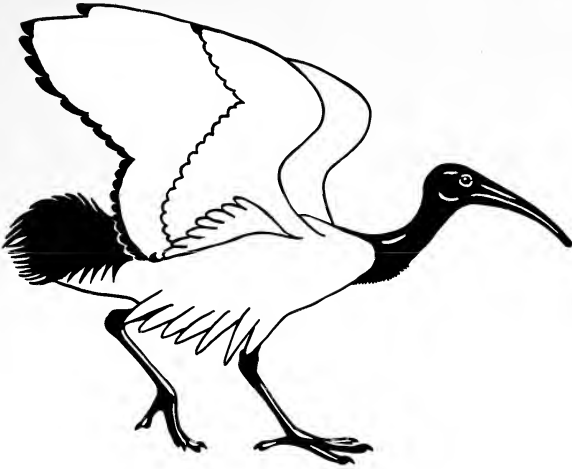


DS 102

Bulletin of the British Ornithologists' Club

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Volume 132 No. 1
March 2012

FORTHCOMING MEETINGS

See also BOC website: <http://www.boc-online.org>

MEETINGS are open to all, not just BOC members and are free.

Evening meetings commence with the talk at 6.00 pm. After the talk the cash bar opens and at 7.30 pm there is a light buffet supper (sandwiches etc.) costing **£15 per person** which must be ordered in advance. Vegetarian and gluten-free options can be ordered. Meetings are in the Tower Rooms, Section A, Sherfield Building, Imperial College, South Kensington, London SW7 2AZ. The entrance is opposite the Queen's Tower in the main quadrangle. The nearest Tube station is at South Kensington. For maps, see: <http://www3.imperial.ac.uk/campusinfo/southkensington>

27 March 2012 at 6.00 pm—Julian Greenwood—*A long-term study of the Black Guillemot colony at Bangor, Co. Down*

Abstract: The talk will examine the history of Black Guillemots *Cephus grylle* nesting in Bangor, Co. Down, and the patterns revealed by this long-term study. Results demonstrate that an advance in timing of breeding is associated with temperature rise in seawater and hence to climate change. Evidence is also gathering to show that Black Guillemots don't always play 'happy families', with both site and mate unfaithfulness occurring. Ringing recoveries have revealed the dispersal patterns of young birds around the Irish coastline.

Biography: Julian Greenwood is co-ordinator of science with education at Stranmillis University College, Belfast, teaching on BEd, PGCE, MEd and life-long-learning programmes. He has had a life-long interest in natural history, particularly birds, and for over 25 years has been working on Black Guillemots in Northern Ireland. He presently serves on RSPB Council.

Those wishing to order the buffet supper should apply to the Chairman (address below) by 13 March 2012
Entry is free but those wishing to attend must notify the Chairman no later than 26 March 2012

12 June 2012 at 5.15 pm—Annual General Meeting; 5.40 pm—Special General Meeting; 6.00 pm—Hein van Grouw—*What colour is that bird? How to recognise and name colour aberrations in birds*

Abstract: Knowledge of pigmentation development and genetics has been mostly gained from studies of domesticated species such as mice and chickens. In the past, when nothing was known about plumage pigmentation and mutations, aberrant-coloured wild birds were often named as new taxa. Now we know that colour aberrations are often due to mutations, but their correct naming remains problematic. Without a good photograph, records of aberrant coloration in some species are often unreliable because of the incorrect identification and / or naming of the mutation. My talk will aim to provide the facts you need to identify colour aberrations in wild birds correctly.

Biography: Hein van Grouw has worked for 15 years as a Bird Curator, first at Naturalis, Leiden, and more recently at the Natural History Museum, Tring. He has a lifelong interest in colour mutations in birds and has been doing practical breeding experiments with domesticated pigeons and doves for 30 years in order to unravel the inheritance of the many mutations present in these species. This, in combination with the examination of many aberrant-coloured bird specimens in museum collection over the last 15 years, has given him insight into the occurrence and nature of mutations in wild birds.

NB—the previously planned programme has been postponed as no offers were received by the published deadline.

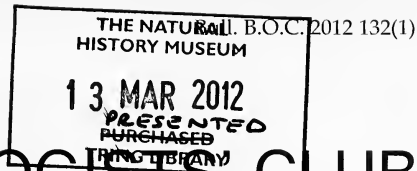
Those wishing to order the buffet supper should apply to the Chairman (address below) by 29 May 2012
Entry is free but those wishing to attend must notify the Chairman no later than 11 June 2012

18 September 2012—Details to be announced.

23 October 2012—BOC is planning to support the Natural History Museum (NHM) and the South London Botanical Institute (SLBI) in organising a one-day conference at the NHM, South Kensington, celebrating the centenary of the death of Allan Octavian Hume (1829–1912). Hume was the Indian ornithologist extraordinaire (he made the largest-ever donation of bird specimens to NHM), founder of the SBLL, enlightened administrator in the Indian Civil Service, and founder and early leading light of the Indian Congress Party. Full details will appear in the June Bulletin, but the day will focus on Hume's scientific legacy and is planned to include three talks on ornithology.

The Chairman: Helen Baker, 60 Townfield, Rickmansworth, Herts WD3 7DD UK. Tel. +44 (0)1923 772441.
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Bulletin of the BRITISH ORNITHOLOGISTS' CLUB



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CLUB ANNOUNCEMENTS

Chairman's message

Subscriptions were due for renewal on 1 January 2012. If you have not already paid, please do so as soon as possible to avoid further reminders. Please remember that the subscription is now £25.

Helen Baker

ANNUAL GENERAL MEETING

The Annual General Meeting of the British Ornithologists' Club will be held in Room SALC3, Sherfield Building, Imperial College, London SW7 2AZ, at 5.15 pm on Tuesday 12 June 2012.

AGENDA

1. Minutes of the 2011 Annual General meeting (see *Bull. Brit. Orn. Cl.* 131: 137–138).
2. Chairman's report.
3. Trustees Annual Report and Accounts for 2011 (both will be available in the room before the start of the meeting).
4. The Bulletin Editor's report—Mr G. M. Kirwan.
5. Election of Officers. The Committee proposes that:
 - i. Dr R. P. Prÿs-Jones be re-elected as *Hon. Secretary*
 - ii. Mr D. J. Montier be re-elected as *Hon. Treasurer*
 - iii. Mr K. F. Betton be elected to serve on the Committee (*vice* Mr M. J. Walton).

No other changes to the Committee are proposed as all other members are eligible to serve at least one more year in office.
6. Any other business, of which advance notice has been given.

Members are reminded that the AGM will be followed by a Special General Meeting to consider a Special Resolution to propose the adoption of the new Rules for the Club and, subject to the adoption of the new Rules, the adoption of the Bye-Laws made under Rule 26 of the new Rules. The proposed new Rules and Bye-Laws were published in *Bull. Brit. Orn. Cl.* 131: 225–232.

REVIEW

Dickinson, E. C., Overstreet, L. K., Dowsett, R. J. & Bruce, M. D. 2011. *Priority! The dating of scientific names in ornithology: a directory to the literature and its reviewers*. Aves Press, Northampton. 320 pp + CD-ROM with 160 pp of supporting data. Available from: Aves Press, Flat 3, 19 Bolsover Road, Eastbourne, East Sussex BN20 7JG, UK, e-mail: info@avespress.com. £80 + £7.50 post & packing.

This is not a book that I will ever read through, and I doubt many others will either, but it is certainly an extremely useful resource for anyone concerned with issues of ornithological nomenclature and I already have cause to be grateful to it. A core component of the *International code of zoological nomenclature* ('the Code'), the bedrock on which the scientific naming of animals is based, is the stress laid on the issue of date priority in determining the correct scientific name for any taxon, e.g. species or subspecies. The arbitrary starting point for all zoological nomenclature is the tenth edition of Linnaeus' *Systema naturae*, fixed at 1 January 1758. However, the precise date on which any scientific name subsequently proposed was first validly published, usually in a book or periodical, can for a whole array of reasons be difficult to establish.

Because of the importance attached to this issue, over the years numerous interested parties have investigated aspects that concerned them. Although often publishing their findings on actual publication dates of books or periodical parts, this literature has tended to be scattered and hard to find, making it all too easy for subsequent workers to overlook relevant findings and waste time 'reinventing wheels'. The great virtue of *Priority!* is not that it solves all dating problems relating to ornithological names, because it

doesn't. Rather, in conveniently standardised fashion it collates, reviews and adds to knowledge concerning 148 books and 121 periodicals that both contain taxon descriptions and pose dating problems, concluding with a clearly stated assessment for each as to whether difficulties can be considered fully resolved, partially resolved or still requiring further investigation.

Prior to the detailed publication by publication consideration that comprises most of the book, there are two useful introductory chapters. The first attempts to summarise exactly what the Code considers validly published work and the nature of the evidence relevant to determining date priority. The second uses over 40 pages to describe how the authors went about their task, including perhaps more than many readers may wish to know about the historical detail of the publishing process. The CD-ROM contains 65 tables referenced in the text under particular publications as providing supporting information and also a long Table 66 'intended to link the work done for this book with the needs of readers of the *Howard & Moore Complete Checklist of the Birds of the World*, 4th Edition, which will be published soon'.

The entire work is very nicely produced, is well referenced and indexed, and provides an extensive glossary to all of the technical publishing terms used in the text. Overall, the authors, who give appropriate credit to a large number of contributors, must be congratulated on a volume that will both save others much time and frustration, and also provides a clearly referenced springboard for further research into an issue that manages to be both esoteric and fundamentally important.

Robert Prŷs-Jones

CORRIGENDA

In the paper describing *Oenanthe lugens warriae* (Shirihai *et al.*, 2011, *Bull. Brit. Orn. Cl.* 131: 270–291), two minor changes of wording came too late to be included. On p. 281, line 33, the word 'distinctly' should be replaced by 'averages', while on p. 284, line 13 of the main text, 'December 2004' should read 'December 2001'.

Geographical variation in Immaculate Antbird *Myrmeciza immaculata*, with a new subspecies from the Central Andes of Colombia

by Thomas M. Donegan

Received 31 May 2010

SUMMARY.—Morphology, biometrics and vocals indicate that the population of Immaculate Antbird *Myrmeciza immaculata* in Colombia's Central Andes is differentiated from other populations. A new subspecies described here differs from nominate *immaculata* in the underparts coloration of females, reduced feathering on the forehead in adult males and a generally slower song with different note shape. Subspecies rank is assigned because differences between the new taxon and allopatric populations do not attain those between sympatric or parapatric *Myrmeciza*. Available data also support splitting Immaculate Antbird into two species, under any modern version of the Biological Species Concept. Western Immaculate (or Zeledon's) Antbird *M. zeledoni* inhabits foothills and mountains from Costa Rica southwards, and includes *M. z. macrorhyncha* of southern Panama to Ecuador. (Andean) Immaculate Antbird *M. immaculata* occurs in the Central, East, Perijá and Mérida Andes of Colombia and Venezuela (and includes the new subspecies). Vocal differences exceed those between parapatric Goeldi's Antbird *M. goeldii* and White-shouldered Antbird *M. melanoceps* and those between sympatric thamnophilids in other genera. Subspecies *macrorhyncha* and the new subspecies can be considered phylogenetic species within *zeledoni* and *immaculata* respectively. *M. i. affinis* of the Mérida Andes is weakly differentiated from *M. i. immaculata*. None of the features used to diagnose *brunnea* (of the Perijá Mountains) is supported. The name *ellisiana* is a junior synonym of nominate *immaculata*. The name *zeledoni* Ridgway, 1909, is selected to have priority over *berlepschi* Ridgway, 1909 (for which *macrorhyncha* is a replacement name) pursuant to an explicit First Reviser action, to stabilise the name of a split *M. zeledoni*.

Immaculate Antbird *Myrmeciza immaculata* is a large thamnophilid of lower to middle elevations in the mountains and some adjacent lowlands from Central America south to Ecuador and the Andean foothills of Colombia and Venezuela (Zimmer & Isler 2003). Although it has served as a study species for ecologists investigating antbirds at army ant swarms (e.g., Hilty 1974, Willis 1985, Vallely 2001, Rios *et al.* 2008), there has been no detailed study of its taxonomy since Cory & Hellmayr (1924), who lacked vocal data and had only limited specimen material available. Recent years have witnessed various taxonomic revisions of thamnophilids which have often shown historical (largely plumage-based) taxonomy to have under-estimated species richness (e.g., Isler *et al.* 1997, 1998, 1999, 2007, 2008, 2009, Isler & Whitney 2011), including in *Myrmeciza* (Chaves *et al.* 2010).

In *M. immaculata*, it is well known that western and eastern populations differ vocally, with the former having a faster paced song (e.g., Zimmer & Isler 2003, Restall *et al.* 2006, Boesman 2007). Moreover, Salaman *et al.* (2002) considered that a female collected in the Serranía de San Lucas, which lies north of the Central Andes of Colombia, probably represented an undescribed subspecies given morphological differences from other Colombian specimens. However, the convoluted taxonomic history of the group, vague

type localities for some names and lack of sound-recordings from San Lucas complicated describing it. In January 2010, with the improving security situation, TMD participated in a further expedition to the Serranía de San Lucas, obtaining two more specimens and sound-recordings of all four major vocalisations of Immaculate Antbirds there. Together with other recordings from Colombia now available, these materials facilitate an overdue taxonomic study.

In suboscine passerines, vocalisations are considered innate and stereotypical (Kroodsma 1984), and in another suboscine genus, *Scytalopus*, these better reflect molecular differences than plumage characters (Arctander & Fjeldså 1994). Helbig *et al.* (2002) suggested that, to assess the rank of allopatric populations, a comparison of observed differences with those between closely related sympatric or parapatric populations known to be species be undertaken. Based on differences between closely related sympatric species of Thamnophilidae, Isler *et al.* (1998) suggested ranking populations as species given three or more diagnostic vocal differences between them, including at least one in male loudsong. These methods have been widely applied in taxonomic studies of this family (e.g., Isler *et al.* 1999, 2006, 2007, 2009, Chaves *et al.* 2010, Isler & Whitney 2011). Further, sympatric Peruvian Warbling Antbird *Hypocnemis peruviana* and Yellow-breasted Warbling Antbird *H. subflava* show no diagnosable differences in male song, but differ in three characters in their calls (Isler *et al.* 2007). For *Myrmeciza*, in particular, two parapatric or sympatric species (Stub-tailed *M. berlepschi* and Esmeraldas Antbirds *M. nigricauda*) are differentiated by only two subjective differences in male loudsong, although they apparently also differ in calls (Chaves *et al.* 2010) and studies of female songs are needed (Remsen *et al.* 2012). However, these *Myrmeciza* are not closely related to *immaculata* (Brumfield *et al.* 2007) and there are various difficulties with the authors' analysis (Remsen *et al.* 2012). Here, morphology and voice are studied in *Myrmeciza* antbirds considered to be related to *immaculata*.

Methods

Molecular data suggest that *M. immaculata* is sister to Sooty Antbird *M. fortis* among taxa sampled to date, and closely related to White-shouldered Antbird *M. melanoceps* and Goeldi's Antbird *M. goeldii*, based on a sequence of a single specimen of subspecies *zeledoni* from Panama (Brumfield *et al.* 2007). Specimens and sound-recordings of all species in this proposed group were studied to understand better the vocal, biometric and plumage differences between them.

A list of museum acronyms with details of specimens examined and their localities appear in Appendix 1. Details of various Colombian specimens at museums not visited are based on Biomap Alliance Participants (2011). The following measurements were taken for each specimen: wing-chord and tail length (to nearest mm), tarsus length, culmen length from skull to tip of mandible (to nearest 0.5 mm) and, from specimen labels, mass (g), where available. There are a few juveniles in museums, identified by their more patchy or darker rufous plumage. Data from such specimens and, for measurements, from body parts in moult, were excluded from analyses.

Vocalisations of *M. immaculata sensu lato* (Appendix 1), *M. fortis*, *M. goeldii* and *M. melanoceps* were studied. Sonograms were generated using the default settings of Raven Lite 1.0, sometimes adjusted for brightness and then expanded for time period and frequency. *M. immaculata* populations possess several different vocalisations. Four of these, for which reasonable samples were available for most populations, were subject to further study. The loudsong (*sensu* Willis 1967, referred to here as 'song' or 'male song') consists of repeated, relatively melodic, similar notes of generally slower delivery than other vocalisations (Fig. 5). Some recordings feature a second individual calling at a higher acoustic frequency and

often faster with a more irregular note shape and frequency variation, in response to the main singing individual. According to recordists' notes on several recordings, such higher and less regular songs correspond to females duetting. Female and putative female songs were treated separately in the analysis. Two call-types were also found in a significant number of recordings and therefore were subject to further analysis. The first ('single-note call': Fig. 6) consists of a single, sharp note, often repeated usually with significant gaps between calls. The second ('multi-note call') consists of an unmelodic, fast churr varying from a handful of notes to several tens (Fig. 7). Other apparent calls of some taxa include single, isolated notes of similar note shape to those in a song or scold; contact calls including single notes and growls with various note shapes; in-hand distress calls by birds mist-netted; and on one apparent recording of *M. fortis*, a minute-long trill. These other calls were not subject to detailed analysis.

Up to three different examples of each vocalisation type were measured from each single recording analysed, resulting in 1,202 vocalisations being studied, comprising 803 male songs, 108 female songs, 169 multi-note calls and 122 single-note calls. Data on numbers of recordings and sonograms are presented in Appendix 3. Appendix 1 contains a gazetteer of recording localities for *immaculata sensu lato*. Locality data for other recordings are available from the author. Recordings of the same individual were treated as one recording and later recordings were excluded from analyses (and the above data), as were recordings of consecutive or close to consecutive serial number in tapes or recordings made within two hours by the same recordist with similar vocal variables. The number of assumed individuals for each vocalisation for each species is stated in Appendix 3. On most recordings, the first three vocalisations were studied, but in some recordings where the individual approached closer permitting greater definition on the sonograms, later recordings were selected. Songs and multi-note calls were analysed where they comprised a sequence of notes broken by gaps significantly longer than intervals between individual notes in a sequence. Data from recordings that were curtailed or included only fragments of a song or call were ignored. As many recordings from as many localities as possible were included, where available, to determine the full range of variables. All recordings of individuals under natural conditions and after playback were included for the same reason. After compiling the data, the highest and lowest recorded values for each variable for each vocalisation for each taxon were double-checked to verify upper and lower limits.

Various vocal variables studied by Isler *et al.* (1999, 2006, 2007, 2009) were considered for further analysis during a preliminary review of sonograms. Data for the following variables were collated and analysed for both male and female songs: (i) number of notes in song; (ii) total song duration; (iii) song speed (calculated by dividing i by ii); (iv) max. acoustic frequency of second note (kHz); (v) max. acoustic frequency of final note (kHz); (vi) acoustic frequency variation (kHz) (iv minus v); (vii) peak in acoustic frequency—the relative position of the highest note (as a percentage, calculated as $(p-1)/(n-1)$ where p is the sequential position of the note with the highest frequency and n is the number of notes in the song, and in recordings with no discernible peak or with no ascending or descending pattern, this was instead determined as 'flat' and the recording was ignored); and (viii) position of trough in acoustic frequency—the relative position of the lowest note (expressed as a percentage, see position of peak); (ix) subjective description of individual note shape; and (x) subjective description of change in note shape. The first note of several *M. goeldii* and *M. melanocephala* songs is often doubled or tripled, whilst in other *Myrmeciza* studied here, songs are evenly paced. To provide comparable song speed data with other species, such doubled and tripled notes were treated as a single note for purposes of counting the number

of notes in songs and song speeds. This aspect was instead treated as a feature of note shape and change in note shape for *M. goeldii* and *M. melanocephala*.

For multi-note calls, the same variables were analysed but frequency data were based on the lowest and highest note at any point, rather than particular notes, and the position of peak and trough were based on the time from the start of the call, rather than by counting notes. Multi-note calls often showed harmonic overtones and undertones. The loudest notes for most taxa were typically (though not always) the second highest set of notes (above a single undertone), so this tone was measured for all recordings of the *immaculata* group and *fortis* including in the few recordings where the undertone was louder. For *goeldii* and *melanocephala*, usually only a single tone was visible and in the few recordings with more than one tone overtones were very weak, so the stronger or sole tone was measured.

For single-note calls, only total call duration (= single note length), max. acoustic frequency (kHz) and note shape were studied.

To assess the rank of the new taxon described here, and to consider species and subspecies limits in *M. immaculata*, biometric and vocal data were subdivided on the basis of currently recognised subspecies and well-known biogeographic divides: (i) Venezuelan or Mérida Andes (including the type locality of *affinis*); (ii) East Andes of Colombia (nominat *immaculata*); (iii) Central Andes, Colombia (new subspecies described below); (iv) Chocó lowlands and adjacent foothills from Ecuador north to Darién (*macrorhyncha*); and (v) northern Panama to Costa Rica (*zeledoni*).

Statistical tests.—Various diagnosability tests were made for pairs of vocal and biometric variables of these populations, following Donegan (2008).

LEVEL 1: statistically significant differences at $p < 0.05$. A Bonferroni correction was applied for both vocal data and biometrics with the number of variables treated separately for each different call type (male and female songs and multi-note calls: eight variables each, $p < 0.0002$); single note calls: two variables, $p < 0.025$; biometrics 5 variables $p < 0.01$). An unequal variance (Welch's) *t*-test was used; for song speeds, a two-sample Kolmogorov-Smirnov test was applied as an additional test that must be satisfied for Level 1, to account for the possibility of a non-normal distribution. These calculations assess the statistical significance of differences between the means of populations, but do not address diagnosability, as they tolerate considerable overlap.

Further calculations, described below, were undertaken to measure inter-population differences in the context of various species and subspecies concepts. In the formulae used below, \bar{x}_1 and s_1 are the sample mean and sample standard deviation of Population 1; \bar{x}_2 and s_2 refer to the same parameters in Population 2; and the *t* value uses a one-sided confidence interval at the percentage specified for the relevant population and variable, with t_1 referring to Population 1 and t_2 referring to Population 2.

LEVEL 2: a '50% / 97.5%' test, following one of Hubbs & Perlmutter's (1942) subspecies concepts, which is passed if sample means are two average standard deviations or more apart controlling for sample size, i.e. the sample mean of each population falls outside the range of 97.5% of the other population: $|\bar{x}_1 - \bar{x}_2| > (s_1(t_{1@97.5\%}) + s_2(t_{2@97.5\%}))/2$.

LEVEL 3: The traditional '75% / 99%' test for subspecies (Amadon 1949, Patten & Unitt 2002), modified to control for sample size, which requires both the following tests to be passed: $|\bar{x}_1 - \bar{x}_2| > s_1(t_{1@99\%}) + s_2(t_{2@75\%})$ and $|\bar{x}_2 - \bar{x}_1| > s_2(t_{2@99\%}) + s_1(t_{1@75\%})$.

LEVEL 4: diagnosability based on recorded values (first part of Isler *et al.*'s 1998 diagnosability test) or, for plumage and subjective vocal characters (note shape and change of note shape), subjective diagnosability.

LEVEL 5: 'Full' diagnosability (where sample means are four average standard deviations apart at the 97.5% level, controlling for sample size) the second part of Isler *et al.*'s (1998) diagnosability test: $|(\bar{x}_1 - \bar{x}_2)| > s_1(t_{1@97.5\%}) + s_2(t_{2@97.5\%})$.

This analysis resulted in pair-wise differences between eight taxa or groups (49 taxa-pairs) under five different statistical tests for 50 characters, a total of c.10,000 pairwise statistical tests. The results of these analyses, together with plumage differences, are set out in Appendix 4.

A separate proposal for ranking species based on scores using a range of characters was recently developed by Tobias *et al.* (2010). Herein, a taxon pair that reaches Level 1 (but does not meet other tests) is treated as conforming to Tobias *et al.*'s (2010) 'minor magnitude' differences (less than two standard deviations between means). Level 2 is equivalent to their 'medium magnitude' (two standard deviations' difference between means), but the statistical test employed is more rigorous in that it also controls for sample size. Tobias *et al.* (2010) use five standard deviations' difference without controlling for sample size for their 'major magnitude' differences; my Level 5 (four standard deviations apart, i.e. no overlap, but controlling for sample size) is treated as equivalent. I do not necessarily endorse any species concept or statistical approach applied in this paper for assessing species rank.

Taxonomic and nomenclatural history

As many as eight different names have been described for *M. immaculata*. Prior to considering species or subspecies limits, it is essential to clarify how described names apply to known populations.

Thamnophilus immaculatus, Lafresnaye, 1845, was based on 'Bogotá' specimens, in a perfunctory description mentioning both male and female plumages. Lafresnaye noted that it was distinguished from other then known antbirds by its uniform, unmarked plumage. Three types (two males and a female-plumaged bird) are now at MCZ (specimen nos. 76756–58; for museum acronyms see Appendix 1). Ten years later, Sclater (1855) described *Pyriglena ellisiana* as a new species, based on a female 'Bogotá' specimen. Sclater (1855) did not mention Lafresnaye's description. Cory & Hellmayr (1924), who later compared the types, considered the female *immaculatus* type and that of *ellisiana* to be identical and that *ellisiana* was therefore a synonym. They also considered the *immaculatus* types to 'agree perfectly' with specimens from near Honda (which, based on elevational data on some specimens in question, were probably collected above this locality, between Honda and Facativá in the East Andes). Lafresnaye's types are consistent with modern specimens from the East Andes, with the female having rather rufous underparts and the males more feathered lores than in populations further west. The type of *ellisiana* (BMNH 1854.5.5.1) is also typical in plumage of an East Andes specimen. There is white only on the wing bend, which excludes *macrorhyncha*, and the underparts are among the more rufous of East Andes specimens. Although 'Bogotá' collections include birds collected elsewhere in Colombia such as the Central Andes (e.g., Donegan & Avendaño 2010), I concur with Cory & Hellmayr (1924) that both *ellisiana* and *immaculatus* should be treated as referring to the East Andes population, probably collected at mid elevations on the west slope of the East Andes below Bogotá.

Cherrie (1891a,b) described two other taxa as subspecies of *Myrmeciza immaculata*, namely *M. i. occidentalis* (type locality: Pozo Azul, Costa Rica) and *M. i. intermedia* (Talamanca, Costa Rica). However, it is clear that Cherrie did not have a good sample of true *immaculata* to hand. As subsequently noted by Salvin & Godman (1888–97) and confirmed through examination of the types (USNM 11949–50: *occidentalis*; USNM 64715: *intermedia*) both are Chestnut-backed Antbirds *Myrmeciza exsul*. *M. i. occidentalis* is now

generally treated as a subspecies of *M. exsul* whilst *M. i. intermedia* has not been recognised in recent works (e.g., Dickinson 2003, Zimmer & Isler 2003).

The next available name, *M. [immaculata] berlepschi*, with a type locality of Chimbo, western Ecuador (holotype USNM 97774) was established by Ridgway (1909), who sought to differentiate Chocó populations from nominate *immaculata*. This subspecies is now referred to as *macrorhyncha* Robbins & Ridgely 1993 (see below) and was originally described as a species separate from *immaculata*, diagnosed as having more extensive white markings on the upper wing (in both sexes extending to the lesser coverts) and a larger bill than *immaculata*.

M. zeledoni Ridgway, 1909 (type locality: Guayabo, Costa Rica) was also originally described as a separate species from *berlepschi* and *immaculata*. This name refers to the population in the mountains of northern / western Panama and Costa Rica, and was considered to have biometrics more similar to *berlepschi* than *immaculata*, but with the white wing markings covering only the anterior margin.

Ridgway (1909) noted that nominate *immaculata* was 'a very different bird' compared to *berlepschi* and *zeledoni* in justifying species rank for all three taxa but Cory & Hellmayr (1924) lumped *zeledoni* and *berlepschi* into *M. immaculata*, recognising all of them as valid subspecies. The same authors also noted differences between Cauca Valley (Central Andes) birds and nominate *immaculata*, considering that 'while typical of *immaculatus* as far as coloration is concerned, [they] approach the western race *berlepschi* by their slightly larger bill and less densely feathered forehead'. Despite this, the Central Andes population apparently lacked further published comment until Salaman *et al.* (2002) reached a similar conclusion to Cory & Hellmayr (1924), considering birds from the northern Central Andes to differ from *berlepschi* and *immaculata*.

Todd (1913) described *M. zeledoni affinis* (type locality: Guarico, Lara, Venezuela) and diagnosed only from *M. zeledoni* of Central America, with no attempt to distinguish it from *berlepschi* or nominate *immaculata*. Cory & Hellmayr (1924) synonymised *affinis* with nominate *immaculata*. They considered the type of *affinis* to be 'practically identical' to the female type of *immaculata* in the 'feathering on the forehead, narrow bill, coloration of the under parts and restriction of white on bend of wing' but also noted that 'additional material from Venezuela should be examined'. Phelps & Phelps (1955) subsequently collected the first specimens from the Perijá in Venezuela and named *M. i. brunnea* based on this series. Robbins & Ridgely (1993) described *M. i. macrorhyncha* as a replacement name for *M. i. berlepschi* due to preoccupation of that name by *Myrmeciza berlepschi* (Hartert, 1898) after Robbins & Ridgely (1991) had transferred *M. berlepschi* to *Myrmeciza* from *Sipia*.

An unidentified antbird was collected in Serranía de los Churumbelos, Cauca, Colombia, in 1998, and was labelled '*Myrmeciza* sp.' in the ICN-UN collection (specimen no. 33244). Salaman *et al.* (1999) reported it as a possible new species. Subsequent review suggests that the specimen represents an undescribed immature male plumage of Spot-winged Antbird *Percnostola leucostigma*, a species common at the locality. It is now labelled as such and databased under that species by Biomap Alliance Participants (2011).

In modern texts, four subspecies of Immaculate Antbird are generally recognised, *immaculata*, *macrorhyncha*, *zeledoni* and *brunnea* (e.g., Hilty & Brown 1986, Ridgely & Tudor 1994, 2009, Salaman *et al.* 2001, 2010, Dickinson 2003, Hilty 2003, Zimmer & Isler 2003, Restall *et al.* 2006). *M. i. immaculata* is treated as occurring in the East and Central Andes of Colombia and the Venezuelan Andes (Hilty & Brown 1986, Hilty 2003, Restall *et al.* 2006). *M. i. brunnea* has been restricted to the Sierra de Perijá (e.g., Hilty & Brown 1986, Hilty 2003) although the name has also been applied to populations on the east slope of the East Andes of Colombia in the Tamá region (Álvarez *et al.* 2007). *M. i. macrorhyncha* occurs in

the western (Chocó) lowlands of Ecuador north to southern Panama as well as on adjacent slopes (Hilty & Brown 1986, Ridgely & Gwynne 1989, Ridgely & Greenfield 2001, Zimmer & Isler 2003), with *M. i. zeledoni* in Costa Rica and northern Panama (Ridgely & Gwynne 1989, Zimmer & Isler 2003). The three other available names—*affinis*, *berlepschi* and *ellisiana*—are not currently in use for the reasons described above.

Names for the Perijá and Mérida populations

Various data relevant to the taxonomic status of populations in the Mérida Andes (for which the name *affinis* is available), Sierra de Perijá (currently known as *brunnea*) and the nominate population in the East Andes were uncovered during this study. The subjective synonymy of *affinis* with nominate *immaculata* by Cory & Hellmayr (1924) was only tentative and the Táchira depression (which separates the East and Mérida Andes) is an important barrier for subspecies of various premontane birds. Comparison of vocalisations of the East Andes and Mérida Andes populations produced statistically significant mean differences in the acoustic frequency of the second note in male songs, and tentatively, based on small samples, the frequency and length of single-note calls (Appendix 4). Females from the Venezuelan Andes are on average also less strongly rufous on the flanks than specimens from Perijá at COP. However, there may be limited contact between the Mérida and East Andes populations in light of a record close to the depression separating the ranges (Boesman 2007) and distribution mapping, which found the East Andes and Mérida ranges of *immaculata* to be continuous (Fig. 9). *M. i. affinis* could be recognised under more liberal subspecies concepts, but not under those based on full diagnosability or which do not tolerate intermediates. These observed minor variations may be clinal.

The widely recognised subspecies *brunnea* of Perijá is weakly differentiated (if at all) and better treated as a synonym of *immaculata* for now. It was diagnosed from *immaculata* in having 'less rufous, more brownish upper parts' in the female and mandibles being 'greyish white' rather than 'yellowish'. The type of *brunnea* is a female at AMNH (formerly at COP), with a darker brown head and flanks compared to females from the East and Central Andes at AMNH. However, the longer series at COP shows considerable variation in these features and would have been compared directly only with Mérida specimens and one female from the Central Andes in that collection. Photographs of the larger series of females at COP reveals complete overlap in the shade of head, upperparts and underparts between Perijá and Mérida specimens, and this feature is also variable in *immaculata* and the Central Andes population. The only visible difference between Perijá and other specimens at COP is that females have on average slightly more strongly rufous-brown flanks than those in the Central Andes of Colombia and Venezuelan Andes. Differences in bill coloration probably result from comparing old with fresh specimens, as the holotype's bill is now white like other specimens. For example, the Central Andes paratype designated below (collected in 2010) had a greyish mandible when deposited at ICN, whilst the San Lucas paratype (collected in 2001) had the mandible yellowish white by 2010, suggesting decolorisation. The Perijá population appears fully contiguous with *immaculata* further south. Notably, there is a USNM specimen from Ayacucho, Cesar, near the lowest elevation of the 'bridge' between the East Andes and Perijá. Like Perijá specimens, most female *M. i. immaculata* have more strongly rufous flanks than Central Andes specimens. Although no vocal data are available from Perijá and insufficient materials were studied to consider biometric variation, none of the diagnosis of *brunnea* is supported by this study.

Myrmeciza fortis incanescens

Of the other species in this study, only *M. fortis* is historically treated as polytypic. The type locality of *M. fortis* is in Loreto, Peru. Todd (1927) described *M. f. incanescens*, which has been recognised tentatively by most subsequent authors (e.g., Dickinson 2003). However, Zimmer & Isler (2003) considered it of doubtful validity. It was described on the basis of its supposed darker mandible, but incorrectly assumed that the feature was yellow in the nominate. As noted above, original mandible coloration is lost as specimens in this genus age. The type locality of *incanescens* is Tonantins, near the Colombian border of Brazil and the Amazon. Recordings near the *incanescens* type locality (e.g., XC 58407 from Leticia, Colombia, and ML 117193–94 from Amazonas, Brazil) produce vocal data very close to the average for other recordings of *M. fortis*. As a result, the *fortis* sample was not subdivided for analysis. Neither subspecies limits in *M. fortis* nor geographic variation in other *Myrmeciza* species are considered further here.

Genus names

Generic limits in *Myrmeciza* have also been rather fluid. For example, Todd (1927) proposed that *immaculata sensu lato* (including *berlepschi* and *zeledoni*), along with various other species, is better placed in *Myrmelastes* P. L. Sclater, 1858 (of which the type species is Plumbeous Antbird *Myrmeciza hyperythra*). However, Zimmer (1932) considered that the 'genera *Myrmoderus*, *Myrmelastes*, *Myrmophylax*, and *Myrmedestes* are equally unsatisfactory and intergrade insensibly with *Myrmeciza*'. Peters (1951) followed Zimmer (1932) for *Myrmelastes* but adopted some of Todd's (1927) other proposals. Robbins & Ridgely (1991) later sunk *Sipia* into *Myrmeciza*.

Molecular phylogenies suggest that *Myrmeciza* is polyphyletic (Brumfield *et al.* 2007, Tavares *et al.* 2011). The type of the genus, White-bellied Antbird *M. longipes*, was not included in either of these studies, but it would be surprising if it grouped with *immaculata*, *fortis*, *melanoceps* and *goeldii*. If that is the case, another genus name will ultimately be needed for the group studied here. Merging these birds with the apparently related Black-headed Antbird *Percnostola rufifrons*, the *Pyriglena* fire-eyes and / or *Gymnocichla* at generic level may be necessary based on data presented by Brumfield *et al.* (2007). Notably, *ellisiana* was originally described in *Pyriglena* by Sclater (1855) so such a treatment would not be novel. Moreover, *M. goeldii* shares the bright red eye of *Pyriglena* and *Percnostola rufifrons* (others in the clade possess red-brown or rufous to brownish irides) and all of the *Pyriglena* / *Gymnocichla* / *Myrmeciza* clade have fairly uniform black male and brownish female plumages, with some species having white interscapular patches and wing-covert fringes. Songs of *Pyriglena* and *Gymnocichla* are similarly structured to those of *Myrmeciza*, involving repeated notes at more or less the same frequency and with a similar note shape to *zeledoni* and *macrorhyncha* (e.g., Fig. 5). A more rational generic placement of the birds studied here requires further research, so I follow prevailing literature in using *Myrmeciza*.

Description of new subspecies

None of the available names discussed above is associated with a type specimen from the Central Andes. Despite that Cory & Hellmayr (1924) and Salaman *et al.* (2002) drew attention to morphological differences between this and other populations, the Central Andes population is undescribed to date. The following name is proposed:

Myrmeciza immaculata concepcion subsp. nov.

Holotype.—Instituto de Ciencias Naturales, Universidad Nacional, Bogotá, Colombia (ICN 38162; see also Fig. 1). Adult male collected by TMD above Santa Cecilia, Santa Rosa del Sur municipality, dpto. Bolívar, Colombia, in premontane forest on the east slope of Serranía de San Lucas (07°58'33"N, 74°12'55"W; 1,550 m) on 9 January 2010. Tissue sample (heart) and skeleton also deposited at ICN. The bird foraged with others of the same species and was lured into a mist-net using playback of the song of nominate *M. immaculata* on Álvarez *et al.* (2007). Sound-recordings of the holotype are available on www.xeno-canto.org, see Appendix 1 and Vocalisations.

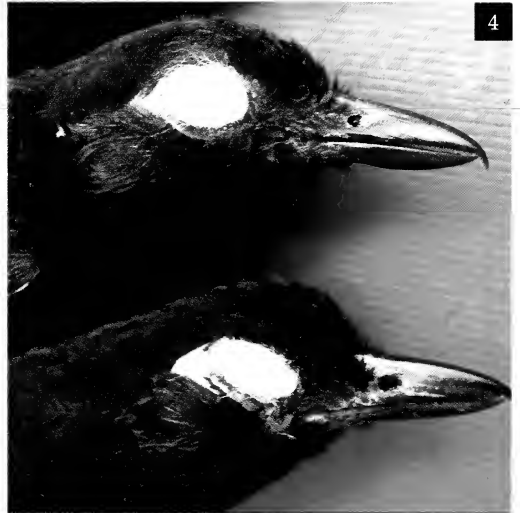
Paratype.—ICN 38161 is an immature male (with plumage similar to the female) collected by TMD at the type locality on 7 January 2010 (*cf.* Fig. 2).

Other specimens.—ICN 34181 (*cf.* Fig. 3) is an adult female collected by P. G. W. Salaman, A. M. Cuervo & TMD at El Retén, near La Punta, Santa Rosa del Sur, Serranía de San Lucas, Bolívar (08°08'47"N, 74°12'48"W; 1,400 m). (Note: the different coordinates specified in Salaman & Donegan (2001) are widely known to be incorrect. The coordinates here are based on re-geo-referencing of the locality in January 2010.) USNM 392891 is an adult female collected by M. A. Carriker at Volador, Santa Rosa del Sur municipality (c.07°58'N, 74°15'W; 800–1,500 m, *per* Paynter 1997), 25 miles west of Simití at 2,600–3,000 ft. USNM 392795 (*cf.* Fig. 4) is an adult male with similar data. Other Central Andes specimens referable to the new subspecies are listed in Appendix 1.

Diagnosis.—Referred to *Myrmeciza* Gray, 1841, due to its medium size for an antbird, resembling *Gymnocichla* but loreal and suborbital regions more feathered (only the postocular and rictal regions naked), adult male without white tips to wing-coverts, bill shorter than head and slender to moderately stout, culmen distinctly curved and gonyes convex and prominent basally, nostril exposed and lack of rictal bristles, rounded wing, tail rounded, tarsus much longer than culmen and generally uniform, dull plumage (Ridgway 1911), but see Genus names above. Referred to *M. immaculata sensu lato* due to its similar plumage, biometrics and voice to other populations, including its generally uniform black (male) or brown (female) plumages with no strong markings except white on the wing bend and its bluish and whitish bare facial skin. Within *M. immaculata*, it is closest to the nominate subspecies of the adjacent East Andes.

M. i. concepcion has a generally slower song than *M. i. immaculata* which permits >90% of recordings to be identified, although there is marginal overlap (Appendix 3; Figs. 5 & 8). Additionally, in *concepcion* individual notes have shorter termini and most are less downslurred over the first 2/3 of the note than in East and Mérida Andes recordings (Fig. 5). In *concepcion*, single-note calls are given in duets by pairs, with the second (higher) note generally being more downstroke-like or an up-downstroke (Fig. 6) but no other Immaculate Antbird recordings showed duetting in this type of call or similar single-note call shapes.

Morphological differences between the new subspecies and other populations are more subtle. Cory & Hellmayr (1924) considered birds now referred to *concepcion* to have more extensive bare skin and less extensive feathering on the lores and forehead than East Andes specimens. This hypothesis is supported by comparing certain specimens prepared by the same collector (Fig. 4), but it should be regarded as a tentative difference. Female *M. i. concepcion* also has a different (generally less strongly rufous and paler) shade of brown on the flanks and undertail-coverts. Compared to East Andes specimens, *concepcion* is more extensively greyish on the mid-belly (although this is shared by Mérida Andes specimens).



Compared to western *zeledoni* and *macrorhyncha*, male song in the new subspecies differs diagnosably in three or more variables (speed, number of notes and note shape vs. *macrorhyncha*; max. frequency of second note, max. frequency of final note, note shape and change in note shape vs. *zeledoni*) and *concepcion* also differs in its female songs and single-note calls (Appendix 4). The new subspecies also has less extensive white feathering in the upper wing-coverts than these two taxa, the difference from geographically proximate *macrorhyncha* being greatest. *M. i. concepcion* has limited contrast between the shade of brown on the crown (more rufous) and mantle (more brown) whereas in *zeledoni* and *macrorhyncha* these are more concolorous. The female is darker and less rufous overall than *macrorhyncha* (7.5YR 3/4: Fig. 3) and *zeledoni*, with the latter again being more similar to *concepcion* in general plumage shade. Differences between *M. i. concepcion* and *M. fortis*, *M. melaniceps* and *M. goeldii* are set out in Appendix 4.

Description of the holotype.—See Fig. 1. Colours follow Munsell Color (1977, 2000). Description taken immediately after collection. Plumage entirely jet black (uncoded) except white (uncoded) on carpal and wing bend. Iris dark red (10R 3/4), bill black, legs dark grey (Gley 1 3/N), soles cream (2.5YR 8/6). Bare postocular skin very pale blue (uncoded) and in front of eye pastel blue (uncoded). Testes: right 4 mm × 2 mm, left 3.5 mm × 2 mm. Skull 100% ossified. Measurements (mm): wing in life 86.0, tail 84.0, tarsus 33.5, bill 22.0; mass 40.8 g.

Female morphology.—See Fig. 3. The following is based on the San Lucas female at ICN, using the specimen label, with bare-part descriptions and other notes from the label, a photograph and field notes. Crown dark rufous-brown (5YR 2.5/2 but redder). Throat, moustachial and lores sooty grey (10YR 2/1). Upper breast greyish dark brown (7.5YR 3/2), paler on belly, legs and tail-coverts (7.5YR 2.5/3). Rump and mantle dark rufous-brown (5YR 2.5/2 but redder, slightly paler than crown). Tail very dark brown (10YR 2/1). Wings very dark brown (10YR 2/1) with more rufous remiges (5YR 3/3). Legs dark bluish grey with yellowish soles. Bill black, mandible grey on distal two-thirds. Irides dark red. Skull 100% ossified, ovaries 9.0 mm, ovi 2.2 mm. Stomach contents: parts of insects including Coleoptera. Measurements (in mm): wing in life 86.0, wing-chord (skin) 76.5, tail 73.0, tarsus 33.5, bill to skull 22.0 mm; mass 39.3 g.

Variation in the series.—The immature male paratype (Fig. 2) is similar to the female but has the throat, moustachial and lores black (not coded) and upper breast less greyish (7.5YR 2.5/2), iris dark brown (5YR 2.5/2), bill black with basal mandible more greyish (Gley 1 4/N). Bare skin in front of eye bluish (not coded) and behind eye white (not coded). Legs black and soles cream (2.5Y 8/6). Measurements (in mm): wing-chord 79.0, tail 83.0, tarsus 33.5, bill to skull 22.5; mass unknown. Skull 100% ossified. Testes very small (not measured). Stomach contents: ants (Formicidae) and beetles (Chrysomelidae and

Legend to plate on facing page

Figure 1. The male *M. i. concepcion* on which the holotype (ICN 38162) is based, prior to its collection (© B. Huertas)

Figure 2. The immature male *M. i. concepcion* on which the paratype (ICN 38161) is based, prior to its collection (© B. Huertas)

Figure 3. Females of *M. i. concepcion* ICN 34181 (left: female, Serranía San Lucas, Bolívar, Colombia) and *M. z. macrorhyncha* ICN 11436 (right: San Antonio de Guaji, Guapi, Cauca, Colombia, collected by A. Olivares, 22 December 1955). Note more extensive white on shoulder of *macrorhyncha* and the differences in plumage shade.

Figure 4. Close-up showing extent of feathering on forehead of males of specimens prepared by M. A. Carriker: (above) *M. i. concepcion* (USNM 392795, Volador, Santa Rosa del Sur, Serranía de San Lucas, Bolívar, 6 May 1947); and (below) *M. i. immaculata* (USNM 411509, Hacienda Santana, Santander, 4 October 1949).

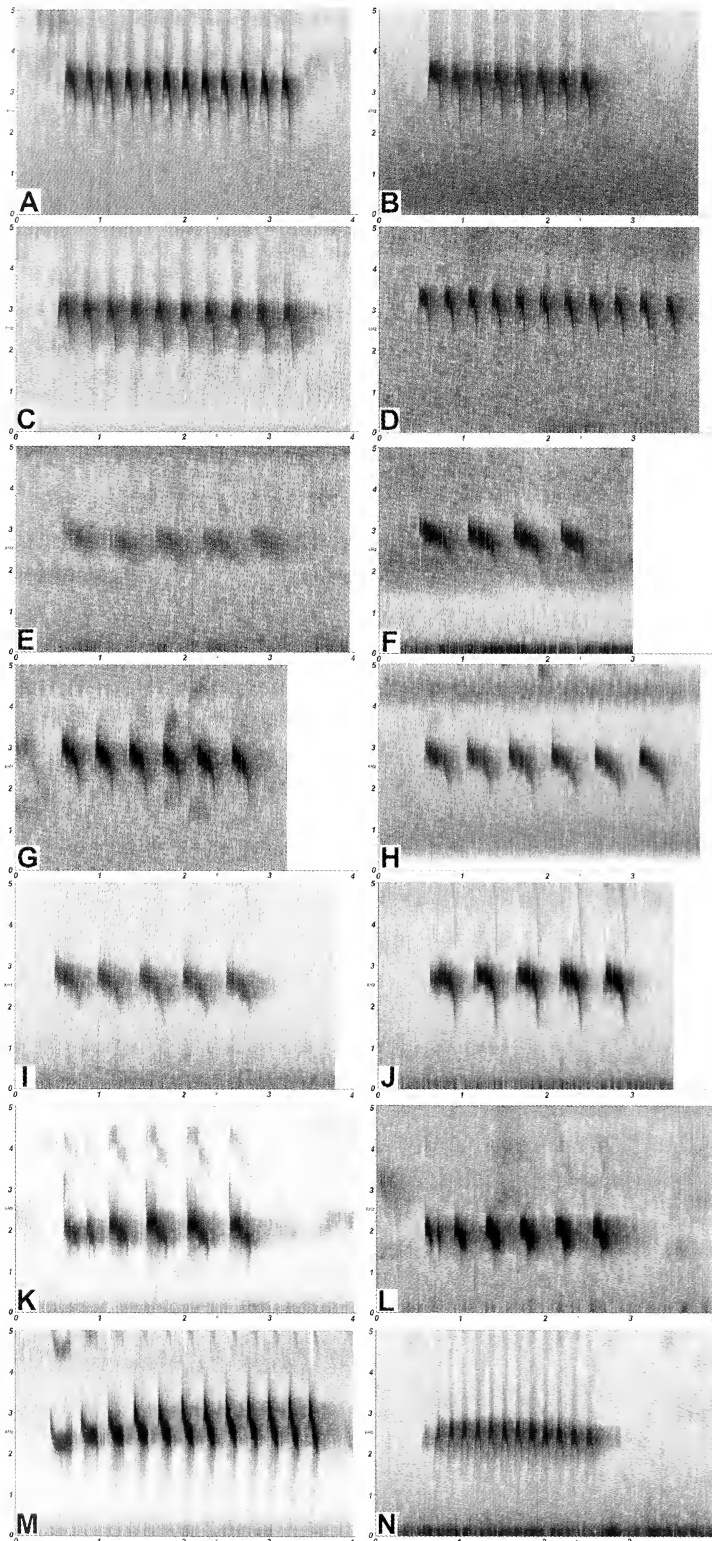


Figure 5. Songs of *Myrmeciza* and other taxa discussed herein. A. *M. z. zeledoni*, Parque Nacional General Omar Torrijos, Coclé, Panama (XC31340: R. Moore). B. *M. z. zeledoni*, La Paz Waterfall Garden, Costa Rica (ISL-KJZ.123:02: K. J. Zimmer). C. *M. z. macrorhyncha*, Tandayapa Bird Lodge, Tandayapa Valley, Pichincha, Ecuador (Moore *et al.* 1999, track 2.13.1: R. S. Ridgely). D. *M. z. macrorhyncha*, Parque Nacional Natural Tatamá, Pueblo Rico, Risaralda, Colombia (XC55196: P. Flórez). E. *M. i. conception*, type locality, Colombia, holotype prior to collection (XC92160: T. M. Donegan). F. *M. i. conception*, Cañon del río Claro, Antioquia, Colombia (XC18153: H. van Oosten). G. *M. i. immaculata*, Laguna Tabacal, Cundinamarca, Colombia (XC59290: F. Lambert). H. *M. i. immaculata*, Toledo, Parque Nacional Natural Tamá, sector San Isidro, Norte de Santander, Colombia (Álvarez *et al.* 2007, track 4.4(a)). I. *M. i. immaculata*, La Soledad, 20 km north-west of Barinitas, Barinas, Venezuela (XC6086: C. Parrish). J. As previous (XC42299: J. G. León). K. *M. melanoceps*, Sucusari Camp, north bank of río Napo, Loreto, Peru (ML34319: T. A. Parker). L. *M. goeldii*, Cocha Cashu Biological Station, Manu National Park, Peru (ML29817: T. A. Parker). M. *M. fortis*, north bank of río Napo, Peru, as above (ML34309: T. A. Parker). N. *Pyriglena leuconota*, El Limo, Loja, Ecuador (XC4240: W. Halfwerk). Note faster song speed and more up-down note shape in A–D (*zeledoni* group) compared to E–J (*immaculata* group) and marginally slower speed and longer ‘tails’ in *immaculata* (G–J) compared to *conception* (E–F). Note also broad similarity in song structure between *Pyriglena leuconota* (N) and *M. zeledoni* (A–D).

Erotylidae). The USNM specimens from San Lucas are an adult male and female, similar to those in the ICN series.

Referring to *macrorhyncha* and *zeledoni*, Willis (1985) suggested that *M. immaculata* has two different plumages before reaching adult male plumage, the first being similar to female plumage and the second like the male but with more brownish-black feathering. This pattern appears to be repeated in *concepcion*, with ICN 38161 an immature male essentially with female plumage; and ICN 18977 and USNM 411507 (from Antioquia) have brownish and black plumage, presumably moulting from immature to adult male plumage. The second phase mentioned by Willis (1985) may only be transient. Two USNM female-plumaged specimens from Valdivia are darker and more rufous than other females of *concepcion* and may be younger birds, but their undertail and flanks still differ in shade from *immaculata*. Data on variation in biometrics and voice of *M. i. concepcion* appear in Appendices 2–3.

Taxonomic rank.—The new taxon is ranked as a subspecies because the vocal differences between it and nominate *immaculata* fall short of Isler *et al.*'s (1998) 'three differences' benchmark for species rank based on voice and morphological differences are slight. Applying the Tobias *et al.* (2010) scoring system, *vis-à-vis* nominate *immaculata*, the new subspecies scores 3 for voice, 2 (tentatively) for bare skin / forehead feathering differences in males and 1 for the different colour of female underparts. Tobias *et al.* (2010) proposed that species should score at least 7 points, leaving *M. i. concepcion* short. Moreover, *M. i. concepcion* responded to playback of *M. i. immaculata* by coming to a mist-net (although it did not sing), also indicating that subspecies rank is appropriate. Recordist notes (XC63733: J. Tobias & N. Sneddon) report that *macrorhyncha* comes to playback of *M. fortis* (but similarly does not vocalise). Whilst such responses may not be fully indicative of conspecificity, a conservative approach is preferred.

Observed vocal differences do not appear to represent clinal variation. The slowest male songs (<1.9 notes / second) are from Tolima (southern Central Andes), Antioquia (northern Central Andes) and Bolívar (Serranía de San Lucas), i.e. across the entire known range of the new subspecies. Moreover, songs of the more proximate East Andes population of *immaculata* average faster than the Mérida population (Appendix 3).

Distribution.—Apparently restricted to the premontane slopes and foothills of the Central Andes, from dpto. Valle del Cauca on the west slope and dpto. Tolima on the east slope, north to Serranía de San Lucas, dpto. Bolívar. The San Lucas range and adjacent northernmost Central Andes near Anorí appear to support an important population, with a slower gradient at suitable elevations compared to further south in the Central Andes.

The southernmost points of the Central and East Andes populations of *M. immaculata* (see Fig. 9) coincide with known major distributional limits of birds in Colombia (Graham *et al.* 2010). The occurrence of related but different taxa in the Central and East Andes is a pattern echoed in several species in the foothill and subtropical zone that occupy the same forests as *M. immaculata*, e.g. Black-winged Saltator *Saltator atripennis*, the woodnymphs *Thalurania fannyi* / *colombica* and Lineated Foliage-gleaner *Syndactyla subalaris* (e.g., Hilty & Brown 1986).

Notes on the type locality.—The highest elevations of the San Lucas range have long been one of the most exciting remaining examples of terrestrial *tierra incognita*. The mountains reach >2,300 m, are isolated by 100 km below the 1,000 m contour from the nearest mountain range—the Central Andes—and may support other undescribed taxa. Carriker collected here in the 1940s but only reached foothill or lower montane forest, wherein he collected specimens of the new subspecies. In 1998–2002, several attempts were made to study these mountains. Two expeditions were aborted due to the security situation

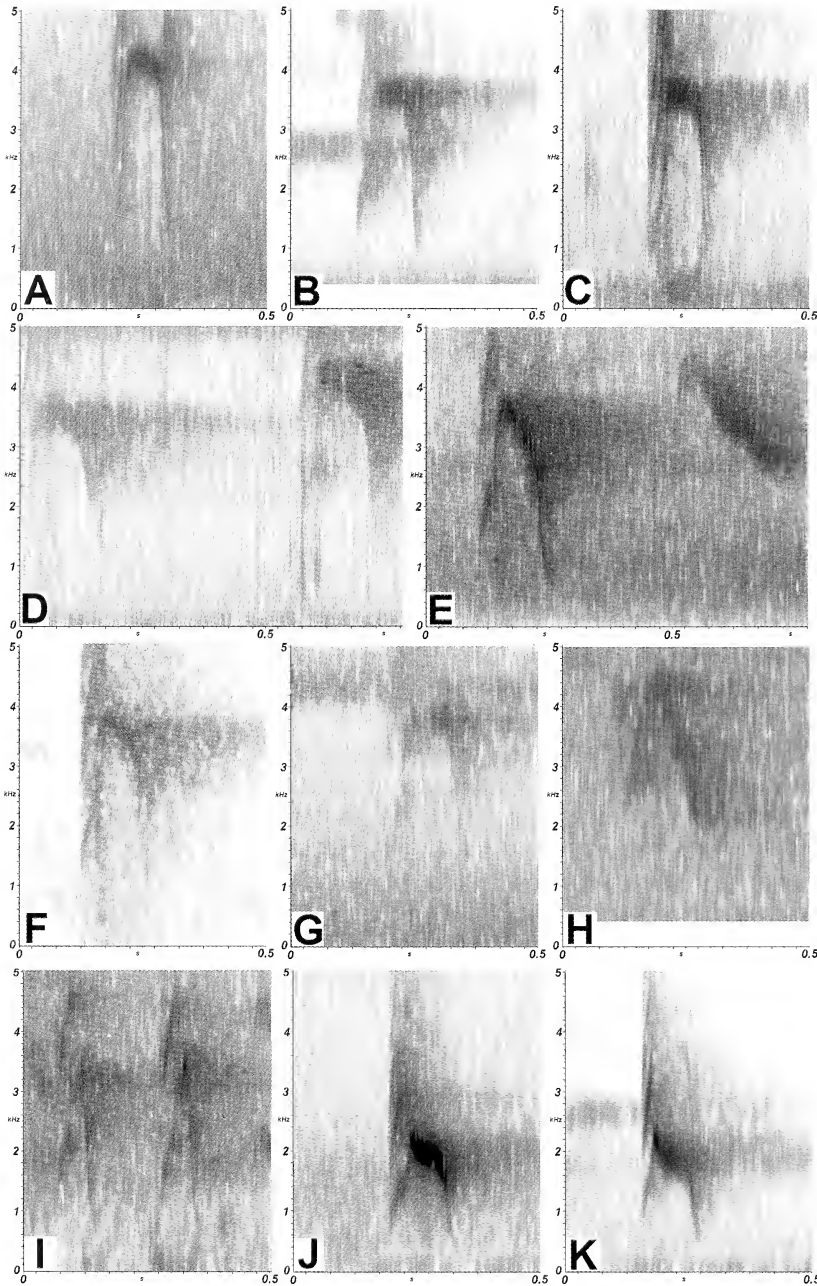


Figure 6. Single-note calls. A. *M. z. zeledoni*, La Virgen del Socorro, Costa Rica (ISL-KJZ.003:24: K. J. Zimmer). B. *M. z. macrorhyncha*, río Anchicayá Valley, Alto Yunda, Valle del Cauca, Colombia (ML83761: S. L. Hilty). C. *M. z. macrorhyncha*, Tinalandia, Pichincha, Ecuador (Krabbe & Nilsson 2003, track 80.15). D. *M. i. conception*, duet of group including holotype, type locality (XC92160: T. M. Donegan). E. *M. i. conception*, duet, La Pradera, Estación, Risaralda / Antioquia, Colombia (Álvarez *et al.* 2007, track 4.4(c)). F. *M. i. immaculata*, San Isidro, Barinas, Venezuela (XC43139: J. Klaiber). G. *M. i. immaculata*, Toledo, Parque Nacional Natural Tamá, sector San Isidro, Norte de Santander, Colombia (IAVH586: M. Álvarez). H. *M. i. immaculata*, El Talisman, San Vicente de Chucurí, Serranía de los Yariguíes, Santander, Colombia (XC92165: T. M. Donegan). I. *M. fortis*, duet, Huampami, río Cenepa, Amazonas, Peru (ML17544: T. A. Parker). J. *M. melanoceps*, Sabalillo, Loreto, Peru (XC27856: D. Edwards) K. *M. goeldii*, Collpa de Guacamayos, río Tambopata, Madre de Dios (ML75916: C. A. Marantz).

and two others resulted in the participants being detained (Salaman & Donegan 2001). In 2010, with the improving security situation, we managed to get higher than any previous study, with observations to 1,700 m, and studied the interior of premontane forest at the *concepcion* type locality (1,500–1,600 m). However, access to the very highest elevations remains restricted due to security issues and land-use conflicts. Other results of this study will appear elsewhere.

Etymology.—The new subspecies' name is a Spanish-language word *concepcion* and therefore non-variable. The full species and subspecies name taken together are intended to constitute a memorable name, referring to a religious concept recognised by the main branch of Christianity followed in the study region.

Species limits

Novel information relevant to species limits was uncovered during the preparation of the above description. Here, I discuss how various *Myrmeciza* antbirds would be treated under some recently proposed species-ranking tests and concepts.

It has been argued that any re-evaluation of the rank of allopatric populations should first consider observed differences between 'good' sympatric or parapatric species which are closely related (Helbig *et al.* 2002, Remsen 2005). *M. fortis* is sympatric with *M. goeldii* and *M. melanoceps* across broad parts of Amazonia. It exhibits six diagnosable differences in male song from *M. goeldii*, as well as three in female song, three in multi-note calls and two in single-note calls. *M. fortis* also differs considerably in voice from *M. melanoceps*, having four diagnosable differences in male song, two in female song, four in multi-note calls and two in single-note calls (see Appendix 4). In each case, these differences greatly exceed the benchmark for species limits in antbirds suggested by Isler *et al.* (1998).

In contrast, the parapatric and widely recognised species pair *M. goeldii* and *M. melanoceps* showed only two diagnosable differences in male song with none in other calls. These differences are in position of peak (which passed statistical diagnosability tests to Level 5, but limited overlap was observed doubtless due to the very large samples studied) and a subtle difference in note shape change. There were an unusual number of statistically significant but non-diagnosable vocal differences between this taxon pair, with small differences in male loudsongs, female songs and single-note calls, most of which did not reach the Level 2 test of 50% diagnosability. This pair also shows striking differences in extent of bare skin, iris colour and female plumage, such that no recent author has considered lumping them. This species pair presents a further example of minor vocal differentiation between apparently 'good' species of antbirds (*cf.* Isler *et al.* 2007, Chaves *et al.* 2010).

Turning to *M. immaculata*, this group separates into two internally cohesive groups, in both voice and plumage, which meet statistical tests proposed for diagnosing species under the Biological Species Concept. Populations on the west slope of the Andes and adjacent lowlands and in foothill habitats north to Central America differ diagnosably in their songs from the Central, East and Mérida Andes populations based on quantitative data (Appendices 3–4; Fig. 8) and subjectively by note shape (Fig. 5). The two geographically most proximate populations in these groups: *macrorhyncha* (in the West Andes of Colombia) and *concepcion* (Central Andes) differ diagnosably in three variables in adult male songs (number of notes, speed and note shape), two in female songs (number of notes and speed) and in the note shape of single-note calls, i.e. six diagnostic vocal differences. *M. i. concepcion* further differs diagnosably in six vocal variables in male songs from Central American *zeledoni* (number of notes, speed, max. and min. acoustic frequencies, note shape and change in note shape) and in the note shape of single-note calls. A low sample of female

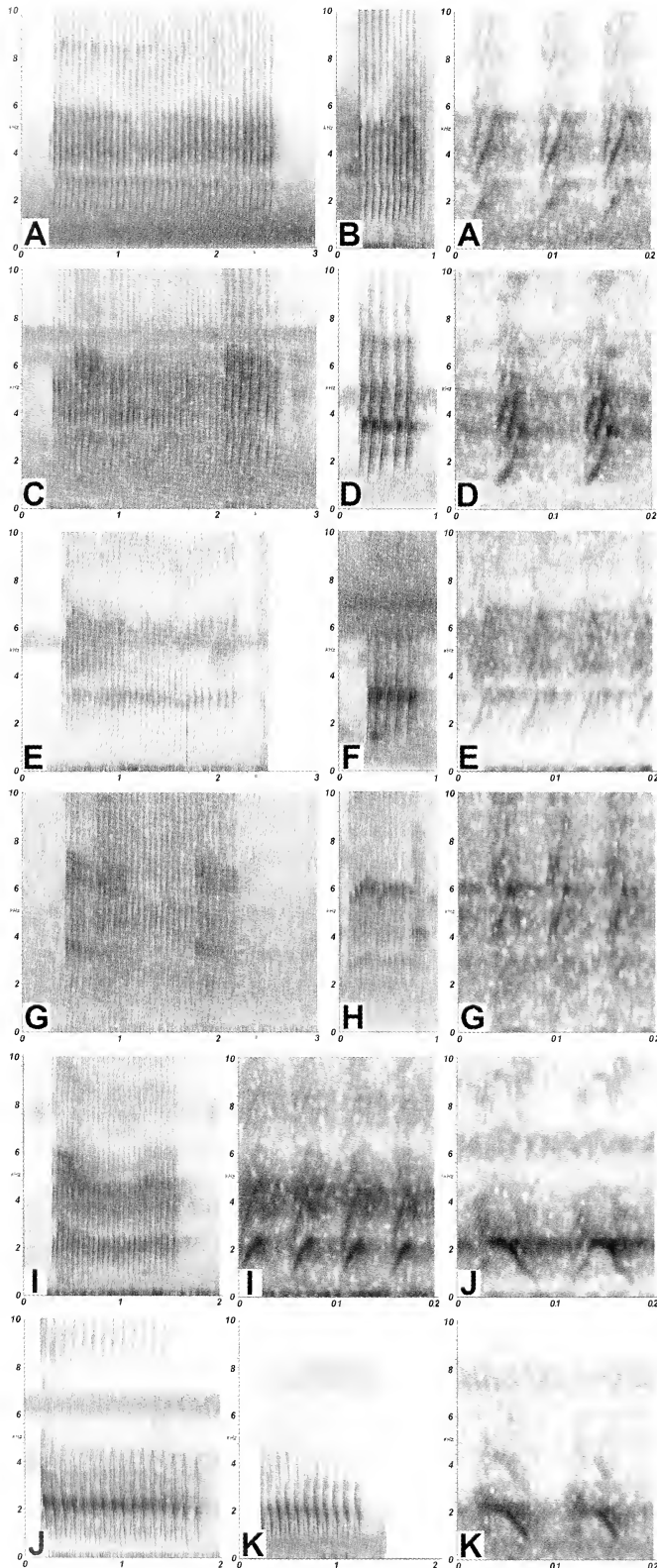


Figure 7. Multi-note calls. For each taxon, sonograms showing examples of entire call and close-up of an extract to show note shape are presented. A. *M. z. zeledoni*, La Virg n del Socorro, Costa Rica (ISL-KJZ.004:17: K. J. Zimmer). B. *M. z. zeledoni*, Boquete road, Bocas del Toro, Panama (ISL-BMW.012:27: B. M. Whitney). C. *M. z. macrorhyncha*, Boca de Cupe, Dari n, Panama (ISL-BMW.078:26: B. M. Whitney). D. *M. z. macrorhyncha*, Buenaventura, 9 km west of Pi nas, El Oro, Ecuador (Moore *et al.* 1999, track 2.13.4: M. Lysinger). E. *M. i. conception*, type locality, Colombia (XC92159: T. M. Donegan). F. *M. i. conception*, La Pradera, Estaci n, Risaralda / Antioquia, Colombia ( lvarez *et al.* 2007, track 4.4(b)). G-H. *M. i. immaculata*, Obra La Toma, T chira, Venezuela (Boesman 2007). I. *M. fortis*, km 37, Maxus road, south of r o Napo, Napo, Ecuador (Krabbe & Nilsson 2003, track 79.10). J. *M. goeldii*, Collpa de Guacamayos, r o Tambopata, Madre de Dios, Peru (ML75579: C. A. Marantz). K. *M. melanoceph*, Tiputini Reserve, Ecuador (ISL-KJZ.058:15: K. J. Zimmer).

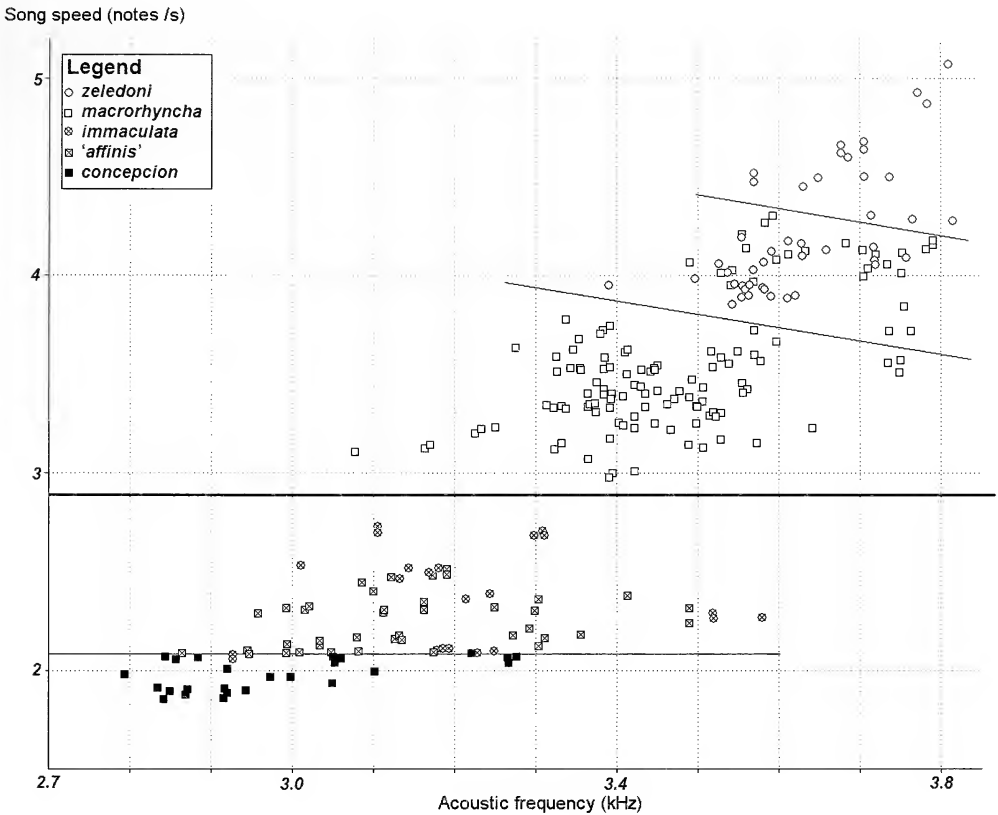


Figure 8. Plot of acoustic frequency of second note of song (x -axis) vs. song speed (y -axis) for all data points for male songs. The complete dark line at song speed = 2.85 notes / second reliably identifies all vocalisations of the two species proposed herein (with all *M. zeledoni* above this line and all *M. immaculata* below it). The narrower, incomplete line at song speed = 2.08 notes / second identifies 94% of *immaculata* recordings (all but 4 of 62) and 93% of *concepcion* recordings (all but 2 of 27). The two narrower, incomplete diagonal lines at higher song speeds show the lower limit of *zeledoni* (lower line) and upper limit of *macrorhyncha* (upper), with the region between them showing the area of overlap in these vocal variables between the taxa.

songs for the Central American population makes diagnosis of relevant variables difficult, but recordings were similar to *macrorhyncha*.

Pairwise comparisons between nominate *immaculata* and each of *macrorhyncha* and *zeledoni* elucidated only two diagnosable differences in male songs, in speed and note shape (Appendix 4). However, the note shapes of single-note calls of *immaculata* constitute a third diagnostic vocal difference and there are also 2–3 diagnosable differences in female songs. The eastern populations therefore also meet the point of reference for species rank proposed by Isler *et al.* (1998) *vis-à-vis* both *macrorhyncha* and *zeledoni*. Observed differences are consistent with those reported between *M. berlepschi* and *M. nigricauda* (Chaves *et al.* 2010), exceed those between some members of the warbling antbird group ranked as species (Isler *et al.* 2006) and exceed those between *M. goeldii* and *M. melanoceps*.

Both *zeledoni* and *macrorhyncha* have more extensive white on the upper wing-coverts in both sexes and a different shade of female plumage compared to the eastern taxa. The two groups may also possess different ecological requirements. Subspecies *immaculata* and *concepcion* are restricted to Andean foothill and premontane forests. Records of *M. i.*

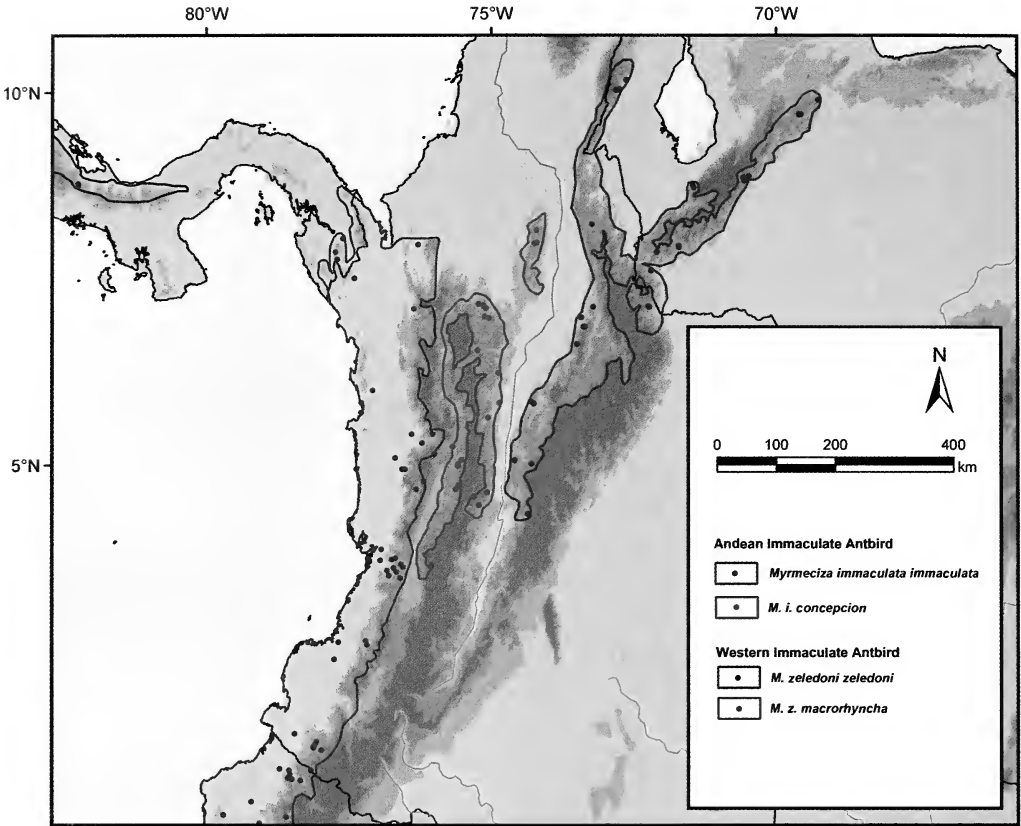


Figure 9. Map showing distribution of *M. immaculata* taxa in Colombia and surrounding regions, based on the new taxonomy established in this paper.

conception around Manizales are at 1,300–2,000 m (Verhelst *et al.* 2007), and in San Lucas and Anorí it has been found at 1,400–1,550 m but was not recorded at a nearby site at 800 m (Salaman & Donegan 2001). Similarly, in Serranía de los Yariguíes, *M. i. immaculata* was found at 1,000–2,000 m but not at lower elevations (Donegan *et al.* 2010; *cf.* Appendix 4). All other modern specimens and sound-recordings are from Andean foothill to lower montane regions. The lowest confirmed record of the split *immaculata* group is a sound-recording of *conception* at 500 m from the Río Claro reserve, Antioquia. The coordinates of another claimed low-elevation record (Boesman 2007: 500 m) map to a higher elevation. Other low-elevation records, especially in northern Antioquia, pertain to old ‘general’ collecting localities also found on labels of other higher elevation species of similar age (e.g., Three-striped Warbler *Basileuterus tristriatus*). Although *macrorhyncha* is also found to 2,000 m and *zeledoni* is a foothill and montane bird in Central America, *macrorhyncha* occurs broadly in the Chocó lowlands (at similar latitudes to *immaculata* and *conception*) down to sea level (Fig. 9).

Application of Isler *et al.*'s (1998) methodology would result in two separate species being recognised for *immaculata* based on three diagnostic vocal differences. Using the Tobias *et al.* (2010) scoring system, the *immaculata* / *conception* vs. *macrorhyncha* / *zeledoni* groups score 1 for biometrics (bill length), 3 for voice (only one character is measured), 3 for the more extensive white shoulder patch in both sexes and conservatively at least 2 (though arguably up to 6) for the different shade of female crown, upperparts and underparts, or a

total of *at least* nine points, exceeding the proposed seven-point test for species rank. It is noteworthy that the Tobias *et al.* (2010) and Isler *et al.* (1998) tests produce similar outcomes, especially given the low weightings in the Tobias *et al.* (2010) tests for vocal characters. Those applying these systems to evaluate species rank should split *M. immaculata* as follows, a return in part to Ridgway's (1909) treatment:

Andean Immaculate Antbird or **Immaculate Antbird** *Myrmeciza immaculata* (Lafresnaye, 1845) includes subspecies *immaculata* Lafresnaye, 1845 (East Andes, Colombia) and *concepcion* (Central Andes, Colombia), along with the doubtful *brunnea* Phelps & Phelps, 1955 (Perijá) and *affinis* Todd, 1917 (Mérida Andes).

Western Immaculate Antbird or **Zeledon's Antbird** *Myrmeciza zeledoni* Ridgway, 1909, including subspecies *zeledoni* Ridgway, 1909 (Costa Rica and northern Panama) and *macrorhyncha* Robbins & Ridgely, 1993 (Ecuador north to southern Panama).

There is a collecting gap between their ranges in the region of Paramillo National Park in the northern foothills of the West Andes (Fig. 9), where subspecies *macrorhyncha* is presumed to occur. The lower slopes have never been extensively collected, nor have they been subject to recent field work due to long-term political instability, and posed a similarly significant gap in connection with the recently proposed split of *M. palliata* (Chaves *et al.* 2010). Although Paramillo should be subject to further study for this and other species if the region stabilises in future, my data suggest that the two groups are sufficiently differentiated in voice that they should be treated as species under the approaches referred to above.

Application of a phylogenetic species concept (e.g., Cracraft 1983) or other diagnosability or pattern-based species concepts would further require *macrorhyncha* and *concepcion* to be afforded species rank. The latter two taxa constitute 'groups' within *zeledoni* and *immaculata* respectively, for purposes of checklists that draw attention to such populations (e.g., Schulenberg 2010).

First Reviser action

Taxa *zeledoni* and *berlepschi* were described on the same page by the same author (Ridgway 1909). Neither has priority in the event that they are treated as conspecific (ICZN 1999, Art. 23) because priority between contemporaneously described names can only be determined pursuant to First Reviser action. Their author does not appear to have preferred either name in any subsequent publication. Ridgway (1911) continued to treat them as different species and he died in 1929, after their synonymisation in 1924, without publishing any relevant work in the interim. Because Cory & Hellmayr (1924) subsumed both names into *immaculata*, they did not act as implicit First Reviser either.

Any First Reviser action should stabilise the nomenclature of species that proponents of widely used species concepts are likely to recognise. Notably, the name *berlepschi* would have to be resurrected for *macrorhyncha* if Stub-tailed Antbird *M. berlepschi* were to be placed in a different genus to *M. zeledoni*. *M. berlepschi* is considered related to Chestnut-backed Antbird *M. exsul*, Dull-mantled Antbird *M. laemosticta*, Magdalena Antbird *M. palliata* and *M. nigricauda* (Brumfield *et al.* 2007, Chaves *et al.* 2010). Based on Brumfield *et al.* (2007), various species in *Pyriglena*, *Percnostola*, *Myrmoborus*, *Gymnocichla* and *Percnostola* would have to be lumped when genus limits are revised, if the two *berlepschi* antbirds are to remain congeneric in the long term. Such a far-reaching generic re-arrangement appears

unlikely, especially due to the position of a member of the morphologically distinctive genus, *Myrmoborus*.

The name *zeledoni* Ridgway, 1909, is hereby selected to take priority over *berlepschi* Ridgway, 1909, pursuant to First Reviser action under Art. 24.2 of the Code. Pursuant to ICZN Art. 24A, it is recommended that the name, spelling or nomenclatural act that best serves stability and universality of nomenclature be adopted. Selecting *zeledoni* promotes stability as the species name of western populations would not change due to differing generic arrangements based on this choice. Also, universality considerations could be thought to include 'position precedence' or 'line priority' (under Art. 69A.10, which applies to the fixation of type species for genera) and *zeledoni* appears first in Ridgway (1909).

Vernacular names

Although some commentators prefer new names for components of split species (e.g., Remsen *et al.* 2012), the name 'Immaculate Antbird' remains appropriate even for a split *M. immaculata*, being a direct translation of the species' scientific name. Cory & Hellmayr (1924) used two uninspiring patronyms for the other group: Zeledon's Ant-catcher for *M. i. zeledoni* and Berlepsch's Ant-catcher for *M. i. berlepschi*. No other vernacular names appear ever to have been used. 'Berlepsch's Antbird' would confuse with Stub-tailed Antbird *M. berlepschi* and the name *berlepschi* is currently replaced by *macrorhyncha*. However, Zeledon's Antbird would be available.

Because patronyms convey little information about birds to their main users—birdwatchers—possible alternative names for *M. zeledoni* require consideration. These antbirds do not lend themselves to plumage-based names due to their strong sexual dichromatism. No obvious plumage patterns unite both sexes and the various populations of the new species. Males are uniform black and females uniform brown but Uniform Antshrike (*Thamnophilus unicolor*) could confuse and 'White-shouldered Antbird' is already used for *M. melanoceps*. A good morphological-based name for *zeledoni* is therefore elusive. Similarly, there is no geographic name available to describe the region from western Ecuador to Costa Rica. Arguably the best approach is to use Western Immaculate Antbird (*zeledoni*) and Andean Immaculate Antbird (*immaculata*). They are clearly related and both have been known as Immaculate Antbirds for a long time.

Conservation

Distribution maps produced by BirdLife International (Fig. 9) yield an estimated Extent of Occurrence (EOO) for Andean Immaculate Antbird of c.92,900 km², comprising c.64,100 km² for *M. i. immaculata* and c.28,800 km² for *M. i. concepcion*. The EOO for Western Immaculate Antbird *M. zeledoni* is c.213,100 km², with c.18,100 km² for *M. z. zeledoni* and c.195,000 km² for *M. z. macrorhyncha*. Neither of the split species approaches the max. range size threshold for Vulnerable under criterion B1 of 20,000 km² (or Area of Occupancy of 2,000 km² for B2), although *zeledoni* and *concepcion* appear to be threatened subspecies. Similarly, range sizes imply that populations of these taxa do not approach as few as 10,000 mature individuals, so criterion C is probably not relevant. It is assumed that only criterion A is potentially relevant for determining threats to these species, with a 30% decline over three generations being the relevant threshold for Vulnerable status. For these antbirds, the relevant time period is estimated at 14 years, based on a generation length of c.4.8 years (BirdLife International unpubl. data).

Andean Immaculate Antbird is a forest-dependent species that occurs at low densities. Much of its Andean foothills range is now deforested, coinciding with the main coffee-

growing region of Colombia, and its elevational range in the Central and East Andes is poorly covered by the national parks network. Deforestation in unprotected rural Colombia, such as the Magdalena Valley slopes, has accelerated recently following the return of improved political stability to many regions. Fundación ProAves (2011) recently estimated that other species in the Central and East Andean foothills, e.g., White-mantled Barbet *Capito hypoleucus* and Sooty Ant Tanager *Habia gutturalis*, have incurred habitat losses of 25–30% during the last 10–20 years. These data suggest that Andean Immaculate Antbird could be categorised as Near Threatened on the basis of a population decline approaching 30% over 14 years. There is however some cause for optimism as to the species' future survival: it occurs in various protected areas in Colombia including national parks in Serranía de los Yariguíes and Tamá, and ProAves reserves in Anorí, Antioquia (Arrieto Antioqueño) and Yariguíes (Reinita Cerulea and *Pauxi pauxi* reserves) (Salaman *et al.* 2010). The Río Claro nature reserve in Colombia and Serranía de las Quinchas are also important sites and there are various national parks and other protected areas in the Mérida Andes, where deforestation pressures may be lower.

Western Immaculate Antbird *M. zeledoni* is assumed to be low risk for now. Although the Chocó lowlands are presently subject to unprecedented deforestation threats, the species' broader range includes an array of other habitats and protected areas in Central America particularly, some of which may be subject to reduced rates of habitat conversion. Its population trends should nonetheless be monitored.

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Appendix 1: materials used in analyses

All specimens, sound-recordings and other records used in analyses are cited. For specimens, coordinates are taken from Paynter (1982, 1997), unless otherwise stated. For sound-recordings, coordinates are taken from the relevant database, publication or recordist and converted where necessary. Dashes refer to a series of different specimens or other cat. nos. starting and ending with the number in question. Taxonomy in all appendices follows the new arrangement presented in the main text. Details of specimen and sound-recording materials studied for *M. fortis*, *M. melanoceps* and *M. goeldii* are available on request.

Specimens.—Listed in order of institution and cat. no., with those personally examined listed first, followed by any data from Biomap Alliance Participants (2011). Acronyms: American Museum of Natural History, New York (AMNH); Academy of Natural Sciences, Philadelphia (ANSP); Natural History Museum, Tring (BMNH); Carnegie Museum of Natural History, Pittsburgh (CM); Colección Ornitológica Phelps, Caracas (COP); Cornell University Museum of Vertebrates (CUMV); Instituto de Ciencias Naturales, Universidad Nacional, Bogotá (ICN); Instituto Alexander von Humboldt, Villa de Leyva, Colombia (IAVH), Museum of Comparative Zoology, Cambridge, MA (MCZ); Museo de Historia Natural, Universidad de la Salle, Bogotá (MLS); Field Museum of Natural History, Chicago (FMNH); Los Angeles County Natural History Museum (LACM); Museum of Natural History, Geneva (MHNG), Smithsonian Institution, National Museum of Natural History, Washington (USNM); Peabody Museum of Natural History, Yale University, Boston (YPM); Louisiana State University Museum of Natural Science, Baton Rouge (LSUMZ); Museum of Zoology, University of Michigan (MZUM); Zoologische Staatssammlung, Munich (ZSM); Museo de Historia Natural, Universidad del Cauca, Popayán (MHNUC); Museo de Historia Natural, Universidad del Valle, Cali (MHNUV); and Museum of Vertebrate Zoology, University of California, Berkeley (MVZUC).

M. i. immaculata Mérida, Venezuela: COP 71720 (Cabudare, Lara, 09°54'N, 69°16'W; 1,200–1,250 m). 81433–34 (Calderas, Barinas, 08°52'N, 70°29'W; 1,250 m) (photographs).

M. i. immaculata Perijá, Venezuela: AMNH numbered COP 57616 (holotype) (Barranguilla, Ranchería Julián, Zulia, 10°10'N, 72°38'W; 960 m). COP 57615–23 (Ranchería Julián, as above), 54865–68 (Kunana, Zulia, 10°02'N, 72°47'W; 1,250–1,300 m), 50051 (Ayapa, Zulia, 10°03'N, 72°45'W; 1,100 m), 54864 (Campamento Pejochaina, Zulia, 10°02'N, 72°49'W; 1,700 m), 6441–12 (La Sabana, Zulia, 10°02'N, 72°45'W; 1,400 m) (photographs).

M. i. immaculata East Andes, Colombia: AMNH 43321 ('New Grenada'), 121938 (Fusagasugá, Cundinamarca, 04°21'N, 74°22'N; 1,829 m), 121939–40 (Honda, Tolima; 1,829 m, presumably to the east and above this locality). BMNH 1881.2.26.25, 1854.5.5.1 (type of *Pyriglena ellisiana*), 1889.9.20.36, 1889.7.10.75 ('Bogotá'). IAVH 10858 (vereda El Diviso, Toledo, Norte de Santander, 07°07'28"N, 72°14'40"W; 1,100 m). ICN 32830–32 (vereda La Grilla, Serranía de las Quinchas, Otanche, Boyacá, 05°51'N, 74°19'W; 1,300–1,500 m, locality data from Múnera & Laverde 2002). MCZ 76756–58 ('Bogotá': types of *M. immaculata*) (photographs). USNM 373499 (Ayacucho, La Gloria, Cesar, 08°36'N, 73°33'W, locality presumably in East Andes above this) (photograph) (note: allocation to 'East Andes' arbitrary: collecting locality near low pass between Perijá and main East Andes), 373622 (Bellavista, Norte de Santander, 08°13'27"N, 73°14'14"W), 411507–09 (Conchal, Lebrija, Santander, 07°07'N, 73°13'W). Biomap data from Colombia: CUMV 7146–48 (El Consuelo, Guaduas, Cundinamarca (above Honda, Tolima; 914 m), 05°04'N, 74°36'W). FMNH 261434 (La Argentina, río Cubugon, Cubará, Boyacá. Paynter's (1997) locality not mapped as too low, presumably near Toledo localities under sound-recordings below). MCZ 47177 ('Bogotá'). MLS 3907 (Fusagasugá). MVZUC 46623 (locality unknown).

M. i. concepcion Central Andes, Colombia: AMNH 94924 (Tolima, unknown locality), 108926 (east of Palmira; 2,073 m), Valle del Cauca (c.03°39'N, 76°04'W), 133498–502 (La Frijolera, Antioquia, 07°10'N, 75°25'W, coordinates not used as this and many other species collected here are higher elevation birds), 491460 (Primavera, 07°09'24"N, 75°14'09"W). COP 64620 (La Frijolera) (formerly AMNH 133501,

photograph). IAVH 11969 (Hacienda Tintina, cuenca del río Tapias, Neira, Caldas, 05°14'55"N, 75°41'06"W; 1,080 m). ICN 18977 ('Antioquia'), 34181 (Retén, near La Punta, Serranía de San Lucas, Santa Rosa del Sur, Bolívar, 08°08'47"N, 74°12'48"W; 1,400 m), 38161 (paratype, see above), 38162 (holotype, see above). USNM 392795, 392891 (Volador, Santa Rosa del Sur, Bolívar, 07°58'N, 74°15'W), 436474 (Hacienda La Sofia, Samaná, Caldas, 05°38'N, 75°04'W), 402390-07 (Valdivia, Antioquia, 07°11'N, 75°27'W, coordinates not used as this and many other species collected here are higher elevation birds).

***M. zeledoni macrorhyncha*: Panama:** AMNH 135740-03, 135743-48 (Tarcuna; 731-1,402 m). USNM 238434-38 (Cana, Panama) (photographs). **Colombia:** AMNH 123340 (Bagadó, Chocó, 05°25'N, 76°24'W; 305 m), 123341-42 (Serranía de Baudó, Chocó, 06°00'N, 77°05'W; 914 m) 111935 (Salencio = Nóvita Trail, Alban, Valle del Cauca, 04°47'N, 76°11'W; 1,676 m), 111936 (exchanged to Museu Zoologia, Universidade de São Paulo, Brazil), 111937-41 (Nóvita, Chocó, 04°57'N, 76°34'W; 122 m). BMNH 1910.5.14.[?]? (Jimenez, 03°45'N, 76°45'W; c.500 m). IAVH 6517 (20 km south-east of Guapí, río Guapí, Cauca, 02°25'24"N, 77°45'21"W). ICN 32275-76 (0.5 km south-east of Altaquer (= Altaguer), Barbacoas, Nariño, 01°15'N, 78°07'W), 31171 (Alto de Pisones, 8 km north-east of Juguadas, Mistrató, Risaralda, 05°25'N, 76°02'W; 1,400-1,850 m), 5037, 5039 (La Guayacana, Tumaco, Nariño, 01°26'N, 78°27'W), 11435-39 (Guajui, San Antonio, Cauca, 02°39'N, 77°41'W). USNM 428205-06, 443155-58 (río Jurubida, Nuquí, Chocó, 05°50'N, 77°17'W), 443158-60, 443269-71 (Base Baudó, río Nuquí, Chocó, 05°42'N, 77°17'W). **Ecuador:** AMNH 119892-95, 124420-21, 129723-25, 171373, 171375-77, 173291, 173295-97, 180247, 193293, 491461-73 (no details taken). BMNH 1860.11.26.82, 1864.8.9.13 ('Quito'), 1889.9.10.1023 (Intaj), 1889.9.20.34 (Nanegal), 1889.9.20.35 ('Ecuador'), 1925.12.24.514 (Mindo) 1940.12.5.313 (Mindo), 1953.68.640 (Guayave, 1,000 m), 1953.68.641 (Guayabe, Imbabura). ICN 5038, 5040 (no details taken). USNM 305181 (río de Oro, Manabi), 97774 (Chimbo, holotype of *berlepschi*). **Unknown:** BMNH 1851.9.11.5 ('Brazil?'). Biomap data from **Colombia:** ANSP 157338, 157340, 159567-69, 160020 (La Guayacana, as above), 157995-8001, 158003, 158005-08 (Santa Cecilia, Pueblo Rico, Risaralda, 05°18'N, 76°13'W), 150792-93, 150795-96 (Ricaurte, Nariño, 01°13'N, 77°59'W), 149867-69, 150797 (Perlasvi = río Peasbi, Nariño, 00°57'N, 78°10'W), 146964-65 (río Baudó, Bajo Baudó, Chocó, 04°57'N, 77°22'W), 147198-99 (río Jurubida, Nuquí, Chocó, 05°50'N, 77°17'W), 137949, 142388, 144685 (río Mechengue, El Tambo, Cauca, 02°40'N, 77°12'W), 73317 (Córdoba, Buenaventura, Valle del Cauca, 03°53'N, 76°56'W), 73318-21 (Andagoya, Istmina, Chocó, 05°06'N, 76°41'W), 491460 (Primavera, Bolívar, Valle del Cauca, coordinates unknown). CM 66771-73 (Córdoba, Buenaventura, as above), 66121-22, 66174, 66227-28, 66248, 66269, 66287-89, 66347-50, 66390, 66417 (Andagoya, as above), 67685 (La Cumbre, Valle del Cauca, 03°39'N, 76°33'W). FMNH 249731-35, 250839-40 (La Guayacana, as above). LACM 30817, 30848-50, 31273-77 (La Guayacana, as above). MCZ 123414 ('Colombia'), 123415-16 (Palmar, Dagua, Valle del Cauca, 03°35'N, 76°40'W), 123419 (La María, Dagua, Valle del Cauca, 03°38'N, 76°43'W) 123417-18 (Pavas, La Cumbre, Valle del Cauca, 03°41'N, 76°35'W). MHNG 1,168,007 (río Huisitó, El Tambo, Cauca, 02°37'N, 77°11'W), 1,141,004, 1,141,008 (La Guayacana, as above), 1,141,009, 1,142,024 (Ricaurte, as above). MHNUC 1290, 1317 and unnumbered (La Guayacana, as above). MHNUV 3540 (Quebrada Lucas, 2 km from La Desembocadura, río Zabaletas, Buenaventura, Valle del Cauca, 03°44'N, 76°57'W), 5104-05 (río Agua Sucia, Cajambre, Boca, Buenaventura, Valle del Cauca, 03°31'N, 77°19'W), 1054-55, 3126 (Corregimiento Loboguerrero, km 28, Dagua, Valle del Cauca, 03°46'N, 76°41'W; 200-250 m), 1705, 1765 (río Blanco, Pacific slope of West Andes, Valle del Cauca, 03°36'N, 76°50'W), 456, 485 (río Anchicayá, Buenaventura, Valle del Cauca, 03°46'N, 77°10'W; 180-220 m). MZUM 153702-05 (La Guayacana, as above), 222928-29 (Pueblo Rico, as above). LSUMZ 38695-97, 45439 (La Guayacana, as above). YPM 27029, 58729-30 (La Guayacana, as above). ZSM 1910.2373 (Pueblo Rico, as above).

***M. z. zeledoni*:** AMNH 390332-33, 390226 (Costa Rica), 390327-31 (Aquinare, Costa Rica; 1,067 m), 390332-33 (Carrillo, Costa Rica), 390334-35 (Santa Cruz de Turrialba; 1,280 m), 390336 (Bonilla; 610 m), 390337 (La Hondura), 390338 (Navarro; 1,219 m), 491474-77 (Cariblanco de Sarapiquí, Costa Rica); 43320, 43322, 187223-38, 491475 (Panama). BMNH 1889.4.10.70, 1889.9.10.74, 1889.9.10.82, 1889.9.10.93, 1889.9.20.88, 1899.6.1.570-71, 1900.9.30.107-09, 1913.10.15.416, 1949.58.398, 1949.58.399-400, 1969.25.119 (no data taken). USNM 209558 (holotype) (Guayabo, Costa Rica). 476076-77 (Bocas del Toro, río Changuena; 732 m), 95049 (El Naranjo, Costa Rica), 209559 (as holotype).

Sound recordings.—Cat. no. acronyms are as follows: XC = www.xeno-canto.org; IAVH = Instituto Alexander von Humboldt's Colección de Sonidos Ambientales; ML = Macaulay Library, Cornell Lab of Ornithology; AV = AVoCet www.avocet.zoology.msu.edu; IBC = Internet Bird Collection (ibc.lynxeds.com); ISL = Mort & Phyllis Isler's antbird sound library. Localities are listed north to south by taxon and then by country.

***M. i. immaculata* Mérida:**

Songs.—**Venezuela** Laguna el Blanquito, PN Yacumbú, Lara (09°42'12"N, 69°34'19"W; 1,450 m) (C. A. Marantz: YAC263 and unnumbered). PN Yacumbú, Lara (09°42'11"N, 69°36'17"W; 1,480 m) (XC6869: N. Athanas; IBC: N. Areta). La Soledad, 20 km north-west of Barinitas, Barinas (08°51'09"N, 70°34'17"W; 1,600-1,630 m) (XC6086: C. Parrish; XC42299: J. G. Leon). San Isidro (08°47'34"N, 70°34'17"W; 1,500 m, XC locality data not used as maps at unfeasibly high elevation, see XC forum 2716) (XC43140-42: J. Klaiber,

first two treated as same recording; ISL-BMW.167:29: B. M. Whitney). Finca Monteverde, Olinda II, Mérida (08°45'N, 71°28'W) (Boesman 2007). Near Azulita, Mérida (08°43'N, 71°27'W; 1,500 m) (ML62071: P. A. Schwarz). 13 km east of Santo Domingo, Barinas (ML52704: S. L. Hilty). Obra La Toma, Táchira (07°56'N, 71°43'W; 1,100–1,250 m) (Boesman 2007). 15 km north-east of Táchira, road from San Cristóbal to La Florida, Táchira (07°51'N, 72°06'W; 1,160 m) (ML62072–73: P. A. Schwarz). Unknown locality (ISL-FSM.002:037: R. A. Behrstock). **Female songs.**—Venezuela ISL-FSM:002.037 (as above). ML62071 (as above). ML62072–73 (as above). Obra La Toma, Táchira (Boesman 2007: same recording as above). **Single-note calls.**—Venezuela XC7002 (as XC6869). XC43138–40 (as XC43140; latter three treated as same recording). **Multi-note calls.**—Venezuela Laguna el Blanquito (as above). Campamento La Trampa, Táchira (07°55'N, 71°43'W; 1,000–1,300 m) (Boesman 2007). Obra La Toma, Táchira (as above but different recording) (Boesman 2007). XC43139 (as above).

M. i. immaculata East Andes:

Male songs.—Colombia Toledo, PNN Tamá, sector San Isidro, Norte de Santander (07°07'N, 72°14'W) (IAVH585, IAVH589 (= Álvarez *et al.* 2007, track 4.4(a)): M. Álvarez). Cerro de la Paz, Zapatoca, Santander (06°58'30"N, 73°25'40"W; 1,000 m) (XC24307: T. M. Donegan). Vereda La Ye, Otanche, Boyacá, Serranía de las Quinchas (05°51'N, 74°19'W; 1,450 m: data from Cuervo 2002) (XC12809, 12847–48: O. Laverde). Laguna Tabacal, Cundinamarca (05°01'05"N, 74°18'07"W; 1,350–2,100 m) (XC59290 = AV12579, XC59308: F. Lambert). **Venezuela** río Negro / río Frio area, Táchira (07°36'N, 72°12'W; 400–500 m' (maps to c.1,000 m)) (Boesman 2007). **Single-note calls.**—Colombia El Taliman, Serranía de los Yariguíes (06°50'57"N, 73°21'51"W; 2,000 m) (XC92165: T. M. Donegan). IAVH586 (as IAVH585).

M. i. conceptioni:

Songs.—Colombia Type locality (XC92160 (holotype), 92181: T. M. Donegan). La Condena, Antioquia (07°06'N, 75°06'W; 1,600–1,750 m) (IAVH19742: A. M. Cuervo). RNA Arrierito Antioqueño, Anorí, Antioquia (06°59'10"N, 75°07'30"W; 1,450 m) (XC51246: D. Geale; XC55371: P. Flórez). La Pradera (parte alta or Don Matías), Estación, Risaralda or Antioquia (06°32'N, 75°15'W; 1,450 m) (ISL-CDC.001:020: C. D. Cadena; IAVH17831, IAVH19741: A. M. Cuervo). Finca la Estrella, Antioquia (IAVH30217: A. M. Cuervo). Cañon del río Claro, Antioquia (05°50'N, 74°52'W; 600 m) (XC18153: H. van Oosten). Clarita Botero, Ibagué, Tolima (04°28'08"N, 75°13'41"W; 1,450 m) (XC32218: N. Athanas). **Female songs.**—Colombia XC55371 (as above). ISL-CDC.001:020 (as above). XC92160 (as above), 92164 (as 92160). **Single-note calls.**—Colombia Type locality (XC92160 (group including holotype, as above). IAVH30503–04 (latter = Álvarez *et al.* 2007, track 4.4(c)) (as IAVH17831). **Duet response or downslurred single-note calls.**—Colombia Type locality (XC92160, group including holotype, as above). IAVH30484–90 (treated as same recording), IAVH30503–04 (treated as same recording), IAVH30976 (as IAVH17831). **Multi-note calls.**—Colombia Type locality (XC92156, 92158–59 (latter two extracts of same recording, details as XC92160 above). Don Matías (as above) (Álvarez *et al.* 2007, track 4.4(b) = ISL-CDC.001:019). **Other calls.**—Colombia Type locality (XC92157, 92161–64, as 92160 above) (holotype and other individuals in hand).

M. z. macrorhyncha:

Songs.—Colombia PNN Tatamá, Pueblo Rico, Risaralda (05°09'N, 76°00'W; 1,510 m) (XC55196: P. Flórez). Near Buenaventura, Valle (03°53'N, 77°04'W; <100 m) (ISL-SLH.004:06: S. L. Hilty). Río Anchicayá (see specimens, above) (ISL-BBC.001:18: B. B. Coffey). **Ecuador** 18.5 km north-west of Alto Tambo, Esmeraldas (00°58'N, 78°43'W; 450 m) (Krabbe & Nilsson 2003, tracks 80.1–80.2). 20 km north-west of Alto Tambo, Esmeraldas (00°57'N, 78°33'W; 325–400 m) (ML63197: M. B. Robbins). El Placer, Esmeraldas (00°52'N, 78°33'W; 670 m) (ML48920, 48958, 48960, 48975: M. B. Robbins; Krabbe & Nilsson 2003, tracks 80.3–80.4). New camp after INEFAN trail, Esmeraldas (00°51'N, 78°31'W; 925 m) (Krabbe & Nilsson 2003, track 80.9). 0.5 km west of El Placer, Esmeraldas (00°51'N, 78°34'W; 650 m) (ML90003: J. Sterling). Estación Biológica Bilsa (00°22'N, 79°42'W) (XC63733: J. Tobias & N. Seddon). Barcelona, Cordillera Toisán, Imbabura (00°20'N, 78°36'W; 1,850 m) (Krabbe & Nilsson 2003, track 80.12). Reserva Mangaloma, Pichincha (00°07'22"N, 78°59'39"W) (XC76266: I. Davies). 23 km west of Lita, Esmeraldas, (00°06'09"N, 78°33'50"W; 600 m) (XC20970: R. Ahlman). Reserva Maquipucana, Pichincha (00°04'48"N, 78°37'12"W; 1,350–1,600 m) (ML50693: P. Coopmans; XC69122–23: J. P. Kjeldsen). Finca Cuatro Rios, San Miguel de Los Bancos, Pichincha (00°04'27"N, 78°58'54"W; 800 m) (XC8082: N. Athanas). Milpe, Pichincha (00°01'43"N, 78°51'46"W; 850–1,100 m) (XC8083, 32252: N. Athanas). Tandayapa Bird Lodge, Tandayapa Valley, Pichincha (00°00'36"N, 78°40'39"W; 1,750–1,780 m) (XC3885: N. Athanas; XC54859: M. Nelson; Moore *et al.* 1999, track 2.13.1: R. S. Ridgely). Bellavista, Tandayapa (00°01'S, 78°41'W; 2,300 m) (XC36991: C. Vogt). Septimo Paraíso, Mindo, Pichincha (00°02'37"S, 78°46'35"W; 1,600 m) (XC20006: C. Vogt). Mindo, Pichincha (00°03'08"S, 78°46'35"W; 1,350 m) (XC13020: R. Ahlman). Tinalandia, Pichincha (00°18'S, 79°00'W; 850 m) (Krabbe & Nilsson 2003, track 80.5). Santo Domingo de los Colorados, Tinalandia, south-east of Santo Domingo, Pichincha (00°18'S, 79°08'W) (ML28481, 28591: A. B. van den Berg). Loma Panecillo, Pichincha (00°32'S, 79°07'W; 700 m) (Krabbe & Nilsson 2003, track 80.11). Milpe road (00°08'34"S, 79°08'29"W; 1,067 m) (ML139034: L. R. Macaulay). 20 km south of Tinalandia, Santo Domingo, Pichincha (00°20'S, 79°20'W; 700 m) (ML31342: B. Spencer). La Delicia, near La Troncal, Cañar (02°34'S, 79°20'W; 600–900 m) (XC3767: D. Jones). Manta Real, Cañar / Azuay (02°34'S, 79°21'W; 250–1,100 m) (Isler

& Whitney 2002, track 2.97 = ISL-TAP.029:09: T. A. Parker). 8–9 km west of Piñas, El Oro (03°39'S, 79°45'W; 900 m) (Krabbe & Nilsson 2003, tracks 80.6–80.8, 80.10; ISL-BMW.072:12: B. M. Whitney). Buenaventura Reserve, El Oro (03°39'S, 79°46'W; 950–1,000 m) (XC6591: N. Athanas; XC17703: A. Spencer). 4.5 km west of Piñas, El Oro (03°42'S 79°42'W; 900 m) (ML43484: M. B. Robbins). Finca 106.5 (coordinates unknown) (XC63734: J. Tobias & N. Seddon). **Female songs.**—**Colombia** SLH.004:06 (as above). **Ecuador** El Placer, Esmeraldas (00°50'N, 78°30'W; 600–700 m) (track 42.1 Boesman 1999, Boesman 2007). Nanegalito, Pichincha (00°02'N, 75°37'W; 1,525 m) (ML78342: M. B. Robbins). ML28481, 28591, 31342, 90003 (as above). XC63734, 69122 (as above). Tracks 80.1–80.3 in Krabbe & Nilsson 2003 (as above). **Single-note calls.**—**Panama** Cana, Darién (07°45'N, 77°42'W; 550–650 m) (ISL-BMW.011:28: B. M. Whitney). ML25767 (as below). **Colombia** Anchiayá Valley at Alto Yunda, Valle del Cauca (03°32'N, 76°48'W; 1,000 m) (ML83761: S. L. Hilty). **Ecuador** Tinalandia, Pichincha (00°16'48"S, 79°04'48"W) (ML84416: R. A. Rowlett). Tinalandia (as others on Krabbe & Nilsson 2003, track 80.15). 20 km north-east of Pedro Vicente, Maldonado, Pichincha (00°15'00"N, 79°04'11"W; 500 m) (XC71228, 71230, 71232–33 (all treated as same individual = ISL-DFL.004:11): D. F. Lane). 17 km north-west of Pedro Vicente, Maldonado, Pichincha (00°08'09"N, 79°08'02"W; 370 m) (XC71261 (= ISL-DFL.004:06): D. F. Lane). Silanche, Pichincha (00°06'N, 79°04'W; 450–500 m) (Krabbe & Nilsson 2003, track 80.16). Maquipucuna, Pichincha (00°05'N, 78°37'W; 1,850–1,950 m) (Krabbe & Nilsson 2003, track 80.17). North-east of Salanguilla, Guayas (01°48'S, 80°32'W; 620 m) (Krabbe & Nilsson 2003, tracks 80.14, 80.18). Buenaventura, 9 km west of Piñas, El Oro (03°39'S, 79°45'W; 900–1,000 m) (Moore *et al.* 1999, track 2.13.3: P. Coopmans). Barcelona, Cordillera Toisán (as above) (Krabbe & Nilsson 2003, track 80.21). 18.5 km north-west of Alto Tambo (as above) (Krabbe & Nilsson 2003, track 80.13). ISL-TAP.029:09 (as above). ML48958 (as above), ML50694 (as ML50693), ML80961 (as ML50693 but G. F. Budney), ML139034 (as above), XC6626 (as XC3885), XC54860 (as XC54859). **Multi-note calls.**—**Panama** Boca de Cupe, Darién (08°02'N, 77°36'W; 500 m) (ISL-BMW.078:26: B. M. Whitney). Cerro Pirre, Darién, (07°51'N, 77°44'W; 500–800 m) (ISL-BMW.002:09, 011:13, 011:30: B. M. Whitney). Cana, Darién (07°50'N, 77°40'W; 600–1,700 m) (Boesman 1999, track 42.2 = Boesman 2007; ML25767: T. A. Parker; ML105191: L. R. Macaulay). ISL-BMW.011:28 (as above). **Colombia** Alto Anchiyaya, Valle del Cauca (03°30'N, 76°36'W; 600 m) (XC68783 = AV9207: F. Lambert). Altaquer, RN Río Nambí, Nariño (01°18'N, 78°05'W; 1,100–1,600 m) (XC12846: O. Laverde). **Ecuador** 2.7 km east of Alto Tambo, Esmeraldas (00°53'31"N, 78°31'58"W; 890 m) (XC72663: D. F. Lane (= ISL-DFL.005:06)). Milpe road, Mindo (00°06'56"S, 78°25'03"W; 1,185 m) (ML139004: L. R. Macaulay). Near Piñas, El Oro (03°40'S, 79°39'W; 1,200 m) (XC9836: A. T. Chartier). Maquipucuna (as above) (Krabbe & Nilsson 2003, track 80.19). Buenaventura (as above) (Moore *et al.* 1999, track 2.13.4: M. Lysinger). El Placer (as above) (Krabbe & Nilsson 2003, track 80.20). Mindo (as above) (Moore *et al.* 1999, track 2.13.2). Krabbe & Nilsson (2003, tracks 80.17, 80.18) (as above). ISL-BMW.035:02 (as ISL-BMW.072:12). ML50689 (as ML50693), ML50694 (as above), XC3766 (as XC3767), XC54860 (as above), XC71261 (as above). **Other call.**—**Ecuador** río Bogotá, Alto Tambo, Esmeraldas (00°07'N, 78°41'W; 700 m) (XC13022: R. Ahlman: see XC forum 1831).

M. z. zeledoni:

Songs.—**Costa Rica** PN Braulio Carillo, San José (10°10'N, 83°58'W) (ISL-KJZ.018:22: K. J. Zimmer). Monteverde Cloud Forest Reserve (10°18'36"N, 84°48'25"W) (XC62677: J. King). Monteverde, Peñas Blancas, Alajuela (10°18'N, 83°48'W; 800 m) (ML72871: D. L. Ross; Ross & Whitney 1995, track 94 (= Ross 1998, track 56; = one of ML72878, 72880 or 72896); ISL-BMW.009:05: B. M. Whitney). La Virgen del Socorro (ISL-KJZ.004:17–18, ISL-KJZ.003:24 (=ISL-KJZ.003:10) & ISL-KJZ.123:29 (=ISL-KJZ.135:29): K. J. Zimmer). Unknown locality (ISL-KJZ.095:01, 095:18: K. J. Zimmer). La Paz Waterfall Garden (ISL-KJZ.123:02 (=ISL-KJZ.135:02): K. J. Zimmer). Puntarenas (1,650 m) (ML53917: D. L. Ross). Finca Fernández, Chiriquí (ISL-BMW.011:03: B. M. Whitney). **Panama** Gualaca–Chiriquí road, Chiriquí (08°46'N, 82°15'W; 1,175 m) (ML54407: M. B. Robbins). PN General Omar Torrijos, Coclé (700 m) (XC31340: R. Moore). Finca Fernandez, Chiriquí (ISL-BMW.011:03: B. M. Whitney). **Female songs.**—**Costa Rica** ISL-KJZ.004:18 (as above). **Panama** ML54407 (as above). **Single-note calls.**—**Costa Rica** ISL-KJZ.003:24 (as above). **Panama** Boquete road, upper Caribbean slope, Bocas del Toro (>800 m) (ISL-BMW.012:27). **Multi-note calls.**—**Costa Rica** ISL-KJZ.004:17–18 (as above). ISL-BMW.012:27 (as above).

Other locality data.—These comprise data from the literature, as well as ML sound-recordings from localities not mentioned above and not presently available in digital form or Isler database recordings not requested from different localities to those above. IAVH = Instituto Alexander von Humboldt AICAs database (<http://aicas.humboldt.org.co>).

M. i. immaculata Mérida Andes, Venezuela Lower Santo Domingo Valley (08°48'32"N, 70°33'43"W; P. Boesman *in litt.* 2011) (Boesman 1998). **East Andes, Colombia** Cerro de la Paz, Zapatoca, Santander, east and west slopes, (06°59'N, 73°26'W; 1,000–1,300 m) (Donegan *et al.* 2010). RNA Reinita Cerulea (06°51'N, 73°23'W; 1,700 m) (Salaman *et al.* 2010). Alto Honduras, El Carmen, Serranía de los Yariquíes, Santander (06°37'N, 73°30'W; 1,600 m) (Donegan *et al.* 2010). Note record in Donegan *et al.* (2010) at Bajo Simacota, Santander (06°46'N, 73°44'W; 100–150 m) was based on a recording of Bare-crowned Antbird *Gymnocichla nudiceps*.

M. i. concepcion Colombia Santa Gertrudis (07°08'N, 75°09'W; 1,420–1,470 m); Bodega Vieja, Antioquia (06°58'N, 75°03'W; 1,300–1,550 m) (Cuervo *et al.* 2008). Embalse de Punchiná, Antioquia (06°14'N, 74°53'W;

200–800 m) (IAVH). Ecoparque Los Alcázares, Manizales, Caldas (05°04'06"N, 75°31'58"W) (Verhelst *et al.* 2007). Playarica, Manizales, Caldas (05°00'54"N, 75°35'20"W) (Verhelst *et al.* 2007). Estación Cenicafé, Manizales, Caldas (04°59'28"N, 75°35'30"W; 1,310–1,425 m) (Verhelst *et al.* 2007, coordinates for last three localities from J. C. Verhelst *in litt.* 2011). Santuario de Flora y Fauna Otún Quimbaya (04°44'01"N, 75°35'16"W; 1,800–2,100 m) (Rios *et al.* 2008). Cañon del río Barbas y Bremen, Risaralda (04°41'N, 75°38'W; 1,600–2,100 m) (IAVH). La Cascada, Tolima (04°35'N, 75°19'W) (A. Quevedo *in litt.* 2011 / ProAves photograph). Anzoategui, Tolima (04°38'27"N, 75°05'03"W) (A. Quevedo *in litt.* 2011).

M. zeledoni macrorhyncha Panama 10 km north of Los Planes, Fortuna Field Station, Chiriquí (08°44'N, 82°15'W; 1,000 m) (ML144050: M. B. Robbins). Gualea (00°07'N, 78°44'W) (Willis 1985), Paramba (00°49'N, 78°21'W) (Willis 1985). Colombia Tukurá, Córdoba (07°57'N, 76°17'W) (Willis 1985). Serranía de Abibe, Chocó (07°05'17"N, 76°21'37"W; 1,500 m) (C. Olaciregui *in litt.* 2011). El Tigre, Chocó (04°57'N, 76°31'W) (Willis 1985). Serranía de los Paraguas, Chocó (04°41'N, 76°19'W; 300–2,700 m) (IAVH). Anchicayá Valley (03°32'N, 76°48'W; 980–1,250 m) (Hilty 1974). RN El Pangán, Nariño (01°20'N, 78°04'W; 600–1,990 m) (Salaman *et al.* 2010; IAVH). RN Río Nambi, Nariño (01°16'N, 78°07'W; 1,100–1,600 m) (IAVH). Ecuador Canandé, Esmeraldas (00°32'N, 79°13'W; 570 m) (ISL-NK_C_136: N. Krabbe). Faisón, Estación, Pichincha (00°20'S, 78°52'W) (ISL-RAB.009.19: R. A. Behrstock). Río Palenque, Los Ríos (00°33'S, 79°22'W; 200–300 m) (ISL-BBC.005:21, 25–26: B. B. Coffey). Above Manta Real, Cañar, Ecuador (02°34'S, 79°21'W) (ML80799: T. A. Parker).

Appendix 2: biometrics

Data are presented as follows: mean ± standard deviation (lowest value–highest value) (*n* = no. of specimens or individuals).

Taxon	Wing-chord from skins (mm)	Tail (mm)	Tarsus (mm)	Culmen (mm)	Body mass (g)
<i>M. i. brunnea</i> (female holotype)	74.0 (<i>n</i> =1)	73.0 (<i>n</i> =1)	32.0 (<i>n</i> =1)	21.0 (<i>n</i> =1)	/
<i>M. i. immaculata</i> (all East Andes)	80.16 ± 3.33 (76.5–89.0) (<i>n</i> =15)	76.52 ± 3.82 (70–83) (<i>n</i> =15)	32.96 ± 1.05 (31.4–34.7) (<i>n</i> =16)	21.24 ± 1.04 (19.5–22.5) (<i>n</i> =16)	41.3 ± 2.46 (38.7–43.6) (<i>n</i> =3)
Males	79.87 ± 3.36 (76.5–89.0) (<i>n</i> =11)	76.24 ± 3.96 (70–83) (<i>n</i> =11)	33.02 ± 1.18 (31.4–34.7) (<i>n</i> =12)	21.28 ± 1.05 (19.5–22.5) (<i>n</i> =12)	42.6 ± 1.41 (41.6–43.6) (<i>n</i> =2)
Females	80.95 ± 3.62 (78–86) (<i>n</i> =4)	77.28 ± 3.86 (72–81) (<i>n</i> =4)	32.78 ± 0.66 (32.0–33.5) (<i>n</i> =4)	21.10 ± 1.14 (19.9–22.5) (<i>n</i> =4)	38.7 (<i>n</i> =1)
<i>M. i. concepcion</i> Specimens	79.07 ± 2.68 (74–86) (<i>n</i> =20)	74.76 ± 3.84 (69–84) (<i>n</i> =20)	33.36 ± 0.84 (31.8–35.5) (<i>n</i> =20)	21.90 ± 0.78 (20.7–23.5) (<i>n</i> =18)	40.05 ± 1.06 (39.3–40.8) (<i>n</i> =2)
Males	80.08 ± 2.85 (74–86) (<i>n</i> =12)	76.34 ± 4.05 (72–84) (<i>n</i> =12)	33.42 ± 1.07 (31.8–35.5) (<i>n</i> =12)	21.99 ± 0.97 (20.7–23.5) (<i>n</i> =10)	40.8 (<i>n</i> =1)
Females	77.55 ± 1.52 (75–80) (<i>n</i> =8)	72.39 ± 1.87 (69–75) (<i>n</i> =8)	33.26 ± 0.36 (32.6–33.5) (<i>n</i> =8)	21.78 ± 0.52 (21.0–22.5) (<i>n</i> =8)	39.3 (<i>n</i> =1)
<i>M. i. concepcion</i> Live birds	83.00 ± 3.10 (79–86) (<i>n</i> =6)	82.40 ± 3.53 (67–85) (<i>n</i> =4)	33.27 ± 0.76 (32.1–34.0) (<i>n</i> =6)	21.47 ± 0.84 (20.5–22.5) (<i>n</i> =6)	40.67 ± 1.01 (39.3–41.6) (<i>n</i> =5)
Males	83.60 ± 3.05 (79–86) (<i>n</i> =5)	84.10 ± 1.15 (83–85.3) (<i>n</i> =3)	33.14 ± 0.77 (32.1–34.0) (<i>n</i> =5)	21.66 ± 0.77 (20.7–22.5) (<i>n</i> =5)	41.00 ± 0.77 (40.0–41.6) (<i>n</i> =4)
Females	80.0 (<i>n</i> =1)	77.3 (<i>n</i> =1)	33.9 (<i>n</i> =1)	20.50 (<i>n</i> =1)	39.30 (<i>n</i> =1)
<i>M. z. macrorhyncha</i>	80.55 ± 3.32 (73–88) (<i>n</i> =117)	70.91 ± 3.52 (63–84) (<i>n</i> =113)	35.49 ± 1.46 (31.6–38.5) (<i>n</i> =115)	23.11 ± 1.08 (20.0–25.5) (<i>n</i> =113)	44.9 ± 4.42 (39.9–48.3) (<i>n</i> =3)
Males	81.53 ± 3.36 (74–88) (<i>n</i> =65)	72.12 ± 3.56 (63–84) (<i>n</i> =64)	35.68 ± 1.37 (32.5–38.5) (<i>n</i> =65)	23.40 ± 0.94 (21.5–25.5) (<i>n</i> =64)	44.1 ± 5.94 (39.9–48.3) (<i>n</i> =2)
Females	79.32 ± 2.84 (73–88) (<i>n</i> =52)	69.33 ± 2.78 (63–76) (<i>n</i> =49)	35.25 ± 1.54 (31.6–38.5) (<i>n</i> =50)	22.73 ± 1.15 (20–25) (<i>n</i> =49)	46.5 (<i>n</i> =1)
<i>M. z. zeledoni</i>	78.18 ± 3.11 (72–85) (<i>n</i> =54)	72.85 ± 3.62 (61–82) (<i>n</i> =53)	33.93 ± 1.16 (30.3–36.0) (<i>n</i> =54)	22.72 ± 0.84 (20.0–24.5) (<i>n</i> =52)	/
Males	78.86 ± 2.82 (72–85) (<i>n</i> =32)	73.21 ± 3.99 (61–82) (<i>n</i> =31)	34.07 ± 1.16 (30.3–36.0) (<i>n</i> =32)	22.89 ± 0.69 (22.0–24.5) (<i>n</i> =30)	/
Females	77.20 ± 3.31 (73–85) (<i>n</i> =22)	72.35 ± 3.05 (67–78) (<i>n</i> =22)	33.71 ± 1.15 (32.0–35.7) (<i>n</i> =22)	22.48 ± 0.97 (20–24) (<i>n</i> =22)	/
<i>M. fortis</i>	81.90 ± 1.84 (78–86) (<i>n</i> =39)	64.27 ± 3.32 (54–71) (<i>n</i> =39)	34.44 ± 1.03 (32–37) (<i>n</i> =39)	22.70 ± 1.04 (20–26) (<i>n</i> =38)	/

Males	82.04 ± 1.53 (78–85) (n=26)	65.08 ± 3.55 (54–71) (n=26)	34.69 ± 0.98 (32.5–37.0) (n=26)	22.69 ± 1.14 (20–26) (n=26)	/
Females	81.62 ± 2.40 (78–86) (n=13)	62.65 ± 2.09 (58–67) (n=13)	33.92 ± 0.95 (32.0–35.5) (n=13)	22.71 ± 0.84 (21–24) (n=12)	/
Live data (Churumbelos, Cauca, Colombia)	83.00 (n=1)	/	/	/	54.00 (n=1)
<i>M. melanoceps</i>	84.23 ± 2.85 (78–91) (n=28)	58.31 ± 3.38 (52–64) (n=26)	32.15 ± 1.16 (30.0–34.5) (n=16)	24.04 ± 1.00 (21.0–25.5) (n=28)	/
Males	86.00 ± 2.48 (80–91) (n=15)	60.36 ± 2.10 (57–64) (n=14)	32.23 ± 1.33 (30.0–34.5) (n=13)	24.4 ± 0.82 (22.5–25.5) (n=13)	/
Females	82.19 ± 1.65 (78–85) (n=13)	55.92 ± 3.03 (52–60) (n=12)	32.08 ± 1.00 (31–34) (n=13)	23.62 ± 1.04 (21–25) (n=13)	/
<i>M. goeldii</i>	85.67 ± 3.51 (82–89) (n=3)	65.00 ± 2.65 (63–68) (n=3)	35.17 ± 1.26 (34.0–36.5) (n=3)	24.00 ± 1.32 (23.0–25.5) (n=3)	/
Males	87.50 ± 2.12 (86–89) (n=2)	65.50 ± 3.54 (63–68) (n=2)	35.75 ± 1.06 (35.0–36.5) (n=2)	24.50 ± 1.41 (23.5–25.5) (n=2)	/
Females	82.0 (n=1)	64.0 (n=1)	34.0 (n=1)	23.0 (n=1)	/

Appendix 3: vocal data

In each table in this appendix, for each taxon / song, data are presented as follows: mean ± standard deviation (lowest value–highest value) (n = no. of vocalisations analysed). $n_{ai} = x$ in respect of each vocalisation for each population, refers to the assumed no. of individuals sampled.

A. Male songs

Taxon	No. of notes	Song duration (s)	Song speed (notes/s)	Max. frequency of second note (kHz)	Max. frequency of last note (kHz)	Frequency variation (kHz)	Position of peak (%)	Position of trough (%)
<i>M. i. immaculata</i> Mérica Andes, Venezuela ($n_{ai}=16$)	5.33 ± 0.98 (3–7) (n=39)	2.39 ± 0.45 (1.25–3.37) (n=39)	2.24 ± 0.14 (2.06–2.51) (n=39)	3.11 ± 0.13 (2.86–3.36) (n=39)	3.06 ± 0.13 (2.86–3.32) (n=38)	0.05 ± 0.05 (-0.02–0.14) (n=38)	0.00 ± 0.01 (0.00–0.08) (n=32)	0.95 ± 0.07 (0.75–1.00) (n=30)
<i>M. i. immaculata</i> East Andes, Colombia ($n_{ai}=9$)	5.65 ± 0.94 (4–8) (n=23)	2.38 ± 0.45 (1.47–3.21) (n=23)	2.40 ± 0.22 (2.09–2.72) (n=23)	3.27 ± 0.16 (3.01–3.58) (n=23)	3.17 ± 0.14 (3.00–3.43) (n=23)	0.10 ± 0.05 (0.01–0.20) (n=23)	0.04 ± 0.09 (0.00–0.25) (n=22)	0.98 ± 0.05 (0.80–1.00) (n=22)
<i>M. i. immaculata</i> All ($n_{ai}=25$)	5.45 ± 0.97 (3–8) (n=62)	2.38 ± 0.45 (1.25–3.37) (n=62)	2.30 ± 0.19 (2.06–2.72) (n=62)	3.17 ± 0.16 (2.86–3.58) (n=62)	3.10 ± 0.14 (2.86–3.43) (n=61)	0.07 ± 0.05 (-0.02–0.20) (n=61)	0.02 ± 0.06 (0.00–0.25) (n=54)	0.97 ± 0.06 (0.75–1.00) (n=52)
<i>M. i. concepcion</i> , Central Andes, Colombia ($n_{ai}=11$)	4.89 ± 0.80 (4–6) (n=27)	2.46 ± 0.39 (1.94–3.22) (n=27)	1.98 ± 0.08 (1.85–2.10) (n=27)	2.99 ± 0.15 (2.79–3.28) (n=27)	2.94 ± 0.14 (2.73–3.22) (n=27)	0.06 ± 0.05 (0.00–0.18) (n=27)	0.02 ± 0.10 (0.00–0.50) (n=26)	0.96 ± 0.06 (0.80–1.00) (n=25)
<i>M. z. macrorhyncha</i> Panana to Ecuador ($n_{ai}=49$)	9.63 ± 1.28 (7–13) (n=124)	2.74 ± 0.37 (1.99–3.76) (n=124)	3.54 ± 0.32 (2.97–4.30) (n=124)	3.48 ± 0.14 (3.08–3.79) (n=125)	3.34 ± 0.13 (3.06–3.69) (n=123)	0.14 ± 0.07 (0.01–0.40) (n=123)	0.03 ± 0.06 (0.00–0.25) (n=125)	0.96 ± 0.05 (0.71–1.00) (n=119)
<i>M. z. zeledoni</i> Panama / Costa Rica ($n_{ai}=16$)	9.52 ± 1.46 (7–13) (n=48)	2.27 ± 0.39 (1.50–3.34) (n=48)	4.22 ± 0.32 (3.86–5.06) (n=48)	3.63 ± 0.09 (3.39–3.81) (n=48)	3.49 ± 0.08 (3.34–3.85) (n=48)	0.14 ± 0.05 (0.01–0.22) (n=48)	0.00 ± 0.00 (0.00–0.00) (n=44)	0.97 ± 0.06 (0.83–1.00) (n=44)
<i>M. fortis</i> ($n_{ai}=65$)	9.40 ± 1.76 (4–15) (n=160)	2.67 ± 0.58 (1.10–4.38) (n=160)	3.57 ± 0.40 (2.82–4.43) (n=160)	3.01 ± 0.16 (2.64–3.52) (n=160)	3.27 ± 0.19 (2.65–3.85) (n=160)	-0.26 ± 0.13 (-0.66–0.01) (n=160)	0.64 ± 0.17 (0.33–1.00) (n=155)	0.02 ± 0.05 (0.00–0.33) (n=156)
<i>M. melanoceps</i> ($n_{ai}=56$)	5.61 ± 0.94 (3–8) (n=145)	2.24 ± 0.44 (1.03–3.38) (n=144)	2.53 ± 0.23 (2.08–3.21) (n=144)	2.40 ± 0.12 (2.13–2.68) (n=143)	2.42 ± 0.12 (1.98–2.62) (n=143)	-0.01 ± 0.07 (-0.18–0.31) (n=142)	0.48 ± 0.14 (0.20–1.00) (n=119)	0.19 ± 0.35 (0.00–1.00) (n=133)

<i>M. goeldii</i> ($n_{ai}=75$)	7.17 ± 1.30 (4–11) ($n=175$)	2.40 ± 0.40 (1.31–3.65) ($n=174$)	2.99 ± 0.22 (2.46–3.48) ($n=174$)	2.30 ± 0.08 (2.03–2.50) ($n=179$)	2.29 ± 0.08 (2.01–2.49) ($n=173$)	0.01 ± 0.04 (-0.11–0.17) ($n=173$)	0.01 ± 0.06 (0.00–0.50) ($n=115$)	0.98 ± 0.06 (0.50–1.00) ($n=108$)
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Note shape descriptions: *immaculata*: down-curved with relatively long downward tails, small initial upstroke in some recordings. *concepcion*: as *immaculata* but shorter downward tail at end. *macrorhyncha* and *zeledoni*: inverted chevron, with wider bandwidth in middle section, downstroke section stronger than upstroke in most recordings; initial upstroke small in handful of *macrorhyncha* recordings. *fortis*: starts as flattish or L-shaped notes then changes to thick downstrokes peaking at start of each note and thicker at end (where lower). *melanoceps* and *goeldii*: modulating note, of two parts, the first higher than second, but continuously delivered ('blob-downstroke'), very small upwards tail before note in some recordings.

Change in note shape descriptions: *immaculata*: no material change in most recordings; in some recordings, first note has initial tail descending in frequency, later notes have initial tail increasing in frequency; in some recordings, first note marginally longer; otherwise no change. *concepcion*: no material change in most recordings; marginal differences in note length in some recordings. *macrorhyncha*: none in most recordings; in some, first note marginally longer, otherwise no change. *zeledoni*: first note appreciably longer. *fortis*: first notes flatter or L-shaped, later notes more like downstrokes, with gradual change. *melanoceps*: first 1–3 notes shorter and less varying in frequency than later ones; some recordings have very short note after first note, forming double note. *goeldii*: reduced differences in note lengths compared to *melanoceps*; two very short notes after first note, forming double or triple note.

B. Female songs

Taxon	No. of notes	Song duration (s)	Song speed (notes/s)	Max. frequency of second note (kHz)	Max. frequency of last note (kHz)	Frequency variation (kHz)	Position of peak (%)	Position of trough (%)
<i>M. i. immaculata</i> , Mérida Andes, Venezuela ($n_{ai}=5$)	4.23 ± 0.44 (4–5) ($n=13$)	1.87 ± 0.21 (1.68–2.27) ($n=13$)	2.27 ± 0.06 (2.20–2.38) ($n=13$)	3.31 ± 0.25 (2.99–3.90) ($n=13$)	3.23 ± 0.21 (2.99–3.55) ($n=13$)	0.08 ± 0.10 (-0.03–0.35) ($n=13$)	0.00 ± 0.00 (0.00–0.00) ($n=11$)	1.00 ± 0.00 (1.00–1.00) ($n=11$)
<i>M. i. concepcion</i> , Central Andes, Colombia ($n_{ai}=3$)	4.42 ± 0.53 (4–5) ($n=7$)	2.06 ± 0.25 (1.83–2.54) ($n=7$)	2.15 ± 0.13 (1.97–2.31) ($n=7$)	3.36 ± 0.26 (3.10–3.73) ($n=7$)	3.23 ± 0.07 (3.18–3.35) ($n=7$)	0.13 ± 0.19 (-0.10–0.40) ($n=7$)	0.18 ± 0.24 (0.00–0.67) ($n=7$)	0.86 ± 0.31 (0.17–1.00) ($n=7$)
<i>M. z. macrorhyncha</i> Panama to Ecuador ($n_{ai}=13$)	10.35 ± 2.04 (7–18) ($n=26$)	2.43 ± 0.48 (1.81–4.40) ($n=26$)	4.27 ± 0.43 (3.61–5.02) ($n=26$)	3.78 ± 0.20 (3.55–4.39) ($n=27$)	3.52 ± 0.13 (3.33–3.73) ($n=26$)	0.24 ± 0.08 (0.13–0.41) ($n=26$)	0.01 ± 0.06 (0.00–0.28) ($n=27$)	0.97 ± 0.06 (0.82–1.00) ($n=26$)
<i>M. z. zeledoni</i> Panama / Costa Rica ($n_{ai}=2$)	9.25 ± 1.50 (7–10) ($n=4$)	1.96 ± 0.09 (1.82–2.01) ($n=4$)	4.71 ± 0.58 (3.84–5.01) ($n=4$)	3.85 ± 0.06 (3.77–3.89) ($n=4$)	3.69 ± 0.10 (3.54–3.76) ($n=4$)	0.17 ± 0.04 (0.13–0.23) ($n=4$)	0.00 ± 0.00 (0.00–0.00) ($n=4$)	1.00 ± 0.00 (1.00–1.00) ($n=4$)
<i>M. fortis</i> ($n_{ai}=5$)	7.38 ± 1.41 (5–9) ($n=8$)	2.11 ± 0.34 (1.51–2.51) ($n=8$)	3.52 ± 0.54 (3.00–4.37) ($n=8$)	3.09 ± 0.13 (2.89–3.24) ($n=8$)	3.46 ± 0.34 (3.16–3.93) ($n=8$)	-0.38 ± 0.24 (-0.69–0.09) ($n=8$)	0.83 ± 0.12 (0.63–1.00) ($n=8$)	0.07 ± 0.10 (0.00–0.25) ($n=8$)
<i>M. melanoceps</i> ($n_{ai}=16$)	4.96 ± 0.74 (4–7) ($n=28$)	1.69 ± 0.32 (1.21–2.56) ($n=28$)	2.97 ± 0.22 (2.67–3.49) ($n=28$)	2.63 ± 0.17 (2.15–3.09) ($n=28$)	2.52 ± 0.11 (2.29–2.88) ($n=28$)	0.11 ± 0.17 (-0.33–0.58) ($n=28$)	0.31 ± 0.22 (0.00–0.67) ($n=27$)	0.67 ± 0.43 (0.00–1.00) ($n=28$)
<i>M. goeldii</i> ($n_{ai}=12$)	6.95 ± 1.33 (5–10) ($n=22$)	2.08 ± 0.39 (1.37–3.05) ($n=22$)	3.35 ± 0.25 (2.85–3.77) ($n=22$)	2.53 ± 0.16 (2.30–2.91) ($n=22$)	2.38 ± 0.09 (2.20–2.51) ($n=22$)	0.16 ± 0.13 (-0.06–0.61) ($n=22$)	0.29 ± 0.30 (0.00–1.00) ($n=21$)	0.80 ± 0.40 (0.00–1.00) ($n=21$)

Note shape descriptions: *immaculata*: down-curved. *concepcion*: down-curved in two recordings; inverted chevron, thickest in middle section with downstroke stronger in other recording. *macrorhyncha* and *zeledoni*: inverted chevron, thickest in middle section with downstroke stronger than upstroke in most recordings; upstroke stronger in one *macrorhyncha* recording. *fortis*: flattish or L-shaped notes (at start) and thick downstrokes (towards end). *melanoceps*: blob-downstrokes, up-downstrokes (inverted chevrons) and one double up-down-stroke. *goeldii*: blob-downstrokes, upwards tail before note in some recordings.

Change in note shape descriptions: *immaculata* and *concepcion*: no material change. *macrorhyncha*: none in most recordings; first note marginally longer in some recordings; in one recording notes change from being more upstrokes to more downstrokes. *zeledoni*: first note longer. *fortis*: first notes flatter or L-shaped, later

notes more like downstrokes, with gradual change. *melanoceps*: none in some recordings; first and / or second note shorter and less varying in frequency in others; change from up-down-stroke to blob-downstroke or *vice versa* in some recordings. *goeldii*: none in some recordings; very short second or third notes (as double or triple note) after first note in most.

C. Multi-note calls

Taxon	No. of notes	Song duration (s)	Song speed (notes/s)	Max. frequency of highest note (kHz)	Max. frequency of lowest note (kHz)	Frequency variation (kHz)	Position of peak	Position of trough
<i>M. i. immaculata</i> Mérida Andes, Venezuela ($n_{ai}=4$)	13.56 ± 5.48 (7–24) ($n=9$)	0.78 ± 0.33 (0.41–1.42) ($n=9$)	17.58 ± 0.76 (16.88–19.14) ($n=9$)	6.86 ± 0.55 (6.37–7.38) ($n=9$)	6.02 ± 0.60 (5.46–7.02) ($n=9$)	0.84 ± 0.25 (0.41–1.26) ($n=9$)	0.20 ± 0.23 (0.00–0.56) ($n=9$)	0.46 ± 0.47 (0.00–1.00) ($n=9$)
<i>M. z. concepcion</i> , Central Andes, Colombia ($n_{ai}=3$)	12.13 ± 10.25 (3–29) ($n=8$)	0.80 ± 0.57 (0.23–1.73) ($n=8$)	13.93 ± 2.35 (10.73–16.89) ($n=8$)	6.72 ± 0.43 (6.27–7.34) ($n=6$)	6.24 ± 0.44 (5.61–6.99) ($n=6$)	0.43 ± 0.51 (0.02–1.40) ($n=6$)	0.42 ± 0.33 (0.14–1.00) ($n=8$)	0.56 ± 0.36 (0.00–0.95) ($n=8$)
<i>M. z. macrorhyncha</i> Panama to Ecuador ($n_{ai}=26$)	12.18 ± 6.17 (3–35) ($n=68$)	0.92 ± 0.45 (0.18–2.56) ($n=68$)	13.40 ± 2.37 (9.36–20.61) ($n=68$)	5.48 ± 0.80 (4.20–7.65) ($n=68$)	4.80 ± 0.69 (3.67–6.36) ($n=67$)	0.71 ± 0.58 (0.10–3.58) ($n=67$)	0.22 ± 0.25 (0.01–1.00) ($n=67$)	0.60 ± 0.32 (0.00–1.00) ($n=67$)
<i>M. z. zeledoni</i> Panama / Costa Rica ($n_{ai}=3$)	24.71 ± 11.69 (10–40) ($n=7$)	1.66 ± 0.80 (0.65–2.72) ($n=7$)	14.89 ± 0.30 (14.51–15.41) ($n=7$)	5.46 ± 0.61 (4.59–5.99) ($n=7$)	4.62 ± 0.53 (3.88–5.20) ($n=7$)	0.84 ± 0.16 (0.62–1.04) ($n=7$)	0.42 ± 0.43 (0.04–1.00) ($n=7$)	0.60 ± 0.38 (0.08–1.00) ($n=7$)
<i>M. fortis</i> ($n_{ai}=16$)	20.21 ± 6.55 (8–37) ($n=43$)	1.19 ± 0.44 (0.49–2.21) ($n=43$)	17.48 ± 2.68 (10.61–22.94) ($n=43$)	5.34 ± 0.92 (4.04–7.57) ($n=40$)	4.55 ± 0.82 (3.08–6.22) ($n=41$)	0.78 ± 0.43 (0.13–1.69) ($n=42$)	0.18 ± 0.23 (0.00–1.00) ($n=42$)	0.41 ± 0.39 (0.00–1.00) ($n=41$)
<i>M. melanoceps</i> ($n_{ai}=1$)	15.00 ± 3.61 (11–18) ($n=3$)	1.39 ± 0.36 (1.00–1.72) ($n=3$)	10.81 ± 0.29 (10.47–10.90) ($n=3$)	2.77 ± 0.09 (2.66–2.83) ($n=3$)	2.37 ± 0.04 (2.33–2.40) ($n=3$)	0.39 ± 0.05 (0.33–0.43) ($n=3$)	0.42 ± 0.50 (0.12–0.99) ($n=3$)	0.58 ± 0.14 (0.45–0.73) ($n=3$)
<i>M. goeldii</i> ($n_{ai}=12$)	14.26 ± 5.86 (3–24) ($n=31$)	1.36 ± 0.56 (0.29–2.76) ($n=31$)	10.56 ± 1.82 (8.69–18.15) ($n=42$)	2.70 ± 0.21 (2.38–3.42) ($n=31$)	2.34 ± 0.23 (2.00–2.92) ($n=31$)	0.36 ± 0.17 (0.05–0.73) ($n=31$)	0.11 ± 0.19 (0.01–0.73) ($n=31$)	0.59 ± 0.39 (0.00–1.00) ($n=31$)

Note shape descriptions: *immaculata*, *concepcion*, *macrorhyncha*, *zeledoni*, *fortis*: upstrokes, with small downstroke or blob at end. *melanoceps*: up-down-stroke, with downstroke stronger and very small upstroke. *goeldii*: up-down stroke, with downstroke stronger on most recordings; upstroke part is small on some recordings.

D. Single-note calls

Taxon	No. of notes	Call duration (s)	Max. frequency of highest note (kHz)
<i>M. i. immaculata</i> Mérida Andes, Venezuela ($n_{ai}=2$)	1 (all) ($n=6$)	0.07 ± 0.02 (0.05–0.11) ($n=6$)	4.13 ± 0.14 (3.93–4.30) ($n=6$)
<i>M. i. immaculata</i> East Andes, Colombia ($n_{ai}=2$)	1 (all) ($n=6$)	0.13 ± 0.12 (0.11–0.16) ($n=6$)	4.43 ± 0.21 (4.20–4.67) ($n=6$)
<i>M. i. immaculata</i> All ($n_{ai}=4$)	1 (all) ($n=12$)	0.10 ± 0.04 (0.05–0.16) ($n=12$)	4.28 ± 0.23 (3.93–4.67) ($n=12$)
<i>M. z. concepcion</i> , Central Andes, Colombia up-down ($n_{ai}=2$)	1 (all) ($n=6$)	0.13 ± 0.02 (0.09–0.15) ($n=6$)	3.99 ± 0.06 (3.91–4.05) ($n=6$)
<i>M. z. concepcion</i> downstroke ($n_{ai}=6$)	1 (all) ($n=15$)	0.15 ± 0.04 (0.09–0.20) ($n=15$)	3.91 ± 0.34 (3.49–4.42) ($n=15$)
<i>M. z. macrorhyncha</i> Panama to Ecuador ($n_{ai}=20$)	1 (all) ($n=15$)	0.15 ± 0.04 (0.10–0.20) ($n=15$)	3.91 ± 0.34 (3.49–4.42) ($n=15$)

<i>M. i. zeledoni</i> Panama / Costa Rica ($n_{ai}=2$)	1 (all) ($n=6$)	0.09 ± 0.02 (0.06–0.11) ($n=6$)	4.24 ± 0.24 (4.13–4.79) ($n=6$)
<i>M. fortis</i> ($n_{ai}=4$)	1 (all) ($n=9$)	0.05 ± 0.03 (0.02–0.08) ($n=9$)	3.72 ± 0.22 (3.30–4.02) ($n=9$)
<i>M. melanoceps</i> ($n_{ai}=11$)	1 (all) ($n=26$)	0.11 ± 0.01 (0.06–0.12) ($n=25$)	2.56 ± 0.17 (2.34–3.09) ($n=26$)
<i>M. goeldii</i> ($n_{ai}=7$)	1 (all) ($n=21$)	0.12 ± 0.01 (0.09–0.14) ($n=21$)	2.40 ± 0.13 (2.13–2.56) ($n=21$)

Note shape descriptions: *immaculata*, *concepcion* (up-down) and *fortis*: up-down stroke. *concepcion* downslurred call: downstroke, small blob at start or thin upstroke at start. *macrorhyncha* and *zeledoni*: up-down stroke, thicker and longer at peak in most recordings. *melanoceps* and *goeldii*: up-down stroke, thicker and longer at peak, and skewed higher frequency at start; shape broken in one recording of *goeldii*.

Appendix 4: differences between *Myrmeciza* taxa

Differences between *M. immaculata* populations are shown using diagnosability levels described under Methods.

The following codes are used:

For vocal variables, the first symbol refers to the type of call:

♂: male song

♀: female song

σ: single-note call

Σ: single-note downslurred call of *concepcion*

μ: multi-note call

The following codes refer to vocal variables:

NN: number of notes

SL: song length

SS: song speed

MF: for songs: acoustic frequency of second note; for calls: max. acoustic frequency.

mF: for songs: acoustic frequency of last note; for calls: min. acoustic frequency

FV: acoustic frequency variation

CP: change of pace

PP: position of peak in acoustic frequency

PT: position of trough in acoustic frequency

NS: note shape

CNS: change in note shape

For biometrics, the following codes are used:

WI: wing length

TL: tail length

TR: tarsus length

BL: bill length

BW: bill width

MS: mass.

N/A: no sample available for one of the populations for the type of vocalisation in question

No diff: no observed differences in any variables measured as determined by statistical tests

Degrees of freedom can be calculated by taking the lower value of the two taxa for the relevant variable under '($n=x$)' in Appendices 2–3, and subtracting 1. The taxon with the higher or lower of the relevant variable can be seen in Appendices 1–2. Differences in bold denote that the two taxa are phylogenetic species *sensu* Cracraft 1983) based on the relevant variable. The two layers of shading represent new species limits proposed herein. See the sample sizes in previous appendices when undertaking pairwise comparisons. Note that some populations may appear 'less diagnosable' for certain variables than they may actually be due to sample size: all statistical tests are affected by sample size. For example, there are particularly small samples of biometrics for *goeldii*, of female songs for several populations especially *zeledoni*, and of multi-note calls for *melanoceps*

	<i>M. i. immaculata</i>	<i>M. i. concepcion</i>	<i>M. z. macrorhyncha</i>	<i>M. z. zeledoni</i>	<i>M. fortis</i>	<i>M. melanoceps</i>	<i>M. goeldii</i>
<i>M. i. immaculata</i> Mérida Andes Songs (σ ¹)	X	♂SS(1,2) ♂NS(4)	♂NN(1,2,3) ♂SL(1) ♂SS(1,2,3,4,5) ♂MF(1,2) ♂mF(1) ♂FV(1) ♂NS(4)	♂NN(1,2) ♂SS(1,2,3,4,5) ♂MF(1) ♂mF(1) ♂FV(1,2) ♂PP(1,2,3,4,5) ♂PT(1,2,3,4,5) ♂NS(4) ♂CNS(4)	♂NN(1,2) ♂SS(1,2,3,4,5) ♂MF(1) ♂mF(1,2) ♂FV(1,2) ♂PP(1,2,3,4,5) ♂PT(1,2,3,4,5) ♂NS(4) ♂CNS(4)	♂SS(1) ♂MF(1,2,3,4,5) ♂mF(1,2,3,4,5) ♂FV(1) ♂PP(1,2,3,4,5) ♂PT(1,2) ♂NS(4) ♂CNS(4)	♂NN(1) ♂SS(1,2,3,5) ♂MF(1,2,3,4,5) ♂mF(1,2,3,4,5) ♂FV(1) ♂NS(4) ♂CNS(4)
Songs (♀)	X	♀: No diff.	♀NN(1,2,3,4,5) ♀SL(1) ♀SS(1,2,3,4,5) ♀MF(1) ♀mF(1) ♀FV(1) ♀NS(4)	♀NN(1,2) ♀SS(2,4,5) ♀MF(1,2) ♀mF(1,2) ♀FV(1,2) ♀PP(1,2,3,4,5) ♀PT(1,2,3,4,5) ♀NS(4) ♀CNS(4)	♀SS(1,2,4,5) ♀MF(1,2) ♀mF(1,2) ♀PP(1,2) ♀NS(4) ♀CS(4)	♀NN(1,2) ♀SS(1,2,3,4,5) ♀MF(1,2,4) ♀mF(1,2,3,4,5) ♀PP(1) ♀NS(4) ♀CNS(4)	♀NN(1,2) ♀SS(1,2,3,4,5) ♀MF(1,2,4) ♀mF(1,2,3,4,5) ♀PP(1) ♀NS(4) ♀CNS(4)
Calls	X	♂SL(1) ♂MF(1)	♂SL(1) ♂NS(4)	♂MF(1) ♂NS(4)	♂SL(1) ♂MF(1,2,3,4,5) ♂NS(4)	♂SL(1,2) ♂MF(1,2,3,4,5) ♂NS(4)	♂SL(1,2) ♂MF(1,2,3,4,5) ♂NS(4)
<i>M. i. immaculata</i> East Andes Plumage IX: Songs (σ ¹)	X	μ: No diff. ΣSL(1,2) ΣNS(4)	μSS(1,2) μMF(1) μmF(1)	μSS(1,2,3,4,5) μMF(2,4) μmF(1,2,4)	μMF(1) μmF(1)	μSS(2,3,4,5) μMF(1,2,3,4,5) μmF(1,2,3,4,5) μFV(2) μNS(4)	μSL(1) μSS(1,2,3,5) μMF(1,2,3,4,5) μmF(1,2,3,4,5) μFV(2) μNS(4)
	X	♂SS(1,2) ♂mF(1) ♂NS(4)	♂NN(1,2,3) ♂SS(1,2,3,4,5) ♂MF(1) ♂mF(1) ♂NS(4)	♂NN(1,2) ♂SS(1,2,3,4,5) ♂MF(1,2) ♂mF(1,2) ♂NS(4)	♂NN(1,2) ♂SS(1,2,3,4) ♂MF(1) ♂FV(1,2,3,4,5) ♂PT(1,2,3,4,5) ♂PT(1,2,3,4,5) ♂NS(4) ♂CNS(4)	♂MF(1,2,3,4,5) ♂mF(1,2,3,4,5) ♂FV(1) ♂PP(1,2,3) ♂PT(1,2) ♂NS(4) ♂CNS(4)	♂NN(1) ♂SS(1,2) ♂MF(1,2,3,4,5) ♂mF(1,2,3,4,5) ♂FV(1,2) ♂NS(4) ♂CNS(4)

	<i>M. i. immaculata</i>	<i>M. i. conception</i>	<i>M. z. macrorhyncha</i>	<i>M. z. zelandi</i>	<i>M. fortis</i>	<i>M. melaniceps</i>	<i>M. godditi</i>
Plumage 1X: Songs (♀)	X	♀: N/A	♀: N/A	♀: N/A	♀: N/A	♀: N/A	♀: N/A
Biometrics 1X: Calls	X	σMF(1,2,4)	σSL(1) σMF(1) σNS(4)	σSL(1,2) σNS(4)	σSL(1,2,4) σMF(1,2,4)	σSL(1) σMF(1,2,3,4,5) σNS(4)	σMF(1,2,3,4,5) σNS(4)
		μ: N/A	μ: N/A	μ: N/A	μ: N/A	μ: N/A	μ: N/A
		ΣMF(1) ΣNS(4)					
<i>M. i. immaculata</i> All							
Plumage 1X: Songs (σ)	X	σSS(1,2) σMF(1) σmF(1) σNS(4)	σNN(1,2,3) σSL(1) σSS(1,2,3,4,5) σMF(1,2) σmF(1) σNS(4)	σNN(1,2) σSS(1,2,3,4,5) σMF(1,2,3) σmF(1,2) σNS(4)	σNN(1,2) σSL(1) σSS(1,2,3,4,5) σMF(1) σFV(1,2) σPP(1,2,3,4,5) σPT(1,2,3,4,5) σNS(4) σCNS(4)	σSS(1) σMF(1,2,3,4,5) σmF(1,2,3,4,5) σFV(1) σPP(1,2,3,5) σPT(1,2) σNS(4) σCNS(4)	σNN(1) σSS(1,2,3) σMF(1,2,3,4,5) σmF(1,2,3,4,5) σFV(1) σNS(4) σCNS(4)
Plumage 1X: Songs (♀)	X	♀: No diff.	♀NN(1,2,3,4,5) ♀SL(1) ♀SS(1,2,3,4,5) ♀MF(1) ♀mF(1) ♀FV(1) ♀NS(4)	♀NN(2,4) ♀SS(2,4,5) ♀MF(1,2) ♀mF(1,2) ♀NS(4)	♀NN(1,2) ♀SS(2,4) ♀FV(2,4) ♀PP(1,2,3,4,5) ♀PT(1,2,3,4,5) ♀NS(4) ♀CNS(4)	♀SS(1,2,4,5) ♀MF(1,2) ♀mF(1,2) ♀PP(1,2) ♀NS(4) ♀CS(4)	♀NN(1,2) ♀SS(1,2,3,4,5) ♀MF(1,2,4) ♀mF(1,2,3,4,5) ♀PP(1) ♀NS(4) ♀CNS(4)
Biometrics 1X: Calls	X	σMF(1)	σMF(1) σNS(4)	σNS(4)	σMF(1,2)	σMF(1,2,3,4,5) σNS(4)	σMF(1,2,3,4,5) σNS(4)
		μ: No diff.	μSS(1,2) μMF(1) μmF(1)	μSS(1,2,3,4,5) μMF(2,4) μmF(1,2,4)	μMF(1) μmF(1)	μSS(2,3,4,5) μMF(1,2,3,4,5) μmF(1,2,3,4,5) μFV(2) μNS(4)	μSL(1) μSS(1,2,3,5) μMF(1,2,3,4,5) μmF(1,2,3,4,5) μFV(2) μNS(4)
		ΣSL(1) ΣNS(4)					

	<i>M. i. immaculata</i>	<i>M. i. conception</i>	<i>M. z. macrorhyncha</i>	<i>M. z. zelatonii</i>	<i>M. fortis</i>	<i>M. melaniceps</i>	<i>M. goeldii</i>
<i>M. i. conception</i> Plumage !X: Songs (♂)	Male <i>conception</i> has less extensive feathering on forehead.	X	<p>♂NN(1,2,3,4,5) ♂SS(1,2,3,4,5) ♂MF(1,2,3) ♂mF(1,2) ♂FV(1) ♂NS(4)</p>	<p>♂NN(1,2,3,4,5) ♂SS(1,2,3,4,5) ♂mF(1,2,3,4,5) ♂mF(1,2,3,4,5) ♂FV(1,2,4) ♂PP(1,2,3,5) ♂PT(1,2,3,4,5) ♂NS(4) ♂CNS(4)</p>	<p>♂NN(1) ♂SS(1,2) ♂MF(1,2,3,4,5) ♂mF(1,2,3,4) ♂FV(1) ♂PP(1,2,3) ♂PT(1,2) ♂NS(4)</p>	<p>♂NN(1,2) ♂SS(1,2,3,4,5) ♂MF(1,2,3,4,5) ♂mF(1,2,3,4,5) ♂FV(1) ♂NS(4) ♂CNS(4)</p>	<p>♂NN(1,2) ♂SS(1,2,3,4,5) ♂MF(1,2,4) ♂mF(1,2,3,4,5) ♂FV(1) ♂NS(4) ♂CNS(4)</p>
<i>M. i. conception</i> Plumage !X: Songs (♀)	Female <i>conception</i> has average greyer wash on breast and averages less rufous on undertail-coverts and flanks.	X	<p>♀NN(1,2,3,4,5) ♀SS(2,4,5) ♀MF(2,4) ♀mF(1,2,4) ♀CNS(4)</p>	<p>♀NN(2,4) ♀SS(2,4,5) ♀MF(2,4) ♀mF(1,2,4) ♀CNS(4)</p>	<p>♀NN(2) ♀SS(2) ♀PP(1,2) ♀PT(2) ♀NS(4) ♀CNS(4)</p>	<p>♀SS(1,2,3,4,5) ♀MF(1,2,4) ♀mF(1,2,3,4,5) ♀FV(1,2,4) ♀NS(4) ♀CNS(4)</p>	<p>♀NN(1,2) ♀SS(1,2,3,4,5) ♀MF(1,2,4) ♀mF(1,2,3,4,5) ♀FV(1,2,4) ♀NS(4) ♀CNS(4)</p>
<i>M. i. conception</i> Biometrics !X: Calls	No diff.	X	<p>♂NS(4)</p>	<p>♂SL(1) ♂MF(1,2,4) ♂NS(4)</p>	<p>♂SL(1,2,4) ♂MF(1)</p>	<p>♂MF(1,2,3,4,5) ♂NS(4)</p>	<p>♂MF(1,2,3,4,5) ♂NS(4)</p>
<i>M. z. macrorhyncha</i> Plumage !X: Songs (♂)	Male: <i>macrorhyncha</i> has more extensive white patch on shoulder and less extensive feathering on forehead.	X	<p>♂SL(1) ♂NS(4) ♂mF(1,2)</p>	<p>♂SL(1,2) ♂MF(1) ♂NS(4) ♂mF(4) ♂mF(1,2,4)</p>	<p>♂SL(1,2,4) ♂NS(4)</p>	<p>♂SL(1) ♂MF(1,2,3,4,5) ♂NS(4)</p>	<p>♂SL(1) ♂MF(1,2,3,4,5) ♂NS(4)</p>
<i>M. z. macrorhyncha</i> Plumage !X: Songs (♀)	Male: <i>macrorhyncha</i> has more extensive white patch on shoulder and less extensive feathering on forehead.	X	<p>♂SL(1) ♂SS(1,2) ♂MF(1) ♂mF(1) ♂PP(1) ♂CNS(4)</p>	<p>♂SL(1) ♂SS(1,2,3,4,5) ♂PP(1,2,3,4,5) ♂PT(1,2,3,4,5) ♂NS(4) ♂CNS(4)</p>	<p>♂NN(1,2,3) ♂SL(1) ♂SS(1,2,3) ♂MF(1,2,3,4,5) ♂mF(1,2,3,4,5) ♂FV(1,2) ♂PP(1,2,3,4,5) ♂PT(1,2) ♂NS(4) ♂CNS(4)</p>	<p>♂NN(1) ♂SL(1) ♂SS(1,2) ♂MF(1,2,3,4,5) ♂mF(1,2,3,4,5) ♂FV(1,2) ♂PP(1,2,3,4,5) ♂PT(1,2) ♂NS(4) ♂CNS(4)</p>	<p>♂NN(1) ♂SL(1) ♂SS(1,2) ♂MF(1,2,3,4,5) ♂mF(1,2,3,4,5) ♂FV(1,2) ♂NS(4) ♂CNS(4)</p>

	<i>M. i. immaculata</i>	<i>M. i. conception</i>	<i>M. z. macrorhyncha</i>	<i>M. z. zeledoni</i>	<i>M. fortis</i>	<i>M. melanoceps</i>	<i>M. goeldii</i>
Plumage !X! Songs (♀)	Female <i>macrorhyncha</i> has more extensive white patch on shoulder, less contrasting crown, and more uniform and intensely rufous underparts and upperparts.		X	♀SL(1) ♀CNS(4)	♀NN(1) ♀MF(1,2,3,4) ♀FV(1,2,4) ♀PP(1,2,3,4,5) ♀PT(1,2,3,4,5) ♀NS(4) ♀CNS(4)	♀NN(1,2) ♀SS(1,2) ♀MF(1,2,3,4,5) ♀mF(1,2,3,4,5) ♀NS(4)	♀NN(1,2) ♀SS(1,2) ♀MF(1,2,3,4,5) ♀mF(1,2,3,4,5) ♀NS(4)
Biometrics !X! Calls	BL(1,2) TL(1) TR(1)	TL(1) TR(1) BL(1)	X	♂MF(1)	♂SL(1,2) ♂MF(1) ♂NS(4)	♂MF(1,2,3,4,5) ♂NS(4)	♂SL(1) ♂MF(1,2,3,4,5) ♂NS(4)
<i>M. z. zeledoni</i>				μ: No diff.	μNN(1) μSL(1) μSS(1)	μMF(1,2,3,4,5) μmF(1,2,3,4,5) μFV(1) μNS(4)	μSS(1) μMF(1,2,3,4,5) μmF(1,2,3,4,5) μFV(1) μNS(4)
Plumage !X! Songs (♂)	Male: <i>zeledoni</i> has more extensive white patch on shoulder.	Male: <i>zeledoni</i> has more extensive white patch on shoulder.	Male: <i>zeledoni</i> has less extensive white patch on shoulder.	X	♂SS(1) ♂MF(1,2,3,5) ♂mF(1) ♂FV(1,2,3,4,5) ♂PP(1,2,3,4,5) ♂PT(1,2,3,4,5) ♂NS(4) ♂CNS(4)	♂NN(1,2) ♂SS(1,2,3,4,5) ♂MF(1,2,3,4,5) ♂mF(1,2,3,4,5) ♂FV(1,2) ♂PP(1,2,3,4,5) ♂PT(1,2) ♂NS(4) ♂CNS(4)	♂NN(1) ♂SL(1) ♂SS(1,2,3,4,5) ♂MF(1,2,3,4,5) ♂mF(1,2,3,4,5) ♂FV(1,2) ♂NS(4) ♂CNS(4)
Plumage !X! Songs (♀)	Female: <i>macrorhyncha</i> has more extensive white patch on shoulder, less contrasting crown, and more uniform and intensely rufous underparts and upperparts.	Female: <i>zeledoni</i> has less extensive white patch on shoulder.	Female: <i>zeledoni</i> has less extensive white patch on shoulder.	X	♀MF(1,2,3,4,5) ♀FV(1,2,4) ♀PP(1,2,3,4,5) ♀PT(1,2,3,4,5) ♀NS(4) ♀CNS(4)	♀NN(4) ♀SS(2) ♀MF(1,2,3,4,5) ♀mF(1,2,3,4,5) ♀PP(1) ♀NS(4) ♀CNS(4)	♀SS(2,4) ♀MF(1,2,3,4,5) ♀mF(1,2,3,4,5) ♀PP(1) ♀NS(4) ♀CNS(4)

	<i>M. i. immaculata</i>	<i>M. i. conception</i>	<i>M. z. macrorhyncha</i>	<i>M. z. zeladori</i>	<i>M. fortis</i>	<i>M. melaniceps</i>	<i>M. goeldii</i>
Biometrics !X! Calls	BL(1)	No diff.	WL(1) TR(1) BL(1)	X	σSL(1) σMF(1,2,4) σNS(4)	σMF(1,2,3,4,5) σNS(4)	σSL(1) σMF(1,2,3,4,5) σNS(4)
<i>M. fortis</i>							
Plumage !X! Songs (♂)	<i>M. fortis</i> has greyer mantle and blue (not whitish) bare skin behind eye.	<i>M. fortis</i> has greyer mantle and blue (not whitish) bare skin behind eye.	<i>M. fortis</i> has greyer mantle and blue (not whitish) bare skin behind eye, and less extensive white feathering on shoulder.	<i>M. fortis</i> has greyer mantle and blue (not whitish) bare skin behind eye.	X	σNN(1,2) σSL(1) σSS(1,2) σMF(1,2,3,5) σmf(1,2,3,4,5) σFV(1,2) σPP(1) σPT(1) σNS(4) σCNS(4)	σNN(1) σSL(1) σSS(1) σMF(1,2,3,4,5) σmf(1,2,3,4,5) σFV(1,2) σPP(1,2,3,5) σPT(1,2,3,4,5) σNS(4) σCNS(4)
Plumage !X! Songs (♀)	<i>M. fortis</i> has brighter rufous on crown, paler brown mantle, grey (not brown) on breast and blue (not whitish) bare skin behind eye.				X	♀MF(1) ♀mf(1,2) ♀FV(1,2,4) ♀PP(1,2) ♀PT(1,2) ♀NS(4) ♀CNS(4)	♀MF(1,2,3) ♀mf(1,2,4,5) ♀FV(1,2,4) ♀PP(1,2) ♀PT(1,2) ♀NS(4) ♀CNS(4)
Biometrics !X! Calls	TL(1,2) TR(1) BL(1)	TL(1,2) TR(1)	TL(1) TR(1) BL(1)	WL(1) TL(1,2)	X	σSL(1,2) σMF(1,2,3,4,5) σNS(4)	σSL(1,2,4) σMF(1,2,3,4,5) σNS(4)
						μSS(2,5) μMF(1,2,3,4,5) μmf(1,2,3,4,5) μFV(1) μNS(4)	μNN(1) μSS(1,2) μMF(1,2,3,4,5) μmf(1,2,3,4,5) μFV(1) μNS(4)

	<i>M. i. immaculata</i>	<i>M. i. conception</i>	<i>M. z. macrorhyncha</i>	<i>M. z. zelandi</i>	<i>M. fortis</i>	<i>M. melanoceps</i>	<i>M. goeldii</i>
<i>M. melanoceps</i>							
<i>Plumage</i> (♂)	<i>M. melanoceps</i> has white interscapular patch, more extensive white feathering on shoulder and darker, less extensive bare skin in ocular region.	<i>M. melanoceps</i> has white interscapular patch, and darker, less extensive bare skin in ocular region.	<i>M. melanoceps</i> has white interscapular patch and darker bare skin.	<i>M. melanoceps</i> has white interscapular patch and darker bare skin.	<i>M. melanoceps</i> has white interscapular patch.	X	♂NN(1) ♂SS(1,2) ♂MF(1) ♂mF(1) ♂FV(1) ♂PP(1,2,3,5) ♂PT(1,2) ♂CNS(4) ♀SS(1) ♀mF(1)
<i>Plumage</i> (♀)	<i>M. melanoceps</i> is more orange throughout, has black hood and darker, less extensive bare skin in ocular region.	<i>M. melanoceps</i> is more orange throughout, has black hood and darker, less extensive bare skin in ocular region.			<i>M. melanoceps</i> is more orange throughout and has a black hood, whilst <i>fortis</i> is dingier brown on upperparts, has grey on underparts and brighter blue bare skin in ocular region.	X	
<i>Biometrics</i> (♂)	WL(1) TL(1,2,3,4,5) BL(1,2)	WL(1,2) TL(1,2,3,4,5) BL(1,2)	WL(1) TL(1,2,3,4,5) TR(1) BL(1)	WL(1,2) TL(1,2,3,4,5) TR(1,2) BL(1)	WL(1) TL(1) TR(1) BL(1)	X	♂SL(1) ♂MF(1) μ: No diff.
<i>M. goeldii</i>							
<i>Plumage</i> (♂)	<i>M. goeldii</i> has brighter red (not reddish-brown) wing bend and has white interscapular patch.	<i>M. goeldii</i> has brighter red (not reddish-brown) iris, lacks extensive bare skin in ocular region, lacks white on wing bend and has white interscapular patch.					<i>M. melanoceps</i> has brown (not red) iris and more extensive bare skin in ocular region.
<i>Plumage</i> (♀)	<i>M. goeldii</i> is more orange-brown generally, has whitish tail and has less extensive bare skin in ocular region.	<i>M. goeldii</i> is more orange-brown generally, has whitish (not dark) throat, lacks darker tail and has less extensive bare skin in ocular region.			<i>M. fortis</i> has brighter rufous crown, darker brown mantle and is grey (not orange) on breast.		<i>M. melanoceps</i> has brown (not red) iris and black hood, whilst <i>goeldii</i> has dusky face and whitish throat. <i>M. melanoceps</i> has more extensive bare skin in ocular region.
<i>Biometrics</i>	No diff.	No diff.	No diff.	No diff.	No diff.	No diff.	No diff. X

Note: differences between East Andes and Mérida Andes populations of *M. immaculata* in voice: ♂MF(1). ♀: N/A. ♂SL(1,2,4), ♂MF(1), μ: N/A

Type specimens in the bird collection at Lubango, Angola

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SUMMARY.—Details pertaining to 22 avian holotypes, and one topotype, held in the bird collection of the Instituto Superior de Ciências da Educação, in Lubango, Angola, are presented. Not all of the taxa discussed here are currently treated as valid by at least some checklists or other keynote works.

A number of avian taxa were described by R. K. Brooke, P. A. Clancey, M. P. S. Irwin, W. J. Lawson and A. A. Rosa Pinto from specimens collected in Angola. All of this type material is housed in the bird collection at the Instituto Superior de Ciências da Educação (ISCED) in Lubango, Angola (see Mills *et al.* 2010). There has been some concern as to the whereabouts of these types and their safety—it was thought that the bird collection may have been damaged during the long civil war in Angola, but in fact it is still intact and accessible.

In June 2008, a team comprising the authors of this note spent two weeks cataloguing the bird collection at Lubango (Mills *et al.* 2010). Due to time constraints, only about one-third of the specimen data were captured electronically, but almost all of those catalogue cards for which the data were not captured were digitally photographed, and subsequently used to complete, as far as possible, the catalogue of the collection (some cards were overlooked so the catalogue remains incomplete). In addition to collecting basic data on the specimen labels, we recorded any additional label notes. The 22 name-bearing types, all holotypes, in the collection are not labelled conventionally with a separate red label, but are noted (in red pen or pencil) to be type specimens. Of great concern is that the holotype material in the collection at ISCED is not housed in separate locked storage, but is placed with conspecifics in specimen drawers in the rather crowded collection room (which houses both avian and mammalian material), meaning that there is some potential for type material to be damaged.

The collection also contains 34 specimens of four species labelled 'paratipo' (= paratype), two specimens labelled 'alotipo' (= allotype) and 90 specimens of 15 species labelled 'topotipo' (topotypes). Details of all holotypes are given below, along with those of one of the topotypes, *Francolinus squamatus schuetti*, which is discussed because of its potential significance in establishing the taxon's type locality. Details of the paratypes and other topotypes can be obtained from the senior author on request.

List of types

Taxonomy and order, with one exception, follows Dean (2000). Abbreviations: c/no = specimen catalogue numbers, OD = original description.

Phasianidae

Francolinus squamatus schuetti Cabanis, 1880, *J. Orn.* 28: 351.

A single adult male in the ISCED collection (c/no 27737), from Mwaoka (07°37'S, 20°52'E), Lunda Norte, Angola, 24 July 1964, collected by 'Sanjinge' is labelled as being a topotype.

The holotype (ZMB 24636), collected by Otto Schütt, on an unknown date, is in the Museum für Naturkunde of the Humboldt-University of Berlin, Germany (Steinheimer & Dean 2007). There is much uncertainty as to where Schütt collected the holotype (Steinheimer & Dean 2007) so the ISCED specimen may be relevant to further research into this question.

Musophagidae

Corythaixoides concolor cuanhamae Rosa Pinto, 1962, *Bol. Inst. Invest. Cient. Ang.* 1: 23

Holotype (c/no 1394), a male, age not given, Pereira d'Éça (now Ondjiva) (17°04'S, 15°43'E), Huíla Province (now Cunene Province), Angola, 14 April 1960, collected by A. A. Rosa Pinto. Included in *C. c. bechuanae* Roberts, 1932, by Dickinson (2003).

Apodidae

Apus horus fuscobrunneus Brooke, 1971, *Durban Mus. Novit.* 9: 33

The holotype (c/no 16161) is in the ISCED collection, but is labelled *Apus t. toulsoni* (Bocage, 1877), an adult female, Rio Curoca (Rio Curoca estuary at Tombua, 15°43'S, 11°55'E), Moçamedes Province (now Namibe Province), Angola, 12 May 1966, collected by M. Loureiro. Recognised by Dickinson (2003) as a subspecies of *A. horus* (Heuglin, 1869). *A. toulsoni* is also sometimes considered to be a local colour morph of *A. horus* (Brooke 1971).

Meropidae

Merops pusillus landanae Rosa Pinto, 1972, *Mem. Trab. Inst. Invest. Cienc. Ang.* 10: 35

Holotype (c/no 29917), male not aged, Malembo (05°20'S, 12°11'E), near Lândana (now Cacongo), Cabinda Province, Angola, 31 August 1969, collected by E. Simões. A second specimen (c/no 29921), collected at the same locality on the same day and labelled as a paratype, is included in the series of measurements for specimens from Cacongo, but not specifically mentioned in the OD. Dickinson (2003) noted that *M. p. landanae* may be a synonym of *M. p. argutus* Clancey, 1967, but requires evaluation.

Merops superciliosus alternans Clancey, 1971, *Durban Mus. Novit.* 9: 42

Holotype (c/no 31558), adult male, Carunjamba (near Lucira, 13°57'S, 12°25'E), Moçamedes Province (now Namibe Province), Angola, 4 December 1969, collected by E. Santos.

Picidae

Jynx ruficollis diloloensis Rosa Pinto, 1962, *Bol. Inst. Invest. Cient. Ang.* 1: 26

Holotype (c/no 157), adult male, Lago Dilolo (11°30'S, 22°05'E), Moxico Province, Angola, 18 August 1958, collected by A. A. Rosa Pinto. A second specimen (c/no 132), an adult female, collected at Reserva da Cameia (11°43'S, 20°48'E), Moxico Province, on 16 August 1958 by A. A. Rosa Pinto is labelled as an allotype. Included in *J. r. ruficollis* Wagler, 1850, by Dickinson (2003). Not recognised by Dowsett *et al.* (2008).

Alaudidae

Mirafra africana anchietae Rosa Pinto, 1967, *Bol. Inst. Invest. Cient. Ang.* 4(2): 29

Holotype (c/no 4097), adult male, Humpata (15°01'S, 13°23'E), Huíla Province, Angola, 27 June 1962, collected by A. M. Ferreira. Included in *M. africana occidentalis* (Hartlaub, 1857) by Dickinson (2003).

Mirafra africana irwini Rosa Pinto, 1968, *Bonn. Zool. Beitr.* 19: 282

Holotype (c/no 16934), adult male, Rio Longa (14°36'S, 18°29'E), Cuando Cubango Province, Angola, 11 June 1966, collected by M. Loureiro. Included in *M. africana gomesi* C. M. N. White, 1944, by Dickinson (2003). Not recognised by Dowsett *et al.* (2008).

Mirafra angolensis niethammeri Rosa Pinto 1968, *Bonn. Zool. Beitr.* 19: 283

Holotype (c/no. 16963), male, not aged, Rio Longa (Longa) (14°36'S, 18°29'E), Cuando Cubango Province, 11 June 1966, collected by D. Mumputu (incorrectly listed as 'Mumputo' in the OD). Included in *M. angolensis antonii* B. P. Hall, 1958, by Dickinson (2003). Needs evaluation.

Hirundinidae

Riparia cincta xerica Clancey & Irwin, 1966, *Durban Mus. Novit.* 8: 30

Holotype (c/no 8828), adult male, Calai, Cuangar (17°54'S, 19°46'E), Cuando Cubango Province, 1 August 1964, collected by A. A. Rosa Pinto.

Motacillidae

Macronyx grimwoodi cuandocubangensis Rosa Pinto, 1968, *Bonn. Zool. Beitr.* 19: 283

Holotype (c/no 16807), adult male, Rio Longa (14°36'S, 18°29'E), Cuando Cubango Province, Angola, 8 June 1966, collected by D. Mumputu. The ISCED collection has 16 specimens labelled as being paratypes, and 19 labelled topotype; the latter all from the type locality. None of the paratypes and topotypes is specifically mentioned in the OD, although all are included in the measurement series. Not recognised by Dickinson (2003) and Dowsett *et al.* (2008), who consider the species to be monotypic.

Turdidae

Monticola brevipes niveiceps Clancey, 1972, *Durban Mus. Novit.* 9: 147

Holotype (c/no 4350), adult female, Tundavala (14°50'S, 13°24'E), Huíla Province, Angola, 28 June 1963, collected by F. Nóbrega. Included in nominate *M. brevipes* (Waterhouse, 1838) by Dickinson (2003).

Sylviidae

Cisticola chiniana huilensis Rosa Pinto, 1967, *Bol. Inst. Invest. Cient. Ang.* 4(2): 30

Holotype (c/no 20230), male, not aged, Lagoa Iventala (15°01'S, 13°23'E), Huíla Province, Angola, 27 July 1967 (incorrectly given as 2 July in the OD), collected by A. M. Ferreira, A. R. Pereira and L. Samahina. Included in *C. c. smithersi* B. P. Hall, 1956, by Dickinson (2003).

Cisticola subruficapilla newtoni Rosa Pinto, 1967, *Bol. Inst. Invest. Cient. Ang.* 4(1): 12

Holotype (c/no 4627), adult male, Major (Caraculo) (15°01'S, 12°25'E), Moçamedes (now Namibe) Province, Angola, 6 August 1963, collected by A. A. Rosa Pinto. A second specimen (c/no 4843), an adult female, collected at the same locality on 21 August 1963 by A. A. Rosa Pinto is labelled as being an allotype.

Achaetops pycnopygius spadix Clancey, 1972, *Durban Mus. Novit.* 9: 151

Holotype (c/no 32110), adult male, Unguéria (15°19'S, 13°32'E), Huíla Province, Angola, 20 May 1970, collected by D. Maputo.

Platysteiridae

Batis molitor pinto Lawson, 1966, *Bull. Brit. Orn. Cl.* 86: 124

Holotype (c/no 8209), adult male, Fazenda do Cuito (Moco) (12°27'S, 15°16'E), Huambo Province, Angola, 19 June 1964, collected by A. A. Rosa Pinto.

Lanioturdus torquatus mesicus Clancey, 1970, *Durban Mus. Novit.* 9: 8

Holotype (c/no 11168), male, not aged, Rio Nompaca, Mupanda (Omupanda) (17°08'S, 15°46'E), Huíla Province (now Cunene Province), Angola, 29 April 1965, collected by A. M. Ferreira. Treated as monotypic by Dickinson (2003).

Timaliidae

Turdoides melanops angolensis Rosa Pinto, 1967, *Bol. Inst. Invest. Cient. Ang.* 4(2): 30

Holotype (c/no 10861), female, not aged, Jau (15°14'S, 13°31'E), Huíla Province, Angola, 29 March 1965, collected by F. Nóbrega. Status uncertain; may be synonymous with nominate *T. m. melanops* (Hartlaub, 1867) (Dickinson 2003).

Nectariniidae

Nectarinia fusca inclusa Clancey, 1970, *Durban Mus. Novit.* 9: 10

Holotype (c/no 30783), male, not aged, Lucira (13°52'S, 12°31'E), Moçamedes (now Namibe) Province, Angola, 12 November 1969, collected by A. M. Ferreira. Now *Cinnyris fuscus inclusus* (Clancey, 1970) following the classification of Irwin (1999).

Malaconotidae

Tchagra australis bocagei Rosa Pinto, 1968, *Bonn. Zool. Beitr.* 19: 284

Holotype (c/no 17552), male, not aged, Cuíto-Cuanavale (15°09'S, 19°10'E), Cuando Cubango Province, Angola, 30 June 1966, collected by M. Loureiro (incorrectly given as 'Loureiro' in the OD).

Sturnidae

Buphagus erythrorhynchus angolensis Rosa Pinto, 1968, *Bonn. Zool. Beitr.* 19: 285

Holotype (c/no 8907), adult male, Sambio (17°53'S, 20°04'E), Cuando Cubango Province, Angola, 3 August 1964, collected by F. Nóbrega. There are seven specimens labelled paratype, none from the type locality, and none specifically mentioned in the OD, although all included (*inter alia* with other specimens) in the measurement series. Recognised by Dowsett *et al.* (2008), but treated as monotypic by Dickinson (2003).

Ploceidae

Sporopipes squamifrons pallidus Rosa Pinto, 1967, *Bol. Inst. Invest. Cient. Ang.* 4(2): 31

Holotype (c/no 4066), male, not aged, Caraculo (15°01'S, 12°40'E), Moçamedes (now Namibe) Province, Angola, 14 June 1962, collected by A. M. Ferreira. The ISCED collection has ten specimens labelled paratype and eight labelled topotype, none from the type locality, and none specifically mentioned in the OD, although all included in the measurement series. Status uncertain; according to Dickinson (2003) the taxon may be synonymous with *S. s. squamifrons* (A. Smith, 1836).

Fringillidae

Serinus citrinelloides martinsi Rosa Pinto, 1962, *Bol. Inst. Invest. Cient. Ang.* 1: 37

Holotype (c/no 460), not aged and sexed, Kalunda (Kalunda) (12°08'S, 23°28'E), Moxico Province, Angola, 11 September 1958, collected by A. A. Rosa Pinto. However, the holotype is in fact a misidentified *S. capistratus capistratus* (Finsch & Hartlaub, 1870) and is held at ISCED under this species name. Pinto (1965) considered *S. citrinelloides martinsi* at Kalunda to be an isolated (and by implication valid) population, but there are no subsequent records of the species from eastern Angola or western Zambia. *S. citrinelloides* is an East African species, and the nearest records to Kalunda are from north-east Zambia (Dowsett *et al.* 2008).

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New information on the distribution and status of birds in Uruguay

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SUMMARY.—Novel distributional data for 19 bird species in Uruguay are provided, including four new for the country: Sharp-billed Treehunter *Heliobletus contaminatus*, Planalto Woodcreeper *Dendrocolaptes platyrostris*, Large-tailed Antshrike *Mackenziaena leachii* and Yellow-olive Flycatcher *Tolmomyias sulphurescens*. The first evidence for the presence of Buff-fronted Owl *Aegolius harrisii* for almost 50 years was also obtained. The status of several other species restricted to forests along the middle Uruguay River is clarified. New data are discussed with reference to available information from neighbouring countries.

Uruguay lies in the Pampas biome of south-eastern South America and >400 species are known from the country. Here we provide novel data for 19 bird species, including four reported for the first time. For most others treated here, there are very few published detailed (i.e., locality and date data) records for Uruguay. Some species were previously included in lists of Uruguayan birds but lack details and / or documentation (Arballo & Cravino 1999, Azpiroz 2001). We also confirm the breeding status of two little-known summer migrants. In many cases, especially for species for which field identification based on morphological characters is difficult, we provide details of available evidence (e.g., specimens, recordings, photographs). Additionally, sound-recordings are available at xeno-canto (www.xeno-canto.org; XC). New records are contextualised with respect to data from neighbouring Argentina and Brazil. Observers are specified in each case (Abente = JSA; Azpiroz = ABA; Calimares = CC; Jaramillo = AJ; Menéndez = JLM; Presa = DP; Saralegui = AR) and localities are shown in Fig. 1.

Species accounts

BLACK-COLLARED HAWK *Busarellus nigricollis*

On 24–25 October 2011 an immature was at Estancia Santo Domingo, dpto. Paysandú (ABA & E. Méndez; Fig. 2). Only four previous reports for Uruguay: Arroyo Laureles, dpto. Rivera, April 1962; isla Arrospide Grande, dpto. Tacuarembó, April 1963; near Paso del Puerto, río Negro, dpto. Río Negro, March 1964 (Gerzenstein 1965); and San Diego, río Yaguarón, dpto. Cerro Largo, October 1988 (Arballo & Cravino 1999). Found in northern and north-east Argentina (Narosky & Yzurieta 2010) with a few records from Rio Grande do Sul, Brazil (Belton 1984, Bencke *et al.* 2003, Accordi & Barcellos 2006). Ours is the first documented record for Uruguay.

WILLET *Catoptrophorus semipalmatus*

One photographed at La Estacada, southern dpto. Montevideo, on 30 November 2008 (A. Mello) and another at José Ignacio, south-west dpto. Maldonado, on 27–28 December 2008 (ABA; Fig. 3). Previous reports concern singles photographed at Playa Penino, south-west dpto. San José in March 1987 (Gambarotta *et al.* 1987) and Punta Carretas, dpto. Montevideo in October 2009 (Gil 2011). There are few published records for Argentina (Chebez 2009)



Figure 1. Localities mentioned in the text. ARTIGAS: 1. Rincón de Franquía (30°11'33"S, 57°38'25"W); 2. Bella Unión (30°15'41"S, 57°35'58"W); 3. La Palma (30°16'24.47"S, 57°21'35.0"W); 4. Isla del Zapallo (30°30'16"S, 57°52'47"W). 5. Rincón de Sepulturas (30°49'31.8"S, 56°01'48"W). RIVERA: 6. FYMSA (31°04'38"S, 55°45'17"W); 7. Bañado de Ataques (31°06'05"S, 55°41'21"W); 8. Valle del Lunarejo (31°08'40.38"S, 55°54'03.42"W). TACUAREMBÚ: 9. Sierra del Infiernillo (c.31°24'46"S, 56°08'03"W); 10. Paso Ceferino (31°31'15"S, 56°04'41"W); 11. Valle Edén (31°49'17"S, 56°10'29"W). PAYSANDÚ: 12. Estancia Santo Domingo (31°49'19"S, 57°39'20"W). CERRO LARGO: 13. Cañada del Burro (32°01'34.6"S, 53°57'39.3"W); 14. Paso Centurión (32°07'56"S, 53°43'58"W); 15. Paso Paiva (32°09'21"S, 53°43'04"W). TREINTA Y TRES: 16. Quebrada de los Cuervos Protected Area (32°55'15"S, 54°27'23"W). 17. Arroyo de las Pavas (c.33°11'51"S, 54°47'35"W). LAVALLEJA: 18. Paso Averías (c.33°36'44"S, 54°19'48"W), Cebollatí River. 19. Cerro Arequita (34°17'26"S, 55°15'58"W). MALDONADO: 20. José Ignacio (34°50'45.80"S, 54°37'58.60"W). MONTEVIDEO: 21. La Estacada (34°55'28"S, 56°09'03"W). COLONIA: 22. Arroyo Limetas, Conchillas (34°09'54"S, 58°05'51"W).

and southern Brazil (Belton 1984). One in Buenos Aires province was assigned to *C. s. semipalmatus* on the basis of alternate plumage (Roesler *et al.* 2004). The bird in December 2008 showed some characters of *C. semipalmatus inornatus* (O'Brien 2006), but could not be certainly identified to subspecies.



Figure 2. Black-collared Hawk *Busarellus nigricollis*, Estancia Santo Domingo, dpto. Paysandú Uruguay, 24 October 2011 (Adrián B. Azpiroz)

Figure 3. Willet *Catoptrophorus semipalmatus*, José Ignacio, dpto. Maldonado, Uruguay, 27 December 2008 (Adrián B. Azpiroz)

Figure 4. Buff-fronted Owl *Aegolius harrisi*, Gajo Medio del Arroyo Tres Cruces, near Paso Ceferino, dpto. Tacuarembó, Uruguay, 30 November 2010 (Adrián B. Azpiroz)

Figure 5. Sharp-billed Treehunter *Heliobletus contaminatus*, río Yaguarón, Paso Paiva, dpto. Cerro Largo, Uruguay, 21 December 2008 (Adrián B. Azpiroz)

Figure 6. Planalto Woodcreeper *Dendrocolaptes platyrostris*, río Yaguarón, Paso Paiva, dpto. Cerro Largo, Uruguay, 15 June 2011 (Adrián B. Azpiroz)

Figure 7. Large-tailed Antshrike *Mackenziaena leachii*, Paso Centurion, dpto. Cerro Largo, Uruguay, 7 March 2011 (Dardo Presa)

Figure 8. Yellow-olive Flycatcher *Tolmomyias sulphurescens*, río Yaguarón, Paso Centurión, dpto. Cerro Largo, Uruguay, 19 November 2011 (Adrián B. Azpiroz)

Figure 9. Female Crested Becard *Pachyramphus validus*, Paso Paiva, dpto. Cerro Largo, Uruguay, 7 March 2011 (José S. Abente)

Figure 10. Golden-rumped Euphonia *Euphonia cyanocephala*, Bella Unión, dpto. Artigas, Uruguay, 9 June 2009 (© Fernando Lapitz)

LONG-TUFTED SCREECH OWL *Megascops sanctaecatarinae*

Several identified by voice at three sites within FYMSA (c.31°04'38"S, 55°45'17"W; 31°03'16"S, 55°45'52"W; 31°04'04"S, 55°44'40"W), northern dpto. Rivera, as follows: 30

January 2004 (one), 22 April (two), 6 September (one), 25 November 2007 (one) and 14 December 2008 (one) (AR). Also singles responded to playback at Valle Edén on 29 April 2010 (photographed; CC & A. Olmos) and 8 November 2011 (photographed; ABA). On 30 April 2010 several were heard and a rufous morph responded to playback at Sierra del Infiernillo, northern dpto. Tacuarembó (CC & A. Olmos). Two rufous morphs were seen and sound-recorded (XC67460) at Valle del Lunarejo, 3.5 km north-west of La Palma (31°08'40.38"S, 55°54'03.42"W), north-west dpto. Rivera, on 12 October 2009 (AJ). Individuals responded to playback near Gajo Medio del Arroyo Tres Cruces, c.11 km north-west of Paso Ceferino, northern dpto. Tacuarembó, on 30 November (one), 8 March 2011 (three, photographed and sound-recorded; XC93329) (ABA & N. Martínez Curci) and 1 November 2011 (two, sound-recorded) (ABA & E. Méndez). Finally, a rufous morph was photographed at Rincón de Sepulturas, c.28 km north of Masoller, south-west dpto. Artigas, on 28 March 2011 (A. Olmos). There are a few old reports for Uruguay. Cuello (1975) mentioned three specimens taken in dptos. Artigas, Cerro Largo and Tacuarembó in 1969–71. In Rio Grande do Sul it is scarce near the Uruguayan border (Belton 1984) and in Argentina it is also relatively rare (Chebez 2009).

FERRUGINOUS PYGMY OWL *Glaucidium brasilianum*

Two photographed at Arroyo de las Pavas, c.38 km west of Treinta y Tres City, dpto. Treinta y Tres, on 2 March 2007 (A. Rocchi & G. Mondón). One photographed and another heard at Quebrada de los Cuervos, dpto. Treinta y Tres, on 3 March 2009 (CC); the species was also observed there in 1999 (CC). Found near Paso Paiva, río Yaguarón, eastern dpto. Cerro Largo on 15 (one) and 16 (two) January 2011; one bird was sound-recorded (ABA, JLM; XC93401). Also photographed at three sites south of Paso Centurión on 6–7 March (DP, JLM, JSA), 9 March (ABA) and 1 November 2011 (JLM, JSA, D. Gil). Singles and pairs were seen repeatedly and photographed at Paso Averías, río Cebollatí, southern dpto. Treinta y Tres, on 18–24 April 2011 (AR & M. Abreu). There are very few previous reports for Uruguay. Wetmore (1926) collected a female near Lascano, dpto. Rocha in February 1921, while Tremoleras (1927) took two at Arroyo Grande, dpto. Flores in 1891 and reported another in dpto. Lavalleja taken prior to 1927, and one was collected at Paso de las Piedras, río Negro, dpto. Durazno, in April 1961 (Cuello & Gerzenstein 1962), but ours are the first records since then. Probably not as rare as previously considered (especially around Centurión) and the species appears to be widespread over the country. It is scarce in Entre Ríos, Argentina (de la Peña 1997) and rare in Rio Grande do Sul, Brazil (Belton 1984).

BUFF-FRONTED OWL *Aegolius harrisii*

One photographed and sound-recorded near Gajo Medio del Arroyo Tres Cruces, c.10 km north-west of Paso Ceferino, northern dpto. Tacuarembó, on 30 November was heard again on 1 December 2010 (ABA & N. Martínez Curci; Fig. 4). Another was photographed and sound-recorded there on 31 October and 1 November 2011 (ABA & E. Méndez). There is only one previous documented record in Uruguay: a female trapped in a mist-net at Estancia Maljos [=Mailhos], Sierra del Infiernillo, Arroyo Tres Cruces, 40 km north of Tacuarembó, in February 1963 (Barlow & Cuello 1964, Gerzenstein 1965, Cuello 1975). All Uruguayan records are from the same general area, very probably <10 km apart. The new records are presumed to represent *A. h. iheringi*, which might be specifically distinct, and is otherwise known from eastern Bolivia, Paraguay, central and eastern Brazil, and north-east Argentina (Marks *et al.* 1999). There are few recent reports from Rio Grande do Sul and north-east Argentina (Bencke *et al.* 2003, Chebez 2009).

BAND-WINGED NIGHTJAR *Caprimulgus longirostris*

Of two specimens collected by members of the Sociedad Guazubirá at Arroyo Limetas, north-west of Conchillas, western dpto. Colonia, on 14 August 1966 and 4 May 1968, one is lost and the other is at MNHM (no. 3957). There are very few published records in Uruguay and none is documented. Vaz-Ferreira & Gerzenstein (1961) mentioned two observations in dptos. San José and Colonia, and Gore & Gepp (1978) reported one in Mariscal, dpto. Lavalleja in September 1967 and another in dpto. Maldonado in 1970. Given the dates of these observations, it is possible that the taxon involved is *C. l. patagonicus*, a winter migrant from Patagonia. Specimens from Rio Grande do Sul, however, belong to *C. l. longirostris* (Straube 1990; G. N. Maurício *in litt.* 2011).

WHITE-BROWED WOODPECKER *Piculus aurulentus*

One heard in gallery forest along the río Yaguarón (on both the Uruguayan and Brazilian banks), south of Paso Centurión, on 31 October 2011 (JLM, JSA, S. Álvarez, D. Gil). Just one previous record in Uruguay: one seen in October 2006 c.300 m south of the new site (Azpiroz & Menéndez 2008).

SHARP-BILLED TREEHUNTER *Heliobletus contaminatus*

Two seen in gallery forest along the río Yaguarón 1.8 km north-west of Paso Paiva on 28 February 2006 (JLM, DP, JSA & S. Álvarez). At the same site, up to four were photographed and sound-recorded on 21 December 2008 (ABA, DP; Fig. 5), 15 February 2010 (JLM; XC93405) and 17 January 2011 (JLM). On 7 March 2011 the species was found a few hundred metres to the south (JLM, JSA). These are the first records in Uruguay and the southernmost ever. It has been found at Vila Basílio in southern Rio Grande do Sul, Brazil, c.70 km north-east of Paso Paiva (Maurício & Dias 2001). Previously known from south-east Brazil, eastern Paraguay and north-east Argentina (Remsen 2003).

PLANALTO WOODCREEPER *Dendrocolaptes platyrostris*

The voice of one was sound-recorded (XC93402) in gallery forest along the río Yaguarón at Paso Paiva on 21 December 2008 (ABA), but went unrecognised for c.2 years. A pair was photographed and sound-recorded (XC93403) in the same area as *Heliobletus contaminatus* on 29 September–1 October 2010 (DP, ABA, JLM, N. Martínez Curci & L. Doño). In the same place two were photographed and sound-recorded (XC93404) on 15 and 17–18 January 2011 (ABA, JLM; Fig. 6). Again heard around Paso Paiva on 7 March 2011 (JLM) and singles and pairs heard, seen or photographed on 5–6 March (JLM), 29–30 October and 2 November (JLM, S. Álvarez, D. Gil) and 19–20 November 2011 (ABA), 1.4 km south-east of Paso Centurión. Known from eastern and south-eastern Brazil, south-east Paraguay and north-east Argentina (Marantz *et al.* 2003), ours are the first records for Uruguay. Paso Paiva is c.90 km south-west of the previously reported southernmost localities in southern Rio Grande do Sul (Rio Piratini and Passo da Orqueta; Maurício & Dias 1998, 2001).

LARGE-TAILED ANTSHRIKE *Mackenziaena leachii*

A female was photographed and sound-recorded in gallery forest at a lagoon 0.7 km south of Paso Centurión on 7–8 March 2011 (JLM, JSA, DP; Fig. 7). A second record was obtained at Cañada del Burro, 16.5 km south-east of Isidoro Noblía, north-eastern dpto. Cerro Largo, where at least one female was photographed on 28–29 August 2011 (M. Abreu & A. Olmos). The two sites are c.25 km apart. These are the first reports for Uruguay and extend the species' known range c.180 km south-west. It was previously known as far south

as Paredão, Rio Camaquã, Rio Grande do Sul, but was expected to occur further south (Maurício & Dias 2001).

GREENISH ELAENIA *Myiopagis viridicata*

This and the next three species were identified primarily by their voices. One in gallery forest of the río Cuareim at Estancia La Palma, northern dpto. Artigas, on 8 November 2011, was sound-recorded (DP; XC93330) and identified subsequently (JLM). The recording matches the third example of this species on López-Lanús (2008). Previously known from one locality in northern dpto. Rivera where it has been observed regularly in spring and summer since 2004 (Saralegui 2008; AR & CC pers. obs.), the new site lies c.180 km to the north-west. Otherwise known in neighbouring areas from northern Rio Grande do Sul and north-east Argentina (Belton 1985, Narosky & Yzurieta 2010).

OLIVACEOUS ELAENIA *Elaenia mesoleuca*

Singles sound-recorded and photographed near Gruta de Piria (c.31°03'16"S, 55°45'50"W), FYMSA, Sierra de la Aurora, c.25 km south-west of Rivera, northern dpto. Rivera, as follows: 27 October and 24 November 2005, 22 and 23 December 2009 (the latter mist-netted) (AR). At Gruta de Piria at least five seen and heard (two photographed) on 8 October 2010 (ABA, AR, CC). Three observations at Cerro Arequita, dpto. Lavalleja: one photographed and sound-recorded (XC16330) on 1 December 2007, one heard and another at a nest with two eggs on 8 and 21 November 2008 (photographed and sound-recorded), and heard in December 2010 (A. Ricetto *in litt.* 2011). Seen in gallery forest along Gajo Medio del Arroyo Tres Cruces and in nearby forest patches, c.11 km north-west of Paso Ceferino, on 1 December 2010 (two, sound-recorded; XC93328), 9 March 2011 (ABA & N. Martínez Curci) and 1 November 2011 (ABA & E. Méndez). Found c.1.5 km south of Paso Centurión on 31 October (sound-recorded and photographed; JLM, JSA, DP, S. Álvarez, D. Gil, A. Chlefe & E. Azpiroz), 2 November (sound-recorded; XC93406, c.500 m to the south; JLM, JSA, S. Álvarez & A. Chlefe) and 19–20 November 2011 (two photographed; ABA). Previously known from four localities in Uruguay (Claramunt & Rocha 2001, Azpiroz & Menéndez 2008), we add three new sites (including the southernmost ever, in dpto. Lavalleja), substantially extend the known dates of occurrence (early October–early March) and provide the first breeding record. A summer resident in neighbouring regions, the species is scarce in north-east Argentina (Narosky & Yzurieta 2010) and abundant, mostly in eastern Rio Grande do Sul (Belton 1985).

LARGE ELAENIA *Elaenia spectabilis*

Singles in the environs of Bella Unión, north-west dpto. Artigas on 1 and 21 April 2007 (JLM & F. Lapitz, respectively), 23 February 2008 (JLM) and 27 February 2009 (JLM, ABA, DP), and at Rincón de Franquía, north of Bella Unión, on 12 October 2009 (JLM) and 30 October 2010 (JLM). Sound-recordings were obtained (XC93399, 93434, 93437). One was also photographed at a nest at Paraje Coronado, 3 km south of Bella Unión, on 7 December 2009 (F. Lapitz *in litt.* 2011). There is only one previous documented report in Uruguay; specimens taken c.7 and 38 km south and south-west of Bella Unión in January and February 1998, respectively (Claramunt & González 1999). Our data suggest this species is a fairly common summer resident in extreme north-west Uruguay and confirm breeding there. Scarce in north-east Argentina (Narosky & Yzurieta 2010) and uncommon to common in western Rio Grande do Sul (Belton 1985).

YELLOW-BELLIED ELAENIA *Elaenia flavogaster*

Two seen and sound-recorded close to a wetland (31°10'58.32"S, 55°53'30.12"W) near the arroyo Lunarejo, Valle del Lunarejo, north-west dpto. Rivera, on 9–10 December 2009 (AJ). The only previous report for Uruguay is that of Abreu *et al.* (2010) who found the species at Lago Merín, south-east dpto. Cerro Largo, c.300 km from our localities, in November 2008 and September 2009. A scarce resident in northern Argentina (Narosky & Yzurieta 2010) but regularly observed year-round in Rio Grande do Sul (Belton 1985).

YELLOW-OLIVE FLYCATCHER *Tolmomyias sulphureus*

One was sound-recorded in gallery forest along the río Yaguarón, c.1.5 km south of Paso Centurión, eastern dpto. Cerro Largo, on 7 March 2011 (JLM; XC93439). On 1 November 2011 two were photographed and sound-recorded (XC93408) in the same area (32°08'50"S, 53°43'57"W; JLM, JSA, DP & S. Álvarez). On 19–20 November 2011, one was photographed c.700 m away (32°08'35"S, 53°43'33"W) on the río Yaguarón (ABA; Fig. 8). Known from neighbouring Rio Grande do Sul, Brazil (Maurício & Dias 1998, 2001), ours are the first records for Uruguay and the southernmost ever.

BOAT-BILLED FLYCATCHER *Megarhynchus pitangua*

Two at Isla del Zapallo, western dpto. Artigas, on 28 February 2008 (ABA, JLM, DP & F. Lapitz). Three were filmed in gallery forest beside the río Cuareim at Estancia La Palma, northern dpto. Artigas, on 8 November 2011 (DP). The only previous report for Uruguay is that of Abente (2010) who observed a pair at the río Cuareim, northern dpto. Artigas, on 2–3 December 2008. In the south of its range the species is regular in northern and central Rio Grande do Sul (Belton 1985), and north-east Argentina, south to northern Corrientes (Narosky & Yzurieta 2010). Two recent records in northern Buenos Aires, eastern Argentina, perhaps involved vagrants (Merlo & Aleman 2010).

CRESTED BECARD *Pachyramphus validus*

A female was photographed c.2 km north-west of Paso Paiva on 7 March 2011 (JSA, JLM; Fig. 9). The species was included in a list of Uruguayan birds by Arballo & Cravino (1999), but without details. Based on unpublished information from the same authors, Claramunt & Cuello (2004) included dpto. Cerro Largo within the species' range. Ours is the first documented record for Uruguay. It is a scarce summer resident in north-east Argentina (Narosky & Yzurieta 2010) and uncommon in Rio Grande do Sul (Belton 1985).

WEDGE-TAILED GRASS FINCH *Emberizoides herbicola*

Several records in northern dpto. Rivera: at Bañado de Ataques on 1 September (two) and 7 December 2005 (three); near Gruta de Piria, FYMSA, on 23 December 2009 (two) and 29 January 2010 (three), respectively (AR); at two sites in the Valle del Lunarejo, on 26 September 2008 (three, sound-recorded), 12 October 2009 (two, sound-recorded) and 7–10 December 2010 (one, photographed and sound-recorded, AJ). *E. herbicola* is readily separated from Lesser Grass Finch *E. ypiranganus* on vocal and plumage differences (Tobias *et al.* 1997). Chebataroff & Gerzenstein (1965) reported that a female was collected at Sierra de Mahoma, dpto. San José, but its whereabouts are unknown, and the record possibly involved an immature Great Pampa Finch *Embernagra platensis*. Moderately common resident in grasslands of Rio Grande do Sul, but not recorded near the Uruguayan border (Belton 1985), and scarce in eastern Argentina (Narosky & Yzurieta 2010).

GOLDEN-RUMPED EUPHONIA *Euphonia cyanocephala*

A male and two females filmed at Bella Unión on 22 July 2009 (DP). The species was observed repeatedly in the same area in May 2009 and males were photographed on 9 June 2009 (Fig. 10) and 28 July 2010 (F. Lapitz *in litt.* 2011). Included by several authors (e.g., Tremoleras 1920, Baratini 1945, Arballo & Cravino 1999, Azpiroz 2001) for Uruguay, but none provided details. Scarce in northern Argentina, south to northern Entre Ríos (Narosky & Yzurieta 2010), and uncommon in Rio Grande do Sul, Brazil (Belton 1985).

Concluding remarks

The majority of species reported here are associated with the Atlantic Forest of south-eastern South America. In recent years many such elements have been found in Uruguay in gallery forest along the río Uruguay (around Bella Unión), and along the Cuchilla de Haedo (Lunarejo Valley and environs) and Cuchilla Grande (Centurión and Sierra de Ríos). The latter two areas are relatively low hills that connect areas of similar topography in southern Brazil. North of Bella Unión a small reserve has been established recently (Rincón de Franquía) and habitat restoration is underway. The Lunarejo Valley has been recently incorporated in the National System of Protected Areas (SNAP) as a 'Protected Landscape' and this measure should contribute to its future preservation. However, the Centurión area, which harbours a large number of Atlantic Forest elements (Azpiroz & Menéndez 2008) has not benefited from such initiatives. Although its addition to the SNAP has been proposed, no concrete measures have been implemented to date. Although none of the species mentioned here are of global conservation concern, several probably are threatened at a national level, especially Buff-fronted Owl, because the Uruguayan population is probably small and perhaps isolated.

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So far from the Andes: Black-and-white Tanager *Conothraupis speculigera*, an unexpected vagrant to French Guiana

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SUMMARY.—A male Black-and-white Tanager *Conothraupis speculigera* was mist-netted on 20 March 2011 at Awala-Yalimapo, north-west French Guiana (05°44'N, 53°55'W), 3,000 km east of its breeding areas and >2,800 km from its principal non-breeding range. This is the first record for north-east South America, and the first away from its restricted breeding range during the nesting period. The alternative hypotheses of exceptionally long-distance vagrancy or the existence of an unknown breeding population between the Andes and French Guiana, are discussed.

The genus *Conothraupis* comprises two range-restricted, medium-sized tanagers, Black-and-white Tanager *C. speculigera* and Cone-billed Tanager *C. mesoleuca*. Males are characterised by their contrasting black and white plumage with a white speculum at the base of the primaries, strikingly reminiscent of some *Sporophila* seedeaters (Isler & Isler 1999, Witt 2005). Females are much duller, predominantly olive in *C. speculigera* and dull brown in *C. mesoleuca*.

C. speculigera breeds in southern Ecuador, mainly in the provinces of Loja and El Oro, and north-west Peru, south to La Libertad, where it occurs mainly during the rainy season in February–May (O'Neill 1966, Best *et al.* 1993, Ridgely & Greenfield 2001, Greeney *et al.* 2006, Ingels 2007, Schulenberg *et al.* 2007). During the non-breeding season, it undertakes a unique trans-Andean migration, south-east into south-west lowland Amazonia, mainly to central and eastern Peru (Isler & Isler 1999, Ridgely & Tudor 2009). It hardly reaches western Brazil, where the species has been recorded only at Seringal Oriente and at Valparaíso on the upper rio Juruá in Acre (Stotz 1990, Whittaker & Oren 1999), and it is only a rare visitor to north-west Bolivia, with one record at Alto Madidi in dpto. La Paz (Parker *et al.* 1991) and an unpublished record in dpto. Cochabamba (S. K. Herzog *in litt.* 2011). Although it commonly nests in secondary habitats in southern Ecuador (Ridgely & Greenfield 2001, Ingels 2007), the species' restricted range, disjunct distribution and possible decline due to loss and degradation of its breeding habitat has led to this tanager being listed as Near Threatened (BirdLife International 2000, 2011).

Given its community of active birdwatchers, new bird species for French Guiana are added annually (Renaudier & CHG 2010, Renaudier *et al.* 2010). However, the capture of a subadult male Black-and-white Tanager at Awala-Yalimapo in north-west French Guiana on 20 March 2011, must rank as one of the most unexpected national 'firsts' to date.

Locality and circumstances

Awala-Yalimapo is in westernmost coastal French Guiana, c.10 km from the border with Suriname in north-east South America. The study site (05°44'N, 53°55'W), locally known as 'la digue' or 'la digue de Panato', is located between the villages of Awala and

Yalimapo. It comprises a dry area on white sand with bushes and low trees, and traditional Amerindian cultures of manioc, surrounded by vast marshes almost at sea level.

The bird was mist-netted during STOC (Suivi Temporel des Oiseaux Communs: Pineau in prep.) surveys on behalf of the Groupe d'Étude et de Protection des Oiseaux en Guyane (GEPOG). Three times p.a. ten mist-nests are erected at the same places within the study area for two consecutive days, covering a total area of c.2 ha. The mist-nets are operated from midday to dusk and the following day from dawn to midday. The net where the bird was caught was placed among bushes and near trees bordering an old manioc 'field'. The Black-and-white Tanager was caught at 08.30 h. When MC brought it to the ringing table none of us could identify the bird.

Description

The bird's general morphology and bill shape and colour clearly indicated it to be a tanager. Its size was approximately that of a *Tachyphonus* or large *Thraupis*, but the glossy black upperparts and head, white lower breast and belly, grey flanks and rump, and striking white speculum at the base of the primaries readily eliminated all species known in French Guiana (Figs. 1–2). The speculum was formed by a clear-cut white patch at the bases of pp3–7 and restricted to the inner web of p8 (numbered descendently). The secondaries also possessed a white basal patch on their inner webs, forming a concealed wingbar. The grey rump and flanks were washed green. In addition, the bird had a concealed white coronal patch, black thighs, dark red eyes, black legs and a dark grey maxilla with a contrasting pale grey mandible. Reference to Restall *et al.* (2006) and Ridgely & Tudor (2009) permitted the bird's identification as a male Black-and-white Tanager. Biometrics: total length 170 mm, wing (flattened) 79 mm, tail 67 mm, mass 25.5 g; belly feathered, and no cloacal protuberance or incubation patch. It exhibited significant fat on the breast (furculum), flanks and axillaries, scoring 3 on a scale of 0–4.

The plumage appeared fresh, in 'perfect' condition and showed no signs of wear or active moult. Traces of green on the rump and flanks, presumably remnants of immature plumage, as well as the pointed rectrices, suggest that the bird was a subadult male with



Figures 1–2. Male Black-and-white Tanager *Conothraupis speculigera*, Awala-Yalimapo, French Guiana, 20 March 2011 (Maxime Cobigo); the missing rectrix was collected for DNA.

retained juvenile tail feathers, although the latter showed no sign of wear nor a distinct coloration. However, the body plumage was almost entirely that of an adult, as were the dark red eyes (Ridgely & Tudor 2009).

The bird was measured, photographed and ringed (Paris SC164426) before being released. On flying into the adjacent understorey, its grey rump was conspicuous.

Discussion

The locality in French Guiana where the Black-and-white Tanager was trapped is 3,000 km east of its breeding range and >2,800 km from its principal non-breeding range. Our record is the longest-distance vagrancy recorded and further demonstrates the species' highly migratory capabilities. Vagrants can clearly be expected elsewhere between its breeding grounds and French Guiana, for example in Colombia, central Amazonian Brazil or Venezuela. A specimen collected on 16 October 1969 in dpto. Putumayo in southern Colombia (Verhelst *et al.* in prep.) is the only record for the country, and is sited on a direct line between the breeding grounds and French Guiana, but 'only' 400 km north-east of the species' breeding areas. There are no records for Venezuela, or central and northern Brazil (Hilty 2003, Ascanio 2009, Pacheco & Agne 2010; D. Ascanio, F. Brammer & J. Kvarnäck *in litt.* 2011). Two males observed in dpto. Cochabamba, central Bolivia, in September 2004 (S. K. Herzog & R. Soria-Auza), 1,700 km from the breeding grounds, represent the longest known movement in a south-easterly direction. Like other migrants, Black-and-white Tanagers are liable to appear outside their usual range, but the distance covered by the Awala bird, in an 'aberrant' north-east direction, is exceptional.

Our record in French Guiana could indicate the existence of a previously unknown population somewhere between the Andes and French Guiana. In such a case, the distance travelled by the Awala bird might not be so great. In late March, this tanager should have been on its breeding grounds. However, Black-and-white Tanager is known to breed only west of the Andes, with all records from east of the Andes being in the non-breeding season (see above). The French Guianan record is the first 'breeding-season' record away from the known breeding range. By modelling environmental characteristics of the known distribution of *C. speculigera*, Verhelst *et al.* (in prep.) highlight a potential area of occurrence in the pantepui of south-east Venezuela and western Guyana. Our record was *c.*700 km further east. However, the model does not discriminate between breeding and non-breeding data, thus the potential distribution includes non-breeding areas.

Although pertaining to two distinct biomes, i.e. dry deciduous montane forest and lowland humid forest, respectively, breeding and non-breeding habitats share certain characteristics (O'Neill 1966). On its breeding grounds, the species occurs in scrubby secondary habitats and clearings within deciduous woodlands, mainly at 500–1,700 m. Such arid habitats are frequented only in the wet season (Best *et al.* 1993, Ridgely & Greenfield 2001, Ingels 2007, Schulenberg *et al.* 2007). Non-breeding, dry-season habitats are more diverse, as the species has been found in xerophytic brushy habitats (O'Neill 1966), riparian thickets and the understorey of riparian forest in south-east Peru and north-east Bolivia (Ridgely & Greenfield 2001, Hennessey *et al.* 2003). The habitat at Awala-Yalimapo matches breeding and non-breeding habitats, comprising mixed, dry brushy and woody white-sand secondary vegetation surrounded by a marsh, thus combining all relevant characteristics, except perhaps altitude.

Finally, there is the question of whether the bird reached French Guiana naturally or if it was an escaped cagebird. Despite its IUCN status, the species is not listed by CITES, making trade legal. While such trade is rather low over most of South America (FAO 2011), the capture and keeping of cagebirds is widespread in the Guianas (Andel *et al.* 2003, Hanks

2005, Mittermeier *et al.* 2010). Local Amerindians and immigrant Surinamese in French Guiana often keep wild songbirds in cages, and frequent movements of people between neighbouring countries, as well as illegal trade, mean that a bird caught in Surinam or Brazil could have been brought to French Guiana. However, the possibility for a cagebird to be carried or traded from Peru or Ecuador to French Guiana appears very low, considering the distance and absence of regular exchange between these countries. Moreover, Black-and-white Tanager is unknown in captivity in Ecuador and Surinam (J. F. Ortiz & M. Sánchez *in litt.* 2011, A. Spaans *vide* J. Ingels *in litt.* 2011).

Despite the date of the French Guiana record being within the species' breeding season, fat accumulation on the bird was also typical of a migrant bird at the onset of migration. Its fresh plumage suggests that it had stayed in the area to moult, and that it was mist-netted potentially just prior to departure. Based on this, the Comité d'Homologation de Guyane validated the record as the first for French Guiana, and has included Black-and-white Tanager in category A of the country's bird list, i.e. a species of wild origin recorded since 1992.

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Status of White-bellied Spinetail *Synallaxis propinqua* in French Guiana and Amapá (Brazil)

by Johan Ingels, Alexandre Renaudier & Kurazo Mateus Okada Aguiar

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The known range of the furtive White-bellied Spinetail *Synallaxis propinqua*, usually described as an obligate river island species (Remsen & Parker 1983, Rosenberg 1990), comprises widely separated localities from eastern French Guiana and northern Brazil throughout Amazonia to extreme south-east Colombia, eastern Ecuador, north-east Peru and north-east Bolivia, where it is locally fairly common along major rivers (Pacheco 1995, Remsen 2003). It prefers early-successional, low brushy growth, mainly on sandbars and river islands, but also on sandy river margins, consisting of dense *Tessaria* thickets and young *Gynerium* cane, interspersed with grass, tangles and low bushes (Remsen 2003). The species is difficult to observe, with singles or pairs moving on or near the ground, almost never in the open. Its presence is usually revealed by its strange, often-heard, low-pitched and nasal song (Ridgely & Tudor 1994, Remsen 2003). We report here on the current status of this spinetail in French Guiana and adjacent Amapá in Brazil.

French Guiana

Tostain *et al.* (1992) mentioned *S. propinqua* as occurring around Saül and in the basin of the Oyapock River in French Guiana. The only evidence for its occurrence there is specimen CM 68107 in the Carnegie Museum of Natural History (Pittsburgh, USA), and there has been some confusion as to the precise collecting locality. Samuel M. Klages collected this adult female *S. propinqua* at Pied Saut on the Oyapock River on 18 March 1918 (Fig. 1). In his own catalogue, Klages gave this specimen the serial no. 16339. Based on it, Vaurie (1980) mentioned the Oyapock River as the north-eastern limit of the species' range, and Tostain *et al.* (1992) included this spinetail in the avifauna of French Guiana.

Stephens & Traylor (1985) considered Pied Saut as being on the 'Oyapock River above Saint Georges (03°53'N, 51°48'W) at foot of rapids; not located'. However, the locality had already been given as Pierre Saut by Haverschmidt (1972), and later corrected to Pied Saut by Parkes (1973). The 1:100,000 tourist map of the French Institut Géographique National for Guyane: Cayenne – Saint-Georges shows a locality Piedsaut on the north bank of the Oyapock River, c.12 km upstream of Saint-Georges, at the foot of the first rapids on this river. Obviously Piedsaut is a misspelling of Pied Saut, meaning 'foot (of) rapid'. Using the same map, we calculate the coordinates of this locality as 03°48'30"N, 51°52'30"W.

For a total of nearly 32 weeks during the period 1999–2009, JI studied the avifauna within c.25 km around Saül, without finding *S. propinqua*. There is no major river with river islands in this region and JI never found other habitat suitable for this spinetail. The only *Synallaxis* that are common in and around Saül are McConnell's *S. macconnelli* and Plain-crowned Spinetails *S. gujanensis*. The former is known in French Guiana from scattered localities in the interior, and the only known population of the latter in the interior of this French department is around Saül (Dick *et al.* 1984, Tostain *et al.* 1992, Restall *et al.* 2006).

In 2010, on 10–13 March and 13–15 April, AR searched for *S. propinqua*, using playback of its typical song, around Ouanary (c.04°13'N, 51°40'W), on the banks of the Ouanary River, and on the river islands of Biche (c.04°07'N, 51°39'W) and Jonc (c.04°10'N, 51°38'W) on the Brazilian side of the river, all in the bay of the Oyapock River. Similar



Figure 1. White-bellied Spinetail *Synallaxis propinqua*, specimen CM 68107, collected by Samuel M. Klages at Pied Saut, French Guiana, on 18 March 1918, and held in the Carnegie Museum of Natural History, Pittsburgh (© Carnegie Museum)

searches were conducted on 12–13 June inland along the Oyapock River, on Îlets Marécage and Barbosa (c.03°50'N, 51°51'W), c.9 km upstream of Saint-Georges, and at Saut Maripa and Saut Cafésoca (c.03°48'N, 51°53'W) near Pied Saut, c.13 km upstream of Saint-Georges. No *S. propinqua* were heard or seen.

None of the islands in the Oyapock River visited by AR was covered by low brushy vegetation, the preferred habitat of *S. propinqua*. Most islands now possess taller second growth, a habitat largely unsuitable for this spinetail. The vegetation of these islands in the early 1900s, when Klages collected his specimen, is unknown. Because of the lack of recent observations, the list of the birds of French Guiana (CHG 2011) now places this spinetail in category B, i.e. a species not recorded since the publication of Tostain *et al.* (1992).



Figure 2. White-bellied Spinetail *Synallaxis propinqua*, Parazinho Island, Reserva Biológica do Parazinho, Amapá, Brazil, 16 September 2005 (Kurazo M. Okada Aguiar)

Amapá (Brazil)

Novaes (1974) did not mention *S. propinqua* for the Território do Amapá. However, KMOA has recently found it at two localities in the state of Amapá in extreme north-east Brazil, adjacent to French Guiana. On Parazinho (00°53'N, 49°59'W), one of the islands of

the Bailique archipelago in the Amazon River mouth, and part of the Reserva Biológica do Parazinho, the species was found at the fringes of the island in riparian vegetation typical of estuarine areas. It was, however rare, as during a seven-day stay on 15–22 September 2005, KMOA mist-netted just one individual, on 16 September (Fig. 2). The Reserva Biológica do Lago Piratuba, is a c.375,000-ha reserve bordered to the south by the Araguari River, to the east and north by the Atlantic Ocean and to the west by the savannas of Amapá (01°10'–01°50'N, 49°34'–50°34'W). Aguiar *et al.* (2010) found *S. propinqua* in this reserve on 3–13 June 2006 during the wet season. It was seen in riparian vegetation consisting of bamboo and mangrove along the Paratur River and on grass-covered islands in the same river, which were inundated at high tide. However, it was not found there on 5–16 November 2005 and 10–30 November 2006, during the dry season. Within inland areas of the reserve, the following spinetails were also observed: Plain-crowned *S. gujanensis*, Pale-breasted *S. albescens* and Yellow-chinned *Certhiaxis cinnamomeus*.

Discussion

It is possible that the preferred habitat of *S. propinqua* in French Guiana has, over the past century, disappeared through a natural evolution of the vegetation of the islands in the Oyapock River, because no suitable habitat was found during the recent searches along this river by AR. We suspect that *S. propinqua* no longer occurs in French Guiana. *S. propinqua* has also been found in the lower Rio Branco basin in Roraima (Pacheco 1995, Naka *et al.* 2006) and therefore the Brazilian states of Amapá and Roraima form the current northern limit of the species' distribution in the Guiana Shield.

We may even speculate whether a breeding population ever existed along the Oyapock, or whether Samuel Klages perhaps collected an individual searching for suitable habitat. The fluvial system of the Oyapock is less dynamic than that of the Amazon because of its lower flow, which does not permit the formation of new islands or the renewal after flooding of the vegetation of existing islands, needed to attract pioneer species.

S. propinqua is usually described as an obligate river island species, specialised on the understorey of successional vegetation. However, this habitat is ephemeral because islands are constantly moving downstream, and are partially or even wholly inundated both by high tides and during the rainy season(s) (Remsen & Parker 1983, Rosenberg 1990, Aguiar *et al.* 2010). Therefore, this spinetail must also possess the ability to wander in search of new suitable habitat, even away from river islands, such as low riparian vegetation on riverbanks and at edges of islands, as demonstrated by our observations in Amapá.

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A replacement name for *Charadrius leschenaultii* *crassirostris* (Severtzov, 1873), a subspecies of Greater Sand Plover

by Caio J. Carlos, C. S. (Kees) Roselaar & Jean-François Voisin

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Greater Sand Plover *Charadrius leschenaultii* has a large breeding distribution extending from Turkey east to Central Asia. Three subspecies are currently recognised: *C. l. leschenaultii* Lesson, 1826, which breeds in the northern Gobi Desert in Mongolia and in north-west China, and winters in Australasia, South-East Asia and the Indian subcontinent; *C. l. columbinus* Wagler, 1829, which breeds in the Middle East, southern Afghanistan and Azerbaijan, and winters in the Red Sea, Gulf of Aden and the south-east Mediterranean regions; and *C. l. crassirostris* (Severtzov, 1873), which breeds in Turkmenistan to southern Kazakhstan, and winters on coasts of eastern and south-east Africa (C. S. Roselaar *in* Cramp & Simmons 1983, Marchant & Higgins 1993, Piersma & Wiersma 1996, Hirschfeld *et al.* 2000). Hereafter, the last-named is referred to as the Transcaspien Greater Sand Plover.

Severtzov (1873: 146) originally described the Transcaspien Greater Sand Plover as a species named *Eudromias crassirostris*. He listed three type specimens, said by him to have been sent to the Russian Academy of Science in St. Petersburg: the first was collected at Perovsk fort (modern-day Kyzylorda in Kazakhstan; c.44°51'N, 65°30'E) on 30 June 1858, the second was taken at Lake Chatir-Kul at c.3,500 m (modern-day Chatyrkel in south-central Kyrgyzstan; c.40°37'N, 75°17'E) on 26 July 1867, and the third on the eastern shore of the Caspian Sea, in Krasnovodsk Bay near Pel'tsamom in western Turkmenistan, in August 1867. We were unable to locate Pel'tsamom, but the shape of Krasnovodsk Bay varies

greatly due to water-level fluctuations and the sites of many former villages are either inundated or are deserted due to drought. All of the above-mentioned dates are presumably Julian calendar dates, used by Russia until the early 20th century, and thus 13 days should be added to identify the Gregorian date.

Eudromias crassirostris, when included in the genus *Charadrius*, as it is by most authors (e.g. Bock 1958, C. S. Roselaar in Cramp & Simmons 1983, Marchant & Higgins 1993, Piersma & Wiersma 1996), becomes a junior homonym of *Charadrius crassirostris* Spix, 1825, which is now treated as a subspecies of Wilson's Plover *C. wilsonia* of northern and north-east Brazil (Carlos & Voisin 2011). Therefore, according to Arts. 23.1 and 60.3 of the *International code of zoological nomenclature* (ICZN 1999) *E. crassirostris* Severtzov must either be replaced by a pre-existing name or by proposing a new one.

Of all taxa related to Greater Sand Plover, both valid and synonyms, only *E. crassirostris* was partially based on breeding birds, the others being described from migrants / wintering individuals (Hirschfeld *et al.* 2000). At least two localities from which the Transcaspiian Great Sand Plover was described, Perovsk fort and 'east shore of the Caspian', lie within its breeding range, while the other is not known to possess breeding Greater Sand Plovers. However, the bird from Lake Chatir-Kul probably belongs to the Transcaspiian breeding population, because nominate *leschenaultii* and *columbinus* are unlikely to occur there (Hirschfeld *et al.* 2000). A review of the literature (e.g., Sharpe 1896, Hartert 1920, Peters 1934, Hirschfeld *et al.* 2000) indicated that Severtzov's (1873) name has no available junior synonym, because it has been a stable taxon since its original description. In accordance with the ICZN (1999) we therefore propose for it:

***Charadrius leschenaultii scythicus* nom. nov.**

Etymology.—The adjective *scythicus* (feminine *scythica*, neuter *scythicum*) commemorates the Scyths, an ancient horse-riding nomadic people who lived, from the 8th century BC to the 2nd century AD, in a vast area, known at the time as Scythia, which covers present-day Central Asia, Russia and Ukraine. This region also includes all of this plover's breeding range.

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The nest, eggs and nestlings of Fulvous Antshrike *Frederickena fulva* from north-east Ecuador

by Harold F. Greeney, Rudy A. Gelis, Thierry Garcia & Xavier Amigo

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Originally described as a subspecies of Undulated Antshrike *Frederickena unduligera* by Zimmer (1944), Fulvous Antshrike *F. fulva* was recently elevated to species rank, based largely on vocalisations (Isler *et al.* 2009, Remsen *et al.* 2011). Thus, in all but the most modern treatments, the taxon discussed here was referred to as Undulated Antshrike (e.g., Hilty & Brown 1986, Ridgely & Greenfield 2001, Zimmer & Isler 2003). Fulvous Antshrike, as currently defined, is monotypic and occurs in the lowlands of westernmost Amazonia from southern Colombia to northern Peru (Zimmer & Isler 2003). Here we provide the first data on the reproductive biology of this poorly known species based on a nest in the foothills of eastern Ecuador.

Methods and Results

We found a nest of Fulvous Antshrike on 16 June 2011 at the reserve administered by the Proyecto de Conservación del Río Bigal, Fundación Ecológica Sumac Muyu (600 m), near Loreto (00°38'S, 77°19'W), prov. Napo. The nest contained two eggs when discovered, but we took no further data at this time. When we returned on 30 June, at 16.00 h, one egg had hatched. The nestling inside the second egg was partially visible through a large hole it had opened in the shell, and had fully hatched c.15 minutes later. The hatching egg was still sufficiently intact to accurately measure as being 30.5 × 22.8 mm and 7.9 g. The egg was slightly off-white with copious cinnamon and lavender flecks and narrow scrawls, concentrated at the larger end. The nestling was completely devoid of natal down, with flesh-coloured skin, slightly dusker dorsally. The bill was dark orange, yellower near the tip except for the dorsal portion of the mandible, which was dusky and bore a bright white egg tooth. The rictal flanges were bright yellow and the mouth lining was bright yellow-orange. The nestling weighed 6.5 g and the right tarsus measured 11 mm.

The nest was a large, thin-walled cup, and its contents were partially visible from below. It was attached by the rim, via two sparse 'wings' extending up on opposite sides to two narrow, parallel, horizontal branches (6 and 8 mm diameter). These attachment points extended c.3 cm above the rim and consisted of no more than 15–20 rootlets each. The nest fairly uniformly comprised thin, slightly branched rootlets, crisscrossed and interwoven, with only those circling the slightly thickened rim being coiled. The inner portion had a sparse, poorly defined lining of smooth, un-branched flexible fibres of unknown origin, as well as 4–5 black fungal rhizomorphs. The cup was 10 cm in diameter inside by 7.5 cm deep. Externally the nest was 14 cm wide by 9 cm tall. Photographs of the nest, eggs

and adults are available on the Colaboraciones Americanas Sobre Aves website (<http://avesamericanas.lifedesks.org/pages/103479>).

Sited at the edge of an open gap created by a recently felled tree, adjacent to an area of dense second growth, the nest was 1.6 m above ground in a 2.5 m-tall sapling that had a sparse-leaved vine tangled through it. As the nest was not discovered until after several days of woodcutting, it is difficult to determine how visible the nest would have been under natural conditions. Based on the timing, however, it appears that the nest was constructed after the tree was felled, but before human activity trampled the surrounding vegetation. It was fairly exposed from one side, but fairly hidden from the other and we suspect that it would have been well hidden in the tangle under natural conditions.

Both adults brooded and fed the nestlings, generally flushing from the nest only when we approached closer than 2 m. When approached while brooding, both sexes flared their substantial crests, but otherwise remained motionless until suddenly leaving the nest and moving off through the low, dense foliage. They did not begin alarm-calling until out of sight and 5–10 m away. Invariably the second adult joined that flushed from the nest within 1–10 minutes. Only the female spent the night on the nest. Based on vocalisations heard very close to nightfall, after the female was sitting for the night, it appeared that the male spent the night c.50 m distant. However, we cannot be sure that these vocalisations were not given by another individual. During the three days we observed the nest we were unable to identify any prey items with certainty, but all appeared to be small arthropods (<50% of the adult's bill size), brought to the nest singly.

Discussion

Molecular evidence (Brumfield *et al.* 2007, Moyle *et al.* 2009) places *Frederickena* within a clade containing *Hypoedaleus*, *Batara*, *Mackenziaena*, *Cymbilaimus* and *Taraba*, and suggests that it is most closely allied to *Mackenziaena*, with which it was formerly merged (Cory & Hellmayr 1924). Comparative data concerning the form and placement of nests are generally scarce. Haverschmidt & Mees (1994) described a nest of Black-throated Antshrike *F. viridis* that generally matches that described here, in both form and placement (open basket in fork low in shrub). Nests are undescribed for both species of *Mackenziaena*, for Spot-backed Antshrike *Hypoedaleus guttatus* and for Bamboo Antshrike *Cymbilaimus sanctaemariae*. However, G. M. Kirwan (*in litt.* 2012) informs us that a nest of Tufted Antshrike *M. severa* he found in Bahia, Brazil, in January 2011, was broadly similar to that described here of *F. fulva*. The nest of Giant Antshrike *Batara cinerea* appears similar, but is described as including leaves in its construction, though sample sizes are very low (Ihering 1914, Zimmer & Isler 2003). Perhaps because of the species' large geographical range, the nest of Great Antshrike *Taraba major* has been described by multiple authors (e.g., Skutch 1969, Wetmore 1972, de la Peña 1995). In fact, the nest photographed by Buzzetti & Silva (2008) is virtually indistinguishable from the nest of Fulvous Antshrike we observed. Across its range, however, there appears to be some variation, with nests from southern South America tending to be externally decorated with leaves, lichens or moss (Fraga & Narosky 1995, di Giacomo 2005), and those from Costa Rica and Ecuador containing dead leaves woven into the structure (Skutch 1969, Sheldon & Greeney 2008). Slightly less well known, but still with several descriptions available, are nests of Fasciated Antshrike *Cymbilaimus lineatus*, which share the rim-attached, bulky-cup architecture of other species in this clade (Skutch 1972, Oniki & Willis 1982, Greeney *et al.* 2004, Kirwan 2009). However, *C. lineatus* frequently builds its nests more than several metres above the ground (Oniki & Willis 1982, Kirwan 2009; HFG pers. obs.). Thus, available evidence suggests that general nest architecture is similar within this group (Moyle *et al.* 2009, Remsen *et al.* 2011), with only slight variations in materials.

Eggs of species within this clade are slightly better known: Great Antshrike (Oates & Reid 1903, Smyth 1928, Sneath 1935, Hellebrekers 1942); Fasciated Antshrike (Skutch 1972, Wetmore 1972); Giant Antshrike (Ihering 1914); Spot-backed Antshrike (Ihering 1900, Oates & Reid 1903); Black-throated Antshrike (Haverschmidt & Mees 1994). Though descriptions vary somewhat, eggs of these species, like those described here, are white to off-white with various combinations of cinnamon and lavender flecking, generally in small, narrow, hair- or scratch-like markings rather than blotches. Nestlings have not been described, with the exception of *Taraba* and *Cymbilaimus*, for any other species, but it comes as no surprise that the nestling of Fulvous Antshrike was born without natal down as is true for all species of *Thamnophilidae* for which data are available (Zimmer & Isler 2003, Collins 2010). It goes without saying that more information is needed for all species in this especially poorly known group of antshrikes.

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On the name of the Canary Blue Tit *Cyanistes teneriffae* from Gran Canaria

by Albrecht Manegold

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In 2008, a new subspecies of Canary Blue Tit, *Cyanistes teneriffae hedwigii* was described from Gran Canaria on the basis of mitochondrial DNA sequence analyses as well as bioacoustic and morphological data, though originally placed in the genus *Parus* (Dietzen *et al.* 2008). The original spelling of the species-group name is incorrect and must be changed in accordance with the *International code of zoological nomenclature* (ICZN 1999, Art. 32.5.1). The epithet ‘*hedwigii*’ is the genitive case of the Latinised *hedwigi*, which is masculine. According to the authors’ etymological explanation, *hedwigi* is derived from the modern German name Hedwig, which usually, however, is a female name. In fact, the new taxon was dedicated to Ms Hedwig Sauer-Gürth (Dietzen *et al.* 2008). Thus, the correct spelling is *Cyanistes teneriffae hedwigae*, because the feminine genitive ending *-ae* is to be added to the stem of this female modern personal name if used as a species-group name (ICZN 1999, Art. 31.1.2; *cf.* Art. 33.2.2 justified emendation). The epithet *hedwigae* must not be confused with the epithet *hedwigii*, which has been correctly applied for several species of algae, bryophytes and fungi, all of them apparently named for Mr Johannes Hedwig, a German botanist and physician of the 18th century (Mägdefrau 1992).

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Two pre-occupied names in African ornithology

by Robert J. Dowsett

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Two pre-occupied names in current use have come to light during revision of the African taxa for the next edition of Dickinson (2003).

CARDINAL WOODPECKER *Dendropicos fuscescens intermedius* Roberts, 1924: 83. Type locality Weenen (28°51'S, 30°05'E), KwaZulu-Natal, South Africa. Holotype in Ditsong National Museum of Natural History (formerly the Transvaal Museum, and hereafter abbreviated as TM).

This name is pre-occupied by the following, if the genus *Thripias* is merged with the earlier *Dendropicos* (as in Dickinson 2003): Bearded Woodpecker *D. namaquus intermedius* (C. H. B. Grant, 1915: 101), type locality Ugogo, Tanzania; holotype at the Natural History Museum, Tring (BMNH). In that case there is an alternative name: *D. fuscescens natalensis* Roberts, 1924: 84, type locality Red Hill (29°47'S, 31°02'E), KwaZulu-Natal coast, South Africa, holotype in TM. *D. f. natalensis* was treated as a synonym of *D. f. intermedius* by W. R. Tarboton in Hockey *et al.* (2005). However, it seems best for now to continue to recognise the genus *Thripias*, pending a complete study of the genera of African woodpeckers, for which the molecular samples of Benz *et al.* (2006) were incomplete.

FOREST CANARY *Crithagra scotops transvaalensis* (Roberts, 1940: 365). Type locality eastern Transvaal to Zoutpansberg, restricted to Woodbush (23°47'S, 30°04'E) (Skead 1960, Dowsett 2011), South Africa. Holotype in TM.

This name is pre-occupied by the following, regardless of whether one uses *Serinus* for these, or *Crithagra* (following Ryan *et al.* 2004): Streaky-headed Seedeater *C. gularis transvaalensis* (Roberts, 1913: 36); type locality Hennops River (25°51'S, 27°56'E), near Pretoria, South Africa; holotype in TM. The later name has been widely used as valid, in error, and both were included by W. R. J. Dean in Hockey *et al.* (2005). There is no other name available (sources examined including Sharpe 1888, Reichenow 1904, Sclater 1930, Roberts 1940, Rand 1968). The only name introduced since 1940 is *C. s. umbrosa* (Clancey, 1964: 184) from Knysna (34°03'S, 23°01'E) in the southern Cape, at the other extreme of the species' distribution. Hence a new name will be needed, and I propose:

Crithagra scotops kirbyi, nom. nov.

This replaces the pre-occupied *C. s. transvaalensis* (Roberts, 1940), nec *C. gularis transvaalensis* (Roberts, 1913). The new name commemorates the collector of the holotype, Frederick Vaughan-Kirby (1868–1945: 'Mfohloza', the native Zulu name by which he was widely known referring to the sound of his long khaki trousers moving through the grass), a game warden who made a valuable contribution to knowledge of the avifauna of south-eastern Africa.

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A proposed new genus of booted eagles (tribe Aquilini)

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Recent evidence from phylogenetic analysis that several long-accepted eagle genera are non-monophyletic, some of them paraphyletic, have realigned boundaries whilst also erecting groups that have yet to be accommodated in taxonomy. All of the above applies in *Aquila*. Sampling mitochondrial or both mitochondrial and nuclear DNA, four studies (Bunce *et al.* 2005, Helbig *et al.* 2005, Lerner & Mindell 2005, Haring *et al.* 2007) broke this traditional genus into well-defined clades the composition of which, within taxon sampling limits, is generally agreed. Up to three of these clades also absorb some or all of the content of other accepted genera.

We focus here on the spotted eagles: Greater Spotted Eagle *Aquila clanga*, Lesser Spotted Eagle *A. pomarina* and their sister taxon Indian Spotted Eagle *A. hastata* whose species rank has been proposed from morphological differences (Parry *et al.* 2002) and genetics (Väli 2006). Taken together, the above analyses identified these three taxa as a clade apart, by Helbig *et al.* (2005) as isolated from the rest by the common ancestor of other *Aquila* species and *Hieraetus* (Booted Eagle *H. pennatus* and allies), a step also indicated by Haring *et al.* (2007) although not figured in other published trees.

Especially as the studies that sampled them (Helbig *et al.* 2005, Lerner & Mindell 2005, Haring *et al.* 2007) shifted one or other of the large-bodied *Hieraetus*, Bonelli's Eagle *H. fasciatus* and African Hawk-Eagle *H. spilogaster*, and also Cassin's (Hawk-) Eagle *Spizaetus africanus*, into another of the *Aquila* clades, a broadening of *Aquila* to cover all of the species involved could have become the recognised arrangement. We believe this ceased to be acceptable with inclusion in the spotted eagle clade by Bunce *et al.* (2005) of monotypic (Indo-Malayan) Black Eagle *Ictinaetus malayensis*, by Helbig *et al.* (2005) of monotypic (Afrotropical) Long-crested Eagle *Lophaetus occipitalis*, and by Lerner & Mindell (2005) and Haring *et al.* (2007) in one or other of their published trees, of both: *Ictinaetus* shown by

Lerner & Mindell to be sister to the spotted eagles, and *Lophaetus* as sister to all of the rest of this clade. For technical reasons, Haring *et al.* (2007) put aside an alternative finding from their mtDNA control region, not corroborated by their cytochrome-*b* results, that rather than being a clade member Black Eagle might instead be linked to Asian *Nisaetus* hawk-eagles, but added that it would still 'be worthwhile to analyse this enigmatic species in more detail using all currently employed markers (nuclear and mitochondrial)'.

Ictinaetus Blyth, 1843, is the older of these two additional names and as a second nomenclatural option could theoretically have been extended to the entire clade (Haring *et al.*'s proposal that the name *Lophaetus* Kaup, 1847, could be so applied overlooked this priority). Black Eagle has a 'pot-hook' sky-dance display similar to that described for Greater Spotted and Lesser Spotted Eagles (Cramp & Simmons 1980, Wells 1999), and for Indian Spotted Eagle (Naoroji 2006), and looks superficially like a classic *Aquila*. However, its peculiar foot morphology plus proportionately long, square-tipped tail and low-loading wings, widest across the 'hand' and primary projection reaching to the tail-tip when folded, which permit this bird's long-sustained, low-speed glides over canopy surfaces in search of small mammals and other prey (including birds' nests, reportedly snatched whole) mark it out as a different kind of predator. Likewise, no one familiar with Long-crested Eagle in the field could easily agree that this black-and-white, buzzard-like bird with a tall, recurved crest, whinnying, kite-like vocalisations and still-hunting behaviour from a low perch (Ferguson-Lees & Christie 2001) is treatable as an *Aquila*, still less that it belongs in *Ictinaetus*; or, conversely (see Helbig *et al.* 2005), that the definition of *Lophaetus* itself be expanded to include spotted eagles.

Taxonomy and nomenclature

In our opinion, on present knowledge and in the absence of genetic distance 'rules' governing recognition of generic splits, parsimony is not served here by adopting compromise solutions. Either these birds are indeed all placed in *Aquila* or they are all different. To break this impasse and eliminate the paraphyly implied we choose to shrink rather than expand definitions, to retain *Ictinaetus* and *Lophaetus* as monotypic and to assign the three spotted eagles a unique genus of their own, in the apparent absence of anything available from synonymy (Sharpe 1874, Peters 1931), under a new name:

Aquiloides, gen. nov.

Type species.—*Aquila clanga* Pallas, 1811.

Diagnosis.—Medium-sized eagles (length 55–71 cm), with medium to notably broad, rounded wings and shortish, rounded tail. The adult head and body are typically uniform brown to blackish brown (except for the pale nape patch on *pomarina*), relieved only by pale-tipped uppertail-coverts, and immatures have buff-fringed breast feathers. Upper wing-coverts are uniform dark brown or buff-fringed in adults, and white-tipped or white-spotted in immatures (never spotted in genus *Aquila* as redefined here; see below). The bill is proportionately smaller and shorter than typical in revised *Aquila*, the nostril is round (vs. oval in *Aquila* except *africana*, *fasciata* and *spilogaster*), and the tibia and tarsus are slender, not robust, and close-feathered ('trouserless') vs. longer feathered, 'baggy-trousered' in *Aquila*, again except for *africana*, *fasciata* and *spilogaster* (none of which is wholly brown-bodied at any life-history stage). Further, the secondaries of adults are longer than those of juveniles, whereas the reverse is true in *Aquila* (see pl. 420 and 422 in Forsman 1999 for this in Greater Spotted).

Taxonomic content.—The genus *Aquiloides* comprises three currently recognised species hitherto included in *Aquila*: *clanga* (Pallas, 1811), *pomarina* (C. L. Brehm, 1831) and *hastata* (Lesson, 1832).

Etymology.—The name *Aquiloides* is derived from the Latin *aquila*, meaning eagle, and the Greek εἶδος, meaning form or likeness, in deference to these birds' *Aquila*-like appearance and behaviour. Following on from *Aquila* and in accordance with Art. 30.1.4.4 of the Code (ICZN 1999), the gender of the new name is designated to be feminine.

A further, incidental advantage of this smaller genus approach is that it facilitates retention of the name *Hieraetus* for eagles related to *pennatus* (Booted Eagle, type species of the genus), i.e., Little Eagle *H. morphnoides* (including the recently proposed split, Pygmy Eagle *H. weiskei*), Wahlberg's Eagle *H. wahlbergi* and Ayres's (Hawk-) Eagle *H. ayresii*.

Lerner & Mindell (2005) recovered molecular evidence (in line with existing morphological clues) that Rufous-bellied Eagle *H. kienerii* is strongly divergent from these other *Hieraetus*. Subsequently, Haring *et al.* (2007) recommended that the monotypic genus *Lophotriorchis* Sharpe, 1874, be resurrected for it.

This then appears to leave genus *Aquila* of Brisson, 1760 (type species *Falco chrysaetos* Linnaeus, 1758) with the following components: Golden Eagle *A. chrysaetos*, Tawny Eagle *A. rapax* (Temminck, 1828), Steppe Eagle *A. nipalensis* Hodgson, 1833, Spanish Imperial Eagle *A. adalberti* C. L. Brehm, 1861, Eastern Imperial Eagle *A. heliaca* Savigny, 1809, Gurney's Eagle *A. gurneyi* G. R. Gray, 1861, Wedge-tailed Eagle *A. audax* (Latham, 1802) and Verreaux's Eagle *A. verreauxii* Lesson, 1831, plus on currently agreed molecular evidence (Haring *et al.* 2007) *A.* (formerly *Hieraetus*) *fasciata* and *spilogaster*, and *A.* (formerly successively *Cassinaetus*, *Hieraetus* and *Spizaetus*) *africana*.

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Authors are invited to submit papers on topics relating to the broad themes of taxonomy and distribution of birds. Descriptions of new species of birds are especially welcome and will be given priority to ensure rapid publication, and can be accompanied by colour photographs or paintings.

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CONTENTS

Club Announcements.....	1
DONEGAN, T. M. Geographical variation in Immaculate Antbird <i>Myrmeciza immaculata</i> , with a new subspecies from the Central Andes of Colombia.....	3
DEAN, W. R. J., FRANKE, U., JOSEPH, G., GONÇALVES, F. M., MILLS, M. S. L., MILTON, S. J., MONADJEM, A. & OSCHADLEUS, H. D. Type specimens in the bird collection at Lubango, Angola.....	41
AZPIROZ, A. B., MENÉNDEZ, J. L., JARAMILLO, A., PRESA, D., CALIMARES, C., SARALEGUI, A. & ABENTE, J. S. New information on the distribution and status of birds in Uruguay.....	46
CLAESSENS, O., CAMBRÉZY, C., COBIGO, M., MAILLÉ, S. & RENAUDIER, A. So far from the Andes: Black-and-white Tanager <i>Conothraupis speculigera</i> , an unexpected vagrant to French Guiana.....	55
INGELS, J., RENAUDIER, A. & AGUIAR, K. M. O. Status of White-bellied Spinetail <i>Synallaxis propinqua</i> in French Guiana and Amapá (Brazil).....	60
CARLOS, C. J., ROSELAAR, C. S. & VOISIN, J.-F. A replacement name for <i>Charadrius leschenaultii crassirostris</i> (Severtzov, 1873), a subspecies of Greater Sand Plover.....	63
GREENEY, H. F., GELIS, R. A., GARCIA, T. & AMIGO, X. The nest, eggs and nestlings of Fulvous Antshrike <i>Frederickena fulva</i> from north-east Ecuador.....	65
MANEGOLD, A. On the name of the Canary Blue Tit <i>Cyanistes teneriffae</i> from Gran Canaria.....	68
DOWSETT, R. J. Two pre-occupied names in Afrotropical ornithology.....	69
WELLS, D. R. & INSKIP, T. A proposed new genus of booted eagles (tribe Aquilini).....	70

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