

A new subspecies of Brown-banded Antpitta *Grallaria milleri* from Antioquia, Colombia

by Paul Salaman, Thomas M. Donegan & Robert Prŷs-Jones

Received 8 October 2007; final revision received 16 January 2009

SUMMARY.—A new subspecies of Brown-banded Antpitta *Grallaria milleri* is described from the northern Central Andes of Colombia, based on a single specimen at The Natural History Museum, Tring, collected in 1878 at Santa Elena, dpto. Antioquia. The new subspecies is separable from *G. m. milleri*, which occurs 140 km further south in the Central Andes, by its considerably shorter tarsus, longer wing and longer tail. Other possible hypotheses for the type specimen's morphology, such as hybridisation or clinal variation, are not supported. Searches at the type locality and in the surrounding region (which are largely deforested at suitable elevations) have failed, suggesting that the new taxon may be either highly endangered or already extinct. Although the new antpitta appears likely to be a phylogenetic species, subspecies rank is assigned conservatively. Its taxonomic rank and status will require review should an extant population be discovered.

Antpittas (Grallariidae) reach their greatest diversity at high elevations in the northern Andes. Although previously treated as part of the Thamnophilidae or Formicariidae, *Grallaria* is now considered part of a smaller family Grallariidae (Irestedt *et al.* 2002, Chesser 2004, Rice 2005a,b, Remsen *et al.* 2008). Grallariidae are secretive species of the understorey, have poor flight and often-small geographical ranges, factors that have contributed to the family being second only to Rhinocryptidae (tapaculos) in the number of new Andean taxa described recently (e.g. Graves 1987, Schulenberg & Williams 1992, Stiles 1992, Krabbe *et al.* 1999, Donegan 2008).

The Central Cordillera of Colombia is the highest (average 3,000 m) and oldest of Colombia's three Andean ranges. It supports a diverse mosaic of habitats, resulting in exceptional biological diversity and intraspecific variation (Orme *et al.* 2005, Phillimore *et al.* 2007). Above 1,000 m, the cordillera supports over 30 restricted-range bird species, one of the largest global concentrations of such montane taxa (Stattersfield *et al.* 1998). Exceptional numbers of *Grallaria* species occur in Colombia's Central Andes, including various endemics to the cordillera (Krabbe & Schulenberg 2003).

During the late 19th and 20th centuries, improved infrastructure encouraged bird collectors to explore the northern Central Cordillera, mainly around Colombia's second-largest city, Medellín, with collections by M. A. Carriker (1941–53: Graves 1987, 1997), K. von Sneider (1938–52: Fjeldså & Krabbe 1990), M. A. Serna (1971–91: SAO 2003) and several American Museum of Natural History (AMNH) expeditions (Chapman 1912, 1917). In the last decade, the northern Central Andes has again been a focus for ornithological research due to the activities of many individuals and groups, including the Sociedad Antioqueña de Ornitología, Medellín's universities, and Fundación ProAves (e.g. Salaman *et al.* 2002, SAO 2003), among others. Despite the region having been better studied than many other parts of the country, the Central Andes have yielded several new bird species in recent years, including two found to date only in the northernmost section, in dpto. Antioquia (Cuervo *et al.* 2001, Donegan 2007).

One of the first significant collections from the northern Central Andes was made by Thomas Knight Salmon, who collected 1,263 bird specimens for the British Museum, now the Natural History Museum (BMNH), in 1872–78. Details, including type specimens of 14 species, were published just after Salmon's death (Sclater & Salvin 1879). Previously, Sclater (1877) had described *Grallaria flavotincta* from a single adult (BMNH 1889.9.20.622) taken by Salmon near Frontino, Antioquia, in 1876. Among the specimens in Salmon's last consignment, collected in September 1878, was an unidentified, plain brown-plumaged *Grallaria* (BMNH 1889.7.10.875). Although details of it were not mentioned by Sclater & Salvin (1879), they did comment on other specimens collected during the same month and referenced the holotype of *G. flavotincta*. The label of 1889.7.10.875 was originally annotated simply '*Grallaria*', but the species name was later added '*flavotincta*' (i.e. Yellow-breasted Antpitta) in a different hand, almost certainly that of P. L. Sclater (handwriting compared against a signed letter). In his account of the Formicariidae for the *Catalogue of the birds in the British Museum*, Sclater (1890) referred to the specimen as a juvenile *G. flavotincta*, although there is no reference to its age on the labels.

Norman Arlott was commissioned to illustrate various antpittas for the *Handbook of the birds of the world* (cf. Krabbe & Schulenberg 2003) and, to this end, in 2001 he visited BMNH. His draft plate for *G. flavotincta* was based solely on specimen 1889.7.10.875, as the holotype was stored in a separate cabinet and BMNH held no other specimens. However, NA soon discovered that his illustration did not match the species' draft text description. *G. flavotincta* is a yellow-breasted endemic of the West Andes, whilst the BMNH skin has dull grey and brown underparts. NA raised the issue with RP-J, and on comparing the specimen with the holotype they realised it could not be of the same species. In early November 2001, PS visited the collection in connection with Project BioMap's databasing of Colombian skins and, on seeing the mystery '*G. flavotincta*' specimen, realised that it more closely recalled Brown-banded Antpitta *G. milleri*. On comparing the single *G. milleri* held at BMNH, a paratype, PS and RP-J noted that the specimen differed from *G. milleri* in various respects.

The incorrect identification of a museum specimen is not uncommon, but in this case it is rather surprising. Sclater described more *Grallaria* species than anyone else, in chronological order: White-bellied Antpitta *G. hypoleuca* and *G. modesta* (now the Thrush-like Antpitta subspecies *Myrmothera campanisona modesta*) (Sclater 1855), Chestnut-naped Antpitta *G. nuchalis* (Sclater 1860), Grey-naped Antpitta *G. griseonucha* (Sclater & Salvin 1871), *G. [nuchalis] ruficeps* (Sclater 1874a), Red-and-white Antpitta *G. erythroleuca* (Sclater 1874b), Rufous-faced Antpitta *G. erythrotis* (Sclater & Salvin 1876), Yellow-breasted Antpitta *G. flavotincta* and Plain-backed Antpitta *G. haplonota* (Sclater 1877), Bicoloured Antpitta *G. rufocinerea* (Sclater & Salvin 1879) and Ochre-striped Antpitta *G. dignissima* (Sclater & Salvin 1880). Particularly noteworthy is that Sclater described *G. flavotincta*.

The collecting locality, Santa Elena, is immediately adjacent to the city of Medellín, and now on the road between the city and its airport. The region had been deforested by the early 1900s (Chapman 1917) and there is little native vegetation today, with pine plantations and other modified habitats predominant (Castaño & Patiño 2000). Recent surveys yielded only 66 bird species. The largest forest fragment covers just 136 ha and the only Grallariidae is the widespread Chestnut-crowned Antpitta *G. ruficapilla* (Castaño & Patiño 2007). Many forest-dependent species collected at the locality by Salmon, including *Grallaria rufocinerea* and Slate-coloured Antpitta *Grallaricula nana*, are no longer present.

Interestingly, Bicoloured Antpitta *G. rufocinerea* also has Santa Elena as its type locality but was not recorded in Antioquia for 130 years until its recent rediscovery at a site 18 km south-east of Santa Elena, at San Sebastián-La Castellana, El Retiro municipality (Ramírez 2006). San Sebastián is considered the best-preserved montane forest fragment (200 ha) in

southern Antioquia and has been subject to much observation over the past decade. It was recently declared an Important Bird Area (Franco & Bravo 2005). *G. ruficapilla*, *G. nuchalis* and *Grallaricula nana* have been found there, but there are no records of *G. milleri* (J. D. Ramírez *in litt.* 2008).

During 2008, Fundación ProAves undertook eight weeks of intensive surveys for *Grallaria* species at seven potential sites within 80 km of Santa Elena and at similar elevations, including the use of regular playback of *G. milleri*. These searches failed to locate *G. milleri* or any similar taxon. Efforts to obtain a useful mtDNA sequence from toe pad scrapings of the mystery BMNH (1889.7.10.875) specimen have also failed, probably because of the specimen's age (N. H. Rice *in litt.* 2006).

Description of new subspecies

We believe that the BMNH skin represents a new taxon and that further delay in alerting ornithologists and conservationists to its existence is not warranted. Given the lack of vocal or molecular data, we conservatively assign it subspecies (rather than species) rank and propose the following name:

Grallaria milleri gilesi subsp. nov. Antioquia Brown-banded Antpitta

Holotype.—See Figs. 1 and 2. Male, reg. no. BMNH 1889.7.10.875, held at the Natural History Museum, Tring, UK; collected in September 1878 by T. K. Salmon (original collector's no. 41) at Santa Elena, 8 km east of Medellín, dpto. Antioquia, Colombia (06°15'N, 75°35'W). Elevation unknown, but within a 10-km radius of Santa Elena elevation does not exceed 2,750 m, with a mean of 2,550 m (<http://earth.google.com>). The label notes the iris as 'dark' and stomach contents included 'insects'.

Diagnosis.—Referred to *Grallaria* Vieillot, 1816 (type: Variegated Antpitta *G. varia*) due to: its medium to large size; long tarsus; culmen very indistinctly (if at all) ridged and gradually but strongly curved from the base; scutellate tarsus; rictal bristles distinct but slender; and chin and upper-throat feathers with long, slender terminal setae (Lowery & O'Neill, 1969). *Grallaria* was treated as comprising several subgenera by Lowery & O'Neill (1969); although some of their proposed subgeneric divisions do not reflect molecular findings (Krabbe & Schulenberg 2003), they are nonetheless of use in considering the possible relations of *G. m. gilesi*. *G. m. gilesi* is apparently a fairly typical member of the plain-coloured group (proposed subgenus *Oropezus* Ridgway, 1909; type species: Rufous Antpitta *G. rufula*), of which *G. milleri* is a member, due to: its relatively small wing (75–103 mm); fairly uniform upperparts and underparts (considered separately) without strong streaks, squamations or bars; tail more than half as long as wing (tail / wing ratio 0.54–0.60); inner edge of tarsus distinctly convolute; and presence of 12 rectrices (Lowery & O'Neill, 1969). However, *G. m. gilesi* falls outside of proposed tarsus / tail and tarsus / wing ratios for the subgenus.

The new taxon immediately recalls *G. m. milleri*, which occurs 140 km further south in the Central Andes (Fig. 3). The holotype shares *G. m. milleri*'s uniform rufous-brown plumage, with whitish lores, throat and belly, and the structural features described for the proposed subgenus *Oropezus* and genus *Grallaria* above. Based on recorded values for *G. milleri* from specimens ($n=10$) and recent field and specimen measurements (Kattan & Beltrán 1999: $n=18$), the *G. m. gilesi* holotype differs from all *G. m. milleri* specimens in hav-

TABLE 1

Comparison of morphometrics of *G. m. gilesi* with *G. m. milleri* (specimens unless otherwise stated). Details of measured specimens are presented under distribution. The mean is given, followed by the standard deviation and then the range, with Kattan & Beltrán (1999) data also presented for comparison.

	Flat wing chord (mm)	Tail length (mm)	Tarsus length (mm)	Maxilla (mm)*	Bill width (gape) (mm)	Body mass (g)	Tail/tarsus ratio	Wing/tarsus ratio
<i>G. m. gilesi</i> (holotype, male)	97.0	55.8	40.8	18.8	12.7	N/A	1.37	2.38
<i>G. m. milleri</i> (n=5 males)	89.1 ± 3.5 (85.0–94.5)	50.4 ± 1.4 (49.2–52.5)	44.4 ± 0.5 (44.0–45.2)	21.1 ± 1.4 (19.5–23.1)	11.3 ± 0.7 (10.3–11.8)	N/A	1.13 ± 0.04 (1.09–1.19)	2.00 ± 0.10 (1.88–2.13)
<i>G. m. milleri</i> (n=10)	88.6 ± 2.9 (85.0–94.5)	49.0 ± 2.9 (43.6–53.0)	44.5 ± 0.6 (43.4–45.5)	21.0 ± 1.9 (19.3–24.7)	11.5 ± 1.0 (10.3–13.0)	N/A	1.10 ± 0.06 (0.98–1.19)	1.99 ± 0.08 (1.88–2.13)
<i>G. m. milleri</i> (Kattan & Beltrán 1999) (n=18 live individuals and specimens)	89.6 ± 3.5	N/A	46.6 ± 2.4	17.1 ± 1.5	N/A	52 ± 3.2	N/A	Based on means: 1.92

* Differences between Kattan & Beltrán (1999) data and ours for maxilla length probably result from differences in measuring technique.

ing a longer wing, longer tail and shorter tarsus (Table 1). It also appears larger bodied than *G. m. milleri*.

Description of the holotype.—The following is based on Munsell Color (2000) codes. *Face* Lores white (Gley 1, 7–8/N) with dark brown feather tips. Ear-coverts warm cinnamon-brown (10YR 3/6) with slightly darker feather tips outlining ear-coverts. Warm cinnamon-brown (10YR 3/6) from ear-coverts to neck-sides and upper breast, forming a breast-band. *Upperparts* Entire upperparts, from the forecrown to the uppertail-coverts, uniform rufous-brown (10YR 3/4). Tail slightly darker rufous-brown (7.5YR 2.5/3). *Wings* As upperparts, with uniform rufous-brown (10YR 3/4) coverts and flight feathers with warm cinnamon-buff (10YR 3/6) underwing-coverts. *Underparts* Throat white (Gley 1 8/N) with warm cinnamon-brown (10YR 3/6) feather tips. Feather tips below culmen modified with exposed, elongated terminal setae, similar in shape (and, doubtless, function) to rictal bristles. Lower underparts to undertail-coverts pale grey (10YR 6/1), being slightly paler whitish and creamy on central belly (10YR 6/3). Sides of throat and malar region pale cinnamon-buff (10YR 3/6), extending around throat to form a distinctive upper-breast-band and extending as broad streaks on mid to lower breast and over flanks. The streaking comprises broad cinnamon (10YR 3/6) fringes to pale grey (10YR 6/1) feathers and darkens to cinnamon-rufous (10YR 3/4) on mid to lower flanks and thighs. *Soft parts* Tarsus scutellate. Irides 'dark' on collection. No bill or leg colour description, but presently faded as in *G. milleri*, with tarsus and culmen dark horn, tipped yellowish horn (10YR 5/6) on both mandibles. See Figs. 1 and 2.

Distribution and specimens examined.—*G. m. gilesi* is known only from the type locality above the Valle de Aburrá, 8 km east of Medellín, Santa Elena municipality, dpto. Antioquia, Colombia (06°15'N, 75°35'W; 2,750 m). The locality is 140 km north of the northernmost known locality of its apparently closest relative, *G. m. milleri*. The holotype was collected within the elevational range of *G. m. milleri* (1,800–2,800 m), suggesting the two taxa may replace one another geographically.

Details are presented below for known localities of *G. m. milleri*. Project BioMap staff and ourselves (*) checked all specimens of *G. milleri* in the following museums: American Museum of Natural History, New York (AMNH*), Academy of Natural Sciences, Philadelphia (ANSP), Natural History Museum, Tring (BMNH*), Instituto de Ciencias Naturales, Universidad Nacional, Bogotá (ICN*), Carnegie Museum, Pittsburgh, USA (CM*) and Museum of Comparative Zoology, Harvard University, Cambridge, MA (MCZ). Recordings from www.xeno-canto.org (XC) were also examined. *G. m. milleri* is currently confirmed to occur only in the middle section of the Central Cordillera in central Colombia, at the following localities south to north:

1. Reserva Natural de las Aves El Mirador (04°09'N, 75°44'W; 2,750 m), sound-recorded, trapped and photographed by Fundación ProAves researchers in 2006 and others subsequently (Alonso Quevedo *et al.*; N. Athanas & F. Lambert: XC 10721, 16777).
2. Río Toche watershed, municipalities of Cajamarca and Ibagué, south-east flank of the Volcán Tolima-Ruiz massif, dpto. Tolima (04°26'N, 75°22'W; 1,800–2,600 m) (López-Lanús *et al.* 2000).
3. Clarita Botero, above Ibagué, dpto. Tolima (04°29'N, 75°13'W; 2,100 m) (M. Moreno-Palacios *in litt.* 2007).
4. Reserva Natural Ibanasca, Cañon del Río Conbeima, dpto. Tolima (04°35'–38'N, 75°14'–19'W; 2,400–2,800m) (M. Moreno-Palacios & D. A. Bejarno-Bonilla *in litt.* 2007).
5. Laguneta (type locality), dpto. Quindío (04°35'N, 75°30'W); specimens at AMNH (111991–94), BMNH (1921.7.3.61, formerly AMNH 111990), MCZ (81785, formerly AMNH 111995)—a small montane forest patch at 2,700–2,800 m on the west slope of the Central Cordillera (Chapman 1912).
6. Above Salento, dpto. Quindío (04°38'N, 75°34'W; 2,745 m); male collected on 6 November 1911 (AMNH 111996) (Chapman 1917) and two males in April 1942 (ANSP 154007–08).
7. Finca San Miguel, 3 km west of Roncesvalles, dpto. Tolima (04°53'N, 75°30'W; 2,750 m) (Cadena *et al.* 2007).
8. Ucumarí Regional Natural Park, dpto. Risaralda (04°42'N, 75°29'W; 2,200–2,600 m). Surveys in 1994–98 yielded 11 birds trapped and six collected (Universidad del Valle 6171, 6178–82; Kattan & Beltrán 1997, 1999).
9. Río Blanco, Manizales, dpto. Caldas (05°05'N, 75°25'W; 2,500 m) (ICN 35692; Verhelst *et al.* 2002, Nieto & Ramírez 2006; B. Davis, D. Bradley, H. van Oosten, A. Spencer & O. Cortés: XC 13896, 17619, 18289, 20505 and 22213).
10. Sancudo (= El Zancudo), 3 km east of Manizales, dpto. Caldas (c.5°05'N, 75°30'W; 2,400 m), where a female was collected (CM 70234) in August 1918.
11. Two 'Bogotá' specimens (AMNH 43555, 43559) were presumably collected in the Central Andes.

The modelled distribution of *G. m. milleri* by J. Velásquez (*in litt.* 2008) using MAXENT 3.0 (Phillips *et al.* 2006) based on topography and climate layers available from Worldclim (Hijmans *et al.* 2005) predicts presence north to Antioquia (Fig. 3). Interestingly, there are no geographical barriers (e.g. significant dry valleys or high mountains) preventing contact



Figure 1. Plate by Norman Arlott showing *Grallaria m. gilesi* (left) and *Grallaria m. milleri* (right).



Figure 2. The *Grallaria m. gilesi* holotype (left three images) and *Grallaria m. milleri* paratype (right three images). © Natural History Museum, Tring.

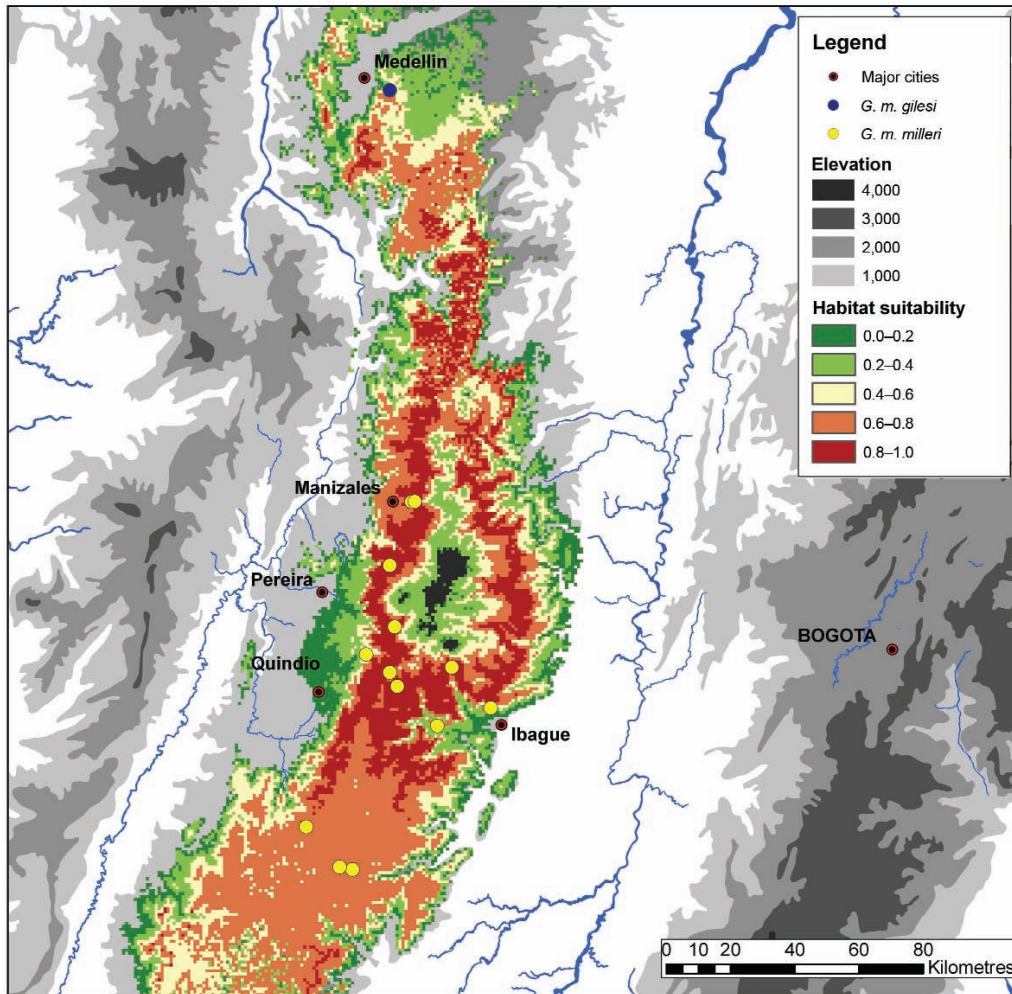


Figure 3. Potential distribution map for *G. milleri*, by J. Velázquez, using MAXENT 3.0 (Phillips *et al.* 2006) and showing locations of records of *G. milleri* and the type locality of *G. m. gilesi* in Colombia, with potential distribution based on topography and climate layers available from Worldclim (Hijmans *et al.* 2005).

between *G. m. milleri* and *G. m. gilesi*, but there is a region showing reduced potential suitability for *G. milleri* between the known range of *G. m. milleri* and the type locality of *G. m. gilesi*. Potentially suitable climatic variables for *G. milleri* are present above Santa Elena, with precipitation (1,887 mm) and temperature (max. 15.3°C) within ranges of these variables at sites where *G. m. milleri* has been recorded (mean rainfall = 1,769 mm; range = 1,178–2,493 mm; mean temperature = 14.0°C; range = 9.8°C–19.2°C: Hijmans *et al.* 2005). However, *G. m. milleri* has been recorded to date only on the slopes of c.4,000 m or higher massifs and at lower latitudes.

Despite climatic similarity, the pattern of a northern subspecies replacing one found further south in the Central Andes is not uncommon. Examples of montane understory species showing apparently similar north–south subspecies replacements in the Central Andes include those of Yellow-breasted Brush Finch *Atlapetes latinuchus elaeoprurus* and *A.l. cauae* (Donegan & Huertas 2006) and Lacrimose Mountain Tanager *Anisognathus lacrymo-*

sus olivaceiceps and *A.l. palpebrosus* (Zimmer 1944). The *Anisognathus* taxa intergrade in dpto. Caldas, but the historical factors underlying these distributions are little studied.

Taxonomic rank.—The following statistical methods were suggested by Donegan (2008) as guidelines for assessing diagnosability and rank where two allopatric populations are compared for continuous, normally distributed variables but where, for one population, there is a sample size of only one. In the formulae below, y is the recorded value for the *G. m. gilesi* type specimen; \bar{x}_1 and s_1 are the sample mean and sample standard deviation of *G. m. milleri*; and the t value uses one-sided confidence intervals at the percentage specified for the degree of freedom for *G. m. milleri* when considering the relevant variable. Tests are based on the highly conservative assumption that the *G. m. gilesi* holotype has unusual biometrics at the highest or lowest 2.5% for each variable studied (whichever is furthest from the *G. m. milleri* mean). Tests also assume that *G. m. gilesi* has similar sample population variance for the relevant variable to *G. m. milleri* and that *G. m. gilesi* does not represent the extreme of a cline, a hypothesis discussed further below.

(A) Traditional '75% / 99%' test for subspecies (Amadon 1949, Patten & Unitt 2002): $y < \bar{x}_1 - (t_{99.0\%} + t_{97.5\%} + t_{75.0\%}) s_1$ or $y > \bar{x}_1 + (t_{99.0\%} + t_{97.5\%} + t_{75.0\%}) s_1$.

(B) Isler *et al.*'s (1999) phylogenetic species test (97.5% / 97.5% diagnosability), adapted: $y < \bar{x}_1 - 3s_1 t_{97.5\%}$ or $y > \bar{x}_1 + 3s_1 t_{97.5\%}$.

A Welch's t -test to compare means (Level 1 of Donegan 2008) is not assessable where only one datum is available for one population. However, var-covar principal components analysis using PAST v1.46 found the *G. m. milleri* specimen to fall outside the 95% ellipse for *G. m. milleri*, using data both from all specimens and from males alone. The *G. m. gilesi* holotype falls outside the range of the *G. m. milleri* sample in wing, tail and tarsus lengths, commissure width (males only), tail / tarsus ratio and wing / tarsus ratio.

Based on data for both sexes of *G. m. milleri* (d.f.=9 for *G. m. milleri*), *G. m. gilesi* passed the 75% / 99% test for subspecies rank for tarsus length (missing the phylogenetic species test by only 0.2 mm or 0.16 t_{s_1}). Based on data for males alone (d.f.=4 for *G. m. milleri*), *G. m. gilesi* passed the 75% / 99% test for subspecies rank for bill width at gape (missing the phylogenetic species test by 0.1 mm or 0.03 t_{s_1}) and tarsus length (missing the phylogenetic species test by 0.3 mm or 0.18 t_{s_1}). *G. m. gilesi* would pass a test for phylogenetic species rank for tarsus length for both males and combined data were the holotype assumed to fall within the most unusual 5% of the hypothetical *G. m. gilesi* population (vs. the most unusual 2.5%, as under the present model). Thus, mensural data suggest that *G. m. gilesi* is at least a subspecies under the Patten & Unitt (2002) 75% / 99% concept, and is also likely a phylogenetic species on biometrics (Cracraft 1983).

Helbig *et al.* (2002) and Remsen (2005) suggested that, to assess taxonomic rank of allopatric populations, a comparison should be undertaken of the observed differences between (i) candidates for species rank and their possible conspecifics; and (ii) congeners known to be good species. *Grallaria* is hardly a model group for such comparisons given that current species limits are poorly defined and frequently a result of historical momentum rather than detailed study (Krabbe & Schulenberg 2003, Remsen *et al.* 2008). Nonetheless, several cases of morphologically rather similar *Grallaria* populations considered biological species (due to sympatry or vocal differences) exist, such as Scaled *G. guatemalensis* and Moustached Antpitta *G. alleni*, and *G. hypoleuca* and *G. flavotincta*. In these species-pairs, morphological differences are subjectively rather small. In *Grallaricula nana*, the only allopatric populations diagnosable by biometrics also have diagnosably different voices and, as here, tarsus length differed markedly between those populations (Donegan 2008).

We conservatively rank *G. m. gilesi* as a subspecies (allospecies) of *G. milleri* pending any vocal or molecular data becoming available. Further data might demonstrate *G. m. gilesi* to be worthy of species rank. Its status should also be re-evaluated as more is learned about the relationship between biometric and vocal variation in *Grallaria*.

Possible other hypotheses.—Describing a new bird taxon based on just one specimen without vocal or molecular data might be considered controversial (e.g. Remsen *et al.* 2008 comments on Graves 1993). However, the other possible alternatives—an aberrant individual of *G. milleri*, clinal variation or a hybrid—are unsupported by the available data.

Hybridisation is exceptionally rare among suboscines other than the Pipridae (e.g. Marini & Hackett 2002, McCarthy 2006), although one case has been documented in *Grallaria* (Cadena *et al.* 2007). Any hybridisation hypothesis would necessarily involve *G. milleri* and would therefore seem biogeographically unlikely, as there are no records of *G. milleri* in the northern Central Andes. Furthermore, *G. m. gilesi* is indistinguishable from some *G. m. milleri* in plumage, meaning that one possible hybrid parent would have influenced only the biometrics of its offspring and left no trace on its plumage.

Assuming that a small population of *G. m. milleri* occurred at or near the type locality of Santa Elena, other possible sympatric *Grallaria* in the Central Andes (not all confirmed to occur in the north) are Undulated *G. squamigera*, Chestnut-naped *G. nuchalis*, Chestnut-crowned *G. ruficapilla*, Bicoloured *G. rufocinerea*, Tawny *G. quitensis*, Scaled *G. guatemalensis*, Moustached *G. alleni*, Rufous *G. rufula*, Plain-backed *G. haplonota* and White-bellied Antpitta *G. hypoleuca*. Of these, *G. milleri* is known to be sympatric only with *G. squamigera*, *G. nuchalis*, *G. ruficapilla* and *G. rufocinerea* (Kattan & Beltrán 1997, Krabbe & Schulenberg 2003) and only *G. rufocinerea*, *G. hypoleuca*, *G. nuchalis*, *G. alleni* and *G. ruficapilla* are known from Antioquia (Hilty & Brown 1986, SAO 2003). Sclater's 'confusion species' *G. flavotincta* is replaced in the Central Andes by *G. hypoleuca* (Krabbe & Schulenberg 2003), so the former is not a plausible parent species.

It is generally expected that hybrids would show intermediate features between their parents (Graves 1990, 1992). No examples of heterosis were noted in the only known case of hybridisation in *Grallaria* (Cadena *et al.* 2007); i.e. the only known hybrid *Grallaria* fell within the range of parent species in biometrics and had intermediate plumage features. Of other *Grallaria* occurring in the Central Andes, *G. squamigera*, *G. guatemalensis*, *G. alleni*, *G. nuchalis*, *G. rufocinerea* and *G. ruficapilla* are so different in plumage from *G. m. gilesi* that they can confidently be excluded as possible parents. None of the *Grallaria* species known to be sympatric with *G. milleri* bears any real resemblance to *G. m. gilesi* in plumage.

Potential parents with nondescript plumage similar to *G. milleri* are *G. hypoleuca*, *G. quitensis* and *G. rufula*. However, none of these is known to be sympatric with *G. milleri* and none is known from the Santa Elena region. *G. hypoleuca* is a vocal species, currently known in Antioquia only from the more humid northern slope of the Central Andes at río Porce, Anorí and Amalfí (Donegan & Salaman 1999), and from older specimens taken at a single locality also on the north slope (Valdivia, Antioquia: USNM 402471–472, FMNH 299492). It has not been recorded at San Sebastián (J. D. Ramírez *in litt.* 2008), nor is it known from historic material taken in the Medellín region or further south in dptos. Quindío or Caldas, despite considerable ornithological work. *G. quitensis* occurs only in very high-elevation páramo, as does *G. rufula*. None of these possible hybrid combinations explains *G. m. gilesi*'s morphometric characters. *G. hypoleuca* (46–49 mm; *n*=5) and *G. quitensis* (c.50 mm; *n*=1: ProAves unpubl. data) have longer, not shorter, tarsi than *G. milleri*, whilst the Central Andes population of *G. rufula* is shorter tailed than *G. milleri* (40.0–42.2 mm; *n*=3: ProAves unpubl. data) and is smaller bodied (mass 40.4–42.0g; *n*=3: ProAves unpubl. data). The larg-

er body, longer tail and shorter tarsus in *G. m. gilesi* permit us to discount these hybrid hypotheses.

G. m. gilesi is unlikely to represent an extreme point of clinal variation within *G. m. milleri*. Bergmann's Rule holds that populations from cooler (here, northern) regions are generally larger bodied. *G. m. gilesi* has a larger body and longer wing and tail than *G. milleri*, which might reflect this. Individuals measured by Kattan & Beltrán (1999) in dpto. Risaralda and the ICN specimen show longer tarsi and slightly longer wing lengths on average than our dpto. Quindío specimen data, in accordance with Bergmann's Rule or possibly reflecting shrinkage in older skins. However, *G. m. gilesi*'s considerably shorter tarsus reverses the general trend observed in *G. milleri* or expected under Bergmann's Rule. Although there are exceptions to Bergmann's Rule in Andean birds and the sample size is small, observed variations in tarsus length are not consistent with a hypothesis of clinal variation.

G. m. gilesi is clearly not a case of an aberrant individual showing 'gigantism', given that its tarsus is shorter than that of *G. m. milleri*.

Sclater (1890) considered the *G. m. gilesi* holotype to be possibly a juvenile. There is some variation in the intensity of rufous plumage in *G. m. milleri*, with AMNH 111991 and 111994 (the holotype) and the *G. m. gilesi* holotype being more rufous than other specimens. The more olivaceous plumage of other AMNH specimens and the BMNH specimen was considered by Chapman (1912) to result from traces of juvenile plumage, a hypothesis supported by the broadly streaked crown of AMNH 111993, clearly a juvenile feature, and its more olivaceous plumage. The pattern of age-related plumage variation in *G. m. milleri* suggests that the *G. m. gilesi* holotype is probably adult (whilst the BMNH *G. m. milleri* paratype is a juvenile) and that Sclater's (1890) note may have been no more than an attempt to explain the differences between it and *G. flavotincta*.

Finally, Tepui Antpitta *Myrmothera simplex* of the Venezuelan and Guianan tepuis is almost identical in plumage to *G. milleri* (Lowery & O'Neill 1969), but *G. m. gilesi* is clearly not a mislabelled *Myrmothera* given its long rectal bristles and more strongly scutellate tarsus.

The description of *G. m. gilesi* is given further weight by the recent discovery of an undescribed species of *Grallaria* by Fundación ProAves researchers in the northernmost West Andes. Its closest relative appears to be *G. milleri*, but it differs in a number of plumage and vocal characters. Notably, the undescribed species is larger bodied and longer winged than *G. m. milleri* (like *G. m. gilesi*) but does not share the short tarsus of *G. m. gilesi*. Biogeographic and biometric considerations suggest that the undescribed species may be closer related to *G. m. gilesi* than to *G. m. milleri*.

Ecology and behaviour.—Beyond its insectivorous diet, *per* the specimen label, no ecological information is available.

Etymology.—The epithet honours O. A. Robert Giles, who has been dedicated to the conservation and study of Colombian avifauna since the early 1990s. He has personally supported the creation of two reserves for threatened birds in Antioquia by Fundación ProAves (Arrierito Antioqueño and Loro Orejamarillo Bird Reserves) and a further two bird reserves elsewhere in Colombia (Reinita Cerúleo and Hormiguero de Torcoroma Bird Reserves). Robert has travelled extensively in Colombia and aided Colombian ornithology by sponsoring research. Colombia's birds are safer due to his generosity and dedication.

Conservation.—The Cordillera Central of Colombia has undergone massive ecological change as Colombia's prime coffee-growing region and represents one of the most human-altered landscapes in the northern Andes. The extensive deforestation of montane forests in the northern Central Andes justifies immediate conservation action for range-restricted taxa found there. Given that searches for the new taxon in remnant forests in the northern Central Andes failed, there is only a remote possibility that *G. m. gilesi* is not already extinct.

Presently, *G. milleri* is considered Endangered (EN: B1a+b(iii,v), VU: C2a(i); D1) with an estimated Extent of Occurrence of 660 km² and known from 2–5 locations (BirdLife International 2008). The information presented here expands the known localities and range of *G. milleri*, although we believe the species remains Endangered (EN: B2b(ii,iii,v), VU: C2a(i)).

G. m. gilesi (when considered separately from *G. m. milleri*) is best categorised as IUCN Critical under category D1, based on a precautionary estimate of its population as <50 mature individuals, consistent with the approach to other bird species on the IUCN Red List for which no population is known, threats are intense, but hope remains for survival (S. H. M. Butchart *in litt.* 2007). As no population of *G. m. gilesi* is known, this description should not materially affect the IUCN assessment of *G. milleri*.

Acknowledgements

We thank Norman Arlott for his beautiful plate. Harry Taylor (BMNH) photographed the specimens in Fig. 2. Jorge Velázquez kindly produced Fig. 3 and discussed ecological issues. Nate Rice (ANSP) and Stephen Rogers (CM) provided photographs and data on *G. milleri* specimens. Paul Sweet & Peg Hart (AMNH), F. Gary Stiles (ICN) and Nate Rice (ANSP) facilitated access to collections. Funding from the Darwin Initiative (UK) and Conservation International for databasing Colombian museum specimens worldwide under Project BioMap (www.biomap.net) was vital in permitting checking for possibly overlooked *Grallaria* specimens by Juan Carlos Verhelst, Carla Isabel Bohórquez, Diana Arzuza, Andrea Morales and Nigel Cleere. We also thank Nick Athanas, Daniel Bejarno-Bonilla, Carl Downing, Miguel Moreno-Palacios, Sergio Ocampo-Tobón, Alonso Quevedo and the other sound recordists and observers mentioned in the text for providing records of *G. milleri*. Niels Krabbe, Thomas Schulenberg, Mary LeCroy and Guy Kirwan provided helpful comments on the manuscript. Pablo Flórez led the searches for *G. milleri* in Antioquia, with assistance from Carlos Andres Páez, Sara Inés Lara and David Caro, and supported by Fundación ProAves and Robert Giles.

References:

- Amadon, D. 1949. The seventy-five per cent rule for subspecies. *Condor* 51: 250–258.
- BirdLife International. 2008. Species factsheet: *Grallaria milleri*. www.birdlife.org (accessed 27 November 2008).
- Cadena, C. D., López-Lanús, B., Bates, J. M., Krabbe, N., Palacio, J. D., Rice, N. H., Stiles, F. G. & Salaman, P. 2007. A rare case of interspecific hybridization in the tracheophone suboscines: *Grallaria nuchalis* × *G. ruficapilla* in a fragmented Andean landscape. *Ibis* 149: 814–825.
- Castaño-V., G. J. & Patiño-Z., J. C. 2000. Cambios en la composición de la avifauna en Santa Elena durante el siglo XX. *Crónica Forestal y del Medio Ambiente* 15: 139–162.
- Castaño-V., G. J. & Patiño-Z., J. C. 2007. Composición de la comunidad de aves en bosques fragmentados en la región de Santa Elena, Andes Centrales Colombianos. *Bol. Cient. Centro Museos, Mus. Hist. Nat. (Univ. Caldas)* 11: 47–64.
- Chapman, F. M. 1912. Diagnoses of apparently new Colombian birds. *Bull. Amer. Mus. Nat. Hist.* 31: 139–166.
- Chapman, F. M. 1917. The distribution of bird-life in Colombia. *Bull. Amer. Mus. Nat. Hist.* 36: 1–728.
- Chesser, R. T. 2004. Molecular systematics of New World suboscine birds. *Mol. Phyl. & Evol.* 32: 11–24.
- Cracraft, J. 1983. Species concepts and speciation analysis. *Current Orn.* 1: 159–187.
- Cuervo, A. M., Salaman, P. G. W., Donegan, T. M. & Ochoa, J. M. 2001. A new species of piha (Cotingidae: *Lipaugus*) from the Cordillera Central of Colombia. *Ibis* 143: 353–368.
- Donegan, T. M. 2007. A new species of brush finch (Emberizidae: *Atlapetes*) from the northern Central Andes of Colombia. *Bull. Brit. Orn. Cl.* 127: 255–268.
- Donegan, T. M. 2008. Geographical variation and species limits in Slate-crowned Antpitta *Grallaricula nana*, with two new subspecies from Colombia and Venezuela. *Bull. Brit. Orn. Cl.* 128: 150–178.
- Donegan, T. M. & Huertas, B. C. 2006. A new brush-finch in the *Atlapetes latinuchus* complex from the Yariquíes Mountains and adjacent Eastern Andes of Colombia. *Bull. Brit. Orn. Cl.* 126: 94–116.
- Donegan T. M. & Salaman P.G.W. (eds.) 1999. Rapid biodiversity assessments and conservation in northeast Antioquia and the Churumbelos highlands. *Colombian EBA Project Rep. Ser. 2*: www.proaves.org.

- Fjeldsá, J. & Krabbe, N. 1990. *Birds of the high Andes*. Zool. Mus., Univ. of Copenhagen & Apollo Books, Svendborg.
- Franco, A. M. & Bravo, G. 2005. Áreas importantes para la conservación de las aves en Colombia. Pp. 117–281 in Boyla, K. & Estrada, A. (eds.) *Áreas importantes para la conservación de las aves en los Andes tropicales: sitios prioritarios para la conservación de la biodiversidad*. BirdLife International & Conservation International, Quito.
- Graves, G. R. 1987. A cryptic new species of antpitta (Formicariidae: *Grallaria*) from the Peruvian Andes. *Wilson Bull.* 99: 313–321.
- Graves, G. R. 1990. Systematics of the “green-throated sunangels” (Aves: Trochilidae): valid taxa or hybrids? *Proc. Biol. Soc. Wash.* 103: 6–25.
- Graves, G. R. 1992. Diagnosis of a hybrid antbird (*Phlegopsis nigromaculata* × *Phlegopsis erythroptera*) and the rarity of hybridization among subspecies. *Proc. Biol. Soc. Wash.* 105: 834–840.
- Graves, G. R. 1993. Relic of a lost world: a new species of sunangel (Trochilidae: *Heliangelus*) from ‘Bogotá’. *Auk* 110: 1–8.
- Graves, G. R. 1997. Colorimetric and morphometric gradients in Colombian populations of Dusky Antbird (*Cercomacra tyrannina*), with a description of a new species *Cercomacra parkeri*. Pp. 21–36 in Remsen, J. V. (ed.) *Studies in Neotropical ornithology honoring Ted Parker*. *Orn. Monogr.* 48.
- Helbig A. J., Knox, A. G., Parkin, D. T., Sangster, G. & Collinson, M. 2002. Guidelines for assigning species rank. *Ibis* 144: 518–525.
- Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G. & Jarvis, A. 2005. Very high resolution interpolated climate surfaces for global land areas. *Intern. J. Climatology* 25: 1965–1978.
- Hilty, S. L. & Brown, W. L. 1986. *A guide to the birds of Colombia*. Princeton Univ. Press.
- Irestedt, M., Fjeldsá, J., Johansson, U. S. & Ericson, P. G. P. 2002. Systematic relationships and biogeography of the tracheophone suboscines (Aves : Passeriformes). *Mol. Phyl. & Evol.* 23: 499–512.
- Isler, M. L., Isler, P. R. & Whitney, B. M. 1999. Species limits in antbirds. The *Myrmotherula surinamensis* complex. *Wilson Bull.* 116: 83–96.
- Kattan, G. H. & Beltrán, W. 1997. Rediscovery and status of the Brown-banded Antpitta *Grallaria milleri* in the Central Andes of Colombia. *Bird Conserv. Intern.* 7: 367–371.
- Kattan, G. H. & Beltrán, W. 1999. Altitudinal distribution, habitat use, and abundance of *Grallaria* antpittas in the Central Andes of Colombia. *Bird Conserv. Intern.* 9: 271–281.
- Krabbe, N. & Schulenberg, T. S. 2003. Family Formicariidae (ground antbirds). Pp. 748–787 in del Hoyo, J., Elliott, A. & Christie D. A. (eds.) *Handbook of the birds of the world*, vol. 8. Lynx Edicions, Barcelona.
- Krabbe, N., Agro, D. J., Rice, N. H., Jacome, M., Navarrete, L. & Sornoza M., F. 1999. A new species of antpitta (Formicariidae: *Grallaria*) from the southern Ecuadorian Andes. *Auk* 116: 882–890.
- López-Lanús, B., Salaman, P. G. W., Cowley, T., Arango, S. & Renjifo, L. M. 2000. The threatened birds of the río Toche, Cordillera Central, Colombia. *Cotinga* 14: 17–23.
- Lowery, G. H. & O’Neill, J. P. 1969. A new species of antpitta from Peru and a revision of the subfamily Grallariinae. *Auk* 86: 1–12.
- Marini, M. Á. & Hackett, S. J. 2002. A multifaceted approach to the characterization of an intergeneric hybrid manakin (Pipridae) from Brazil. *Auk* 119: 1114–1120.
- McCarthy, E. M. 2006. *Handbook of avian hybrids*. Oxford Univ. Press, New York.
- Meyer de Schauensee, R. 1966. *The birds of Colombia and adjacent areas of South and Central America*. Livingston Publishing Co., Narberth, PA.
- Munsell Color. 2000. *Munsell® soil color charts*. GretagMacbeth LLC, New York.
- Nieto-R., M. & Ramírez, J. D. 2006. Notas sobre aves de tierras altas que siguen marchas de hormigas arrieras para su alimentación, en la reserva natural Río Blanco, Manizales, Caldas. *Bol. Soc. Antioqueña Orn.* 16: 59–66.
- Orme, C. D. L., Davies, R. G., Burgess, M., Eigenbrod, F., Pickup, N., Olson, V. A., Webster, A. J., Ding, T.-S., Rasmussen, P. C., Ridgely, R. S., Stattersfield, A. J., Bennett, P. M., Blackburn, T. M., Gaston, K. J. & Owens, I. P. F. 2005. Global hotspots of species richness are not congruent with endemism or threat. *Nature* 436: 1016–1019.
- Patten, M. A. & Unitt, P. 2002. Diagnosability versus mean differences of Sage Sparrows subspecies. *Auk* 119: 26–35.
- Phillimore, A. B., Orme, C. D. L., Davies, R. G., Hadfield, J. D., Reed, W. J., Gaston, K. J., Freckleton, R. P. & Owens, I. P. F. 2007. Biogeographical basis of recent phenotypic divergence among birds: a global study of subspecies richness. *Evolution* 61: 942–957.
- Phillips, S. J., Anderson, R. P. & Schapire, R. E. 2006. Maximum entropy modelling of species geographic distributions. *Ecol. Modelling* 190: 231–259.
- Ramírez, J. D. 2006. Redescubrimiento de *Grallaria rufocinerea* (Formicariidae) en el Valle de Aburrá, Antioquia, Colombia. *Bol. Soc. Antioqueña Orn.* 16: 17–23.
- Remsen, J. V. 2005. Pattern, process, and rigor meet classification. *Auk* 122: 403–413.

- Remsen, J. V., Cadena, C. D., Jaramillo, A., Nores, M., Pacheco, J. F., Robbins, M. B., Schulenberg, T. S., Stiles F. G., Stotz, D. F. & Zimmer, K. J. 2008. A classification of the bird species of South America (version 24 March 2008). www.museum.lsu.edu/~Remsen/SACCBaseline.html.
- Rice, N. H. 2005a. Phylogenetic relationships of antpitta genera (Passeriformes: Formicariidae). *Auk* 122: 673–683.
- Rice, N. H. 2005b. Further evidence for paraphyly of the Formicariidae (Passeriformes). *Condor* 107: 910–915.
- Salaman, P. G. W., Donegan, T. M. & Cuervo, A. M. 2002. New distributional bird records from Serranía de San Lucas and the adjacent Central Cordillera of Colombia. *Bull Brit. Orn. Cl.* 122: 285–304.
- SAO. 2003. *Aves del Valle de Aburrá*. Second edn. Soc. Antioqueña de Orn., Medellín.
- Schulenberg, T. S. & Williams, M. D. 1982. A new species of antpitta (*Grallaria*) from northern Peru. *Wilson Bull.* 94:105–113.
- Sclater, P. L. 1855. Descriptions of some new species of ant-thrushes (Formicariinae) from Santa Fé de Bogota. *Proc. Zool. Soc. Lond.* 1855: 88–90.
- Sclater, P. L. 1860. On some new or little-known birds from the Rio Napo. *Proc. Zool. Soc. Lond.* 1859: 440–441.
- Sclater, P. L. 1874a. [Mr. Sclater exhibited and pointed out . . .] *Proc. Zool. Soc. Lond.* 1873: 728–729.
- Sclater, P. L. 1874b. On Peruvian birds collected by Mr. Whitely. *Proc. Zool. Soc. Lond.* 1873: 779–784.
- Sclater, P. L. 1877. Description of two new antbirds of the genus *Grallaria*, with a list of the known species of the genus. *Ibis* (4)1: 437–451.
- Sclater, P. L. 1890. *Catalogue of the birds in the British Museum*, vol. 15. Trustees of the Brit. Mus., London.
- Sclater, P. L. & Salvin, O. 1871. On Venezuelan birds collected by Mr. A. Goering. *Proc. Zool. Soc. Lond.* 1870: 779–788.
- Sclater, P. L. & Salvin, O. 1876. On new species of Bolivian birds. *Proc. Zool. Soc. Lond.* 1876: 352–358.
- Sclater, P. L. & Salvin, O. 1879. On the birds collected by the late Mr. T. K. Salmon in the State of Antioquia, United States of Colombia. *Proc. Zool. Soc. Lond.* 1879: 486–550.
- Sclater, P. L. & Salvin, O. 1880. On new birds collected by Mr. C. Buckley in eastern Ecuador. *Proc. Zool. Soc. Lond.* 1880: 155–161.
- Stattersfield, A. J., Crosby, M. J., Long, A. J. & Wege, D. C. 1998. *Endemic Bird Areas of the world: priorities for biodiversity conservation*. BirdLife International, Cambridge, UK.
- Stiles, F. G. 1992. A new species of antpitta (Formicariidae: *Grallaria*) from the eastern Andes of Colombia. *Wilson Bull.* 104: 389–399.
- Verhelst, J. C., Rodríguez, J. C., Orrego, O., Botero, J. E., López, J. A., Franco, V. M. & Pfeifer, A. M. 2002. Birds of Manizales, Caldas, Colombia. *Biota Colombiana* 2: 265–283.
- Zimmer, J. T. 1944. Studies of Peruvian birds, no. XLVIII: the genera *Iridosornis*, *Delothraupis*, *Anisognathus*, *Buthraupis*, *Compsocoma*, *Dubusia* and *Thraupis*. *Amer. Mus. Novit.* 1262: 1–21.

Addresses: Paul Salaman, World Land Trust-US, 2806 P Street NW, Washington DC, USA, e-mail: psalaman@worldlandtrust-us.org. Thomas M. Donegan, Fundación ProAves, 33 Blenheim Road, Caversham, Reading RG4 7RT, UK, e-mail: tdonegan@proaves.org. Robert Prÿs-Jones, Bird Group, Dept. of Zoology, The Natural History Museum, Akeman Street, Tring, Herts. HP23 6AP, UK, e-mail: rpp@nhm.ac.uk