M. heteroptera* foraging mostly 4-10 meters above ground, regularly inspecting branches in the interior of trees, often leaning over to search the undersides as they constantly twitch the tail in short, sharp, side-to-side and up-down arcs; he has not observed any of them preferentially for-

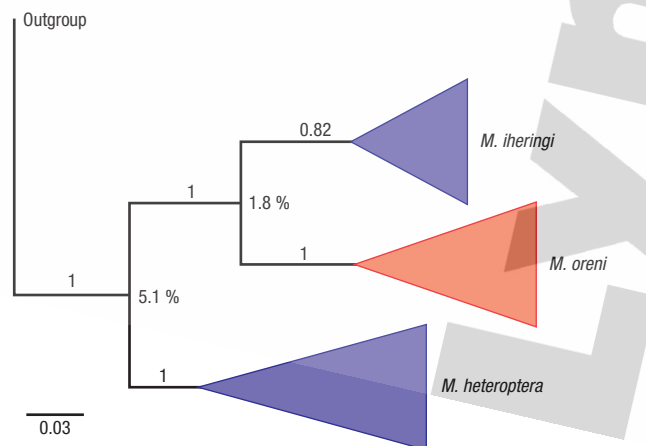


Figure 1. Phylogenetic relationships within *Myrmotherula iheringi* recovered by Bayesian analyses based on 1,683 bp of *cytb* and *ND2* sequences. Numbers refer to posterior probabilities values and genetic distances (% of average uncorrected p sequence divergence) between sister groups associated with the labeled nodes (see SI for detailed information).

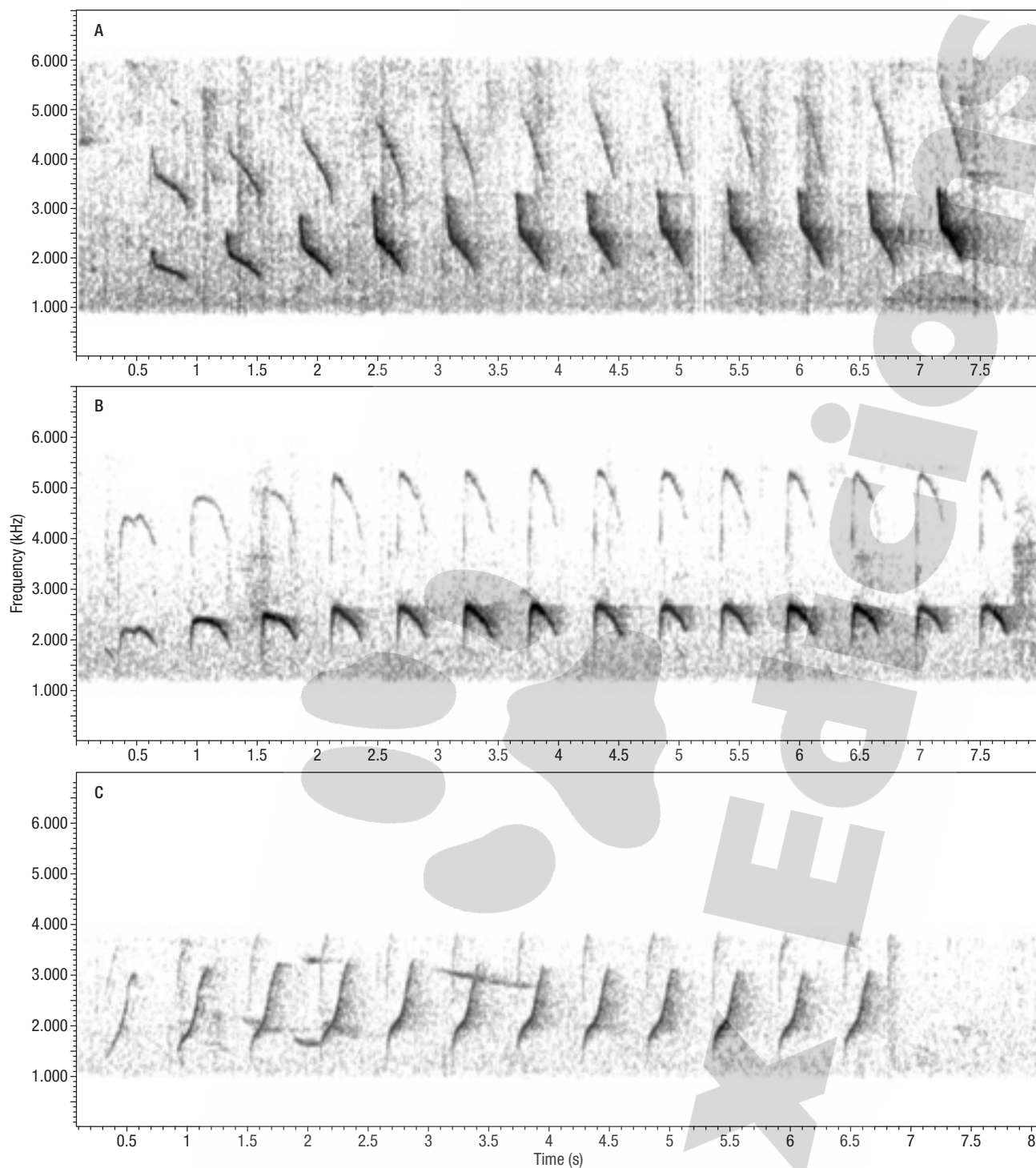


Figure 2. Representative spectrograms of loudsongs of taxa in the *Myrmotherula iheringi* complex: A: *M. iheringi*, Boim, Rio Tapajós, Pará, Brazil (type locality; BMW 108:05); B: *M. oreni*, Manu Lodge, Madre de Dios, Peru (BMW 77:07); and C: *M. heteroptera*, Parque Nacional da Serra do Divisor, Acre, Brazil (BMW 125:01). Recording numbers are from the Isler recording archive.

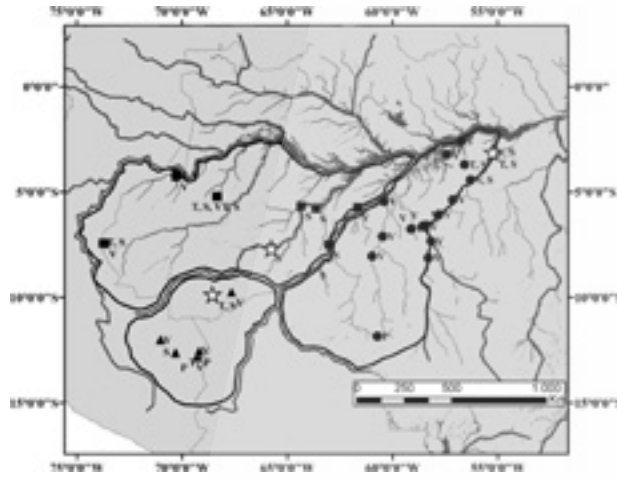
aging from bamboo substrates and the latter two taxa rarely enter bamboo where it is present in their ranges. *Myrmotherula oreni* is reported as uncommon in most places (Schulenberg *et al.* 2000, Aleixo and Guilherme 2010), with an extrapolated density of 3 pairs/100 hectares at Cocha Cashu, Peru (Robinson and Terborgh 1997). Its nest and eggs remain unknown.

Vocalizations.— The song of *M. iheringi*, *M. heteroptera*, and *M. oreni* is a slow series of short notes of about the same frequency, and given at a pace that is steady or slightly accelerating. Within the complex, the song differs among the taxa primarily in the shape of the notes. The song of *M. oreni* is closest to that of nominate *iheringi* in overall structure, but differs by possessing distinctly hill-shaped notes, giving it a higher pitched quality (Fig. 2). In comparison with *M. heteroptera*, the loudsong of *M. oreni* is also distinguished by notes with a completely different structure, and hence the same higher pitched quality (Fig. 2). Calls were not analyzed due to very small sample sizes. It is recommended that interested readers listen to the songs rep-

resented by spectrograms in Figure 2 online at the Internet Bird Collection (IBC) website.

Phylogenetic relationships and taxonomy.— DNA sequence data for the mitochondrial genes cytochrome *b* (cyt *b*, 668 bp) and NADH subunit 2 (ND2, 1,015 base pairs) were obtained for 14 individuals (see Table 6 in the SI file for a list of specimens sequenced) of both taxa grouped under *M. iheringi* (*M. i. iheringi* and *M. i. heteroptera*) in addition to three outgroups. All Bayesian and Maximum Likelihood trees obtained recovered the same topology in which three main lineages not corresponding to current subspecific limits within *M. iheringi* were found (hereafter named as clades A, B, and C; Figs. 1 and 3). Clade A includes specimens inhabiting the Madeira–Tapajós interfluvium, where the type locality of nominate *M. iheringi* is located; clade B includes birds from the southern part of the Inambari area of endemism, which have been treated up to now as *M. i. heteroptera*; finally, clade C groups specimens occurring west of the Madeira river in the northern part of the Inambari area of

Figure 3. Geographic distribution of specimens, vocalizations, and tissues of *Myrmotherula iheringi* (circles), *Myrmotherula heteroptera* (squares), and *Myrmotherula oreni* (triangles) analyzed in this study. Sampling locations include tissues (T), skins (S), photographs (P) and vocal (V) records. Open stars indicate type localities of the different species recognized here in the *Myrmotherula iheringi* complex. The ranges of the three main lineages recovered by the molecular phylogeny, corresponding to *M. iheringi*, *M. oreni*, and *M. heteroptera*, are depicted with solid lines.



endemism (Silva *et al.* 2005) and to which the name *heteroptera* applies (type locality Hyutanaã on the Rio Purus; Fig. 3). Thus, all phylogenies obtained recovered a paraphyletic *M. i. heteroptera* as indicated by current taxonomy (Zimmer and Isler 2003), because clades C (to which the name *heteroptera* truly applies) and B do not share a most recent common ancestor (Fig. 1); instead, clade B is sister to clade A, to which the name *iheringi* applies, hence highlighting the need to name clade B as a new taxon (*oreni*). Clade C is especially well differentiated from its closest relatives (Fig. 1). We recommend that it be known henceforth as *Myrmotherula heteroptera*, Purus Antwren.

Conservation.— *Myrmotherula oreni* is a low-density species in its preferred habitat and has one of the most restricted global populations of any species in the genus *Myrmotherula*. However, because it is endemic to one of the least disturbed parts of Amazonia (the Inambari area of endemism), it is not currently threatened by anthropogenic alteration of its habitat or other sources. Of particular concern in the long term is the recent advancement of deforestation throughout most of the range of *M. oreni* in Acre (Brazil), Madre de Dios (Peru) and Pando (Bolivia). If the advancement of logging and agro-business at the core of *M. oreni*'s range becomes more widespread, it could eventually imperil this and many other endemic *terra-firme* species of the Inambari region.

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Figure 4. The Bamboo Antwren (*Myrmotherula oreni*) is largely restricted to thickets of *Guadua* spp. bamboos in southwestern Amazonia in Brazil, Peru, and northern Bolivia. This adult male was photographed in the buffer zone of Manu National Park in Madre de Dios, Peru, 13 November 2009, by Lars Petersson.

