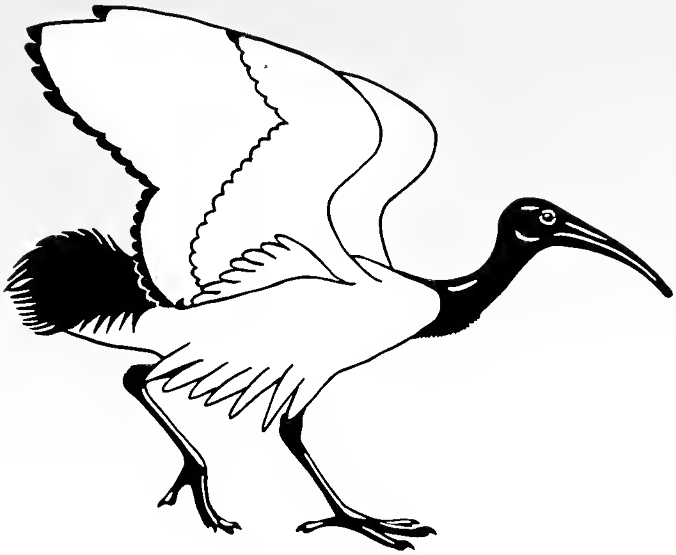
Bulletin of the
British Ornithologists' Club



Volume 134 No. 2
June 2014

FORTHCOMING MEETINGS

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

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

Evening meetings are held in **an upstairs room at The Barley Mow, 104 Horseferry Road, Westminster, London SW1P 2EE**. The nearest Tube stations are Victoria and St James's Park; and the 507 bus, which runs from Victoria to Waterloo, stops nearby. For maps, see http://www.markettaverns.co.uk/the_barley_mow.html or ask the Chairman for directions.

The cash bar opens at **6.00 pm** and those who wish to eat after the meeting can place an order. **The talk will start at 6.30 pm** and, with questions, will last *c*.1 hour.

It would be very helpful if those intending to come can notify the Chairman no later than the day before the meeting.

Tuesday 23 September 2014—6.30 pm—Dr Andrew Gosler—*Ornithology to ethno-ornithology*

Abstract: Why are we ornithologists? Because we are fascinated by birds, yes, but why are humans so captivated by the ecology, evolution and behaviour of another vertebrate group that a UK Government Chief Scientist should complain that a disproportionate amount was spent on bird research to the detriment of other taxa? Whatever the answer to this, the fact that humans everywhere are enthralled by birds should point the way to how we might engage, re-engage or differently engage people in all countries with nature, and so focus resources most effectively for its conservation. Ethno-ornithology is the study of human relationships and associations with birds, be they benign or harmful for the birds themselves. This talk expands on these issues and describes how the speaker's own lifelong engagement with birds led to an interest in the very issue of human interest in birds itself.

Biography: Andy Gosler is University Research Lecturer in Ornithology and Conservation at Oxford University, where he holds a joint position between the Edward Grey Institute of Field Ornithology and the Institute of Human Sciences. His research interests span bird ecology and evolution, through ethno-ornithology to conservation. He is a former Editor of *Ibis*, a recipient of medals from the BTO and BOU and is the originator and Director of EWA: the Ethno-ornithology World Archive.

Saturday 22 November 2014—Joint meeting with the Oriental Bird Club and the Natural History Museum

A one-day meeting in the Flett Theatre, Natural History Museum, South Kensington, London SW7 5BD. The programme will include:

Can the Spoon-billed Sandpiper be saved?—Dr Debbie Pain

AVEntures: new species and rediscoveries of Asian birds?—Dr Pamela Rasmussen

Sumatra: the island that just keeps on giving (but sparingly!). A personal account—John Gregory

Warblers and larks: unexpected relationships and cryptic species—Dr Per Alström

Allan Octavian Hume: the "Pope" of south Asian ornithology—Dr Robert Prŷs-Jones

Full programme details will be made available in the September Bulletin and on the BOC website: http://www.boc-online.org

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Bulletin of the
BRITISH ORNITHOLOGISTS' CLUB

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CLUB ANNOUNCEMENTS

Our long-serving *Hon. Treasurer*, David Montier, has been looking for an opportunity to retire from the Committee for some time and I am pleased to say we have now identified a successor willing to stand. He is Richard Malin, a career banker, who has spent more than 30 years in commercial real estate finance, and much of the last ten years assisting business start-ups and with small business investment. Richard has recently established an invoice-discounting service for small companies. It is therefore proposed to hold a brief Special General Meeting of the Club immediately before the talk at The Barley Mow on 23 September 2014 to propose that Richard takes over as *Hon. Treasurer*. Formal notice of the meeting is given below.

Special General Meeting

A Special General Meeting of the British Ornithologists' Club will be held in the upstairs room at The Barley Mow, Horseferry Road, Westminster, London SW1P 2EE, at 5.30 pm on Tuesday 23 September 2014.

Agenda

The Committee proposes that Richard W. Malin be, and hereby is, appointed *Hon. Treasurer* in place of David J. Montier. No other business will be conducted at this meeting.

Chris Storey

The 975th meeting of the Club was held on Tuesday 19 November 2013 in the upstairs room of the Barley Mow, 104 Horseferry Road, Westminster, London SW1P 2EE. Seven members and four non-members were present. Members attending were: Miss H. BAKER, MR K. F. BETTON, Mr K. HERON JONES, Mr D. J. MONTIER, Dr R. P. PRŶS-JONES, Mr S. A. H. STATHAM and Mr C. W. R. STOREY (*Chairman*).

Non-members attending were: Mrs J. HERON-JONES, Dr C. IERONYMIDOU (*Speaker*), Mrs M. MONTIER and Mrs J. SENA STOREY.

Dr Christina Ieronymidou (BirdLife International) spoke on *Avian responses to land-use in Cyprus, and the potential effects of agricultural change,* which was the focus of her Ph.D. at the Univ. of East Anglia, Norwich. Christina began by describing the context of her work: the ongoing declines in farmland bird populations in Europe. One of the main drivers in the dramatic declines of species that used to be common in farmed countryside, such as Corn Bunting *Miliaria calandra* and Skylark *Alauda arvensis,* is the Common Agricultural Policy (CAP) of the European Union (EU). The original purpose of the CAP was to protect European Economic Community producers, partially by providing subsidies related to production. This led to agricultural intensification, but also made low-intensity farming more expensive, especially in marginal areas. The two opposing types of land-use change, intensification and abandonment, threaten farmland biodiversity, including birds. Since the 1990s, reforms to the CAP have introduced mechanisms to mitigate these threats, including agri-environment measures. Christina explained that in order to optimise these measures, we require an understanding of what land-use practices are most important to birds.

Cyprus, a recently acceded EU member state, still harbours significant populations of bird species that have declined elsewhere in Europe, as it possesses large areas of traditionally managed farmland. The overall aim of Christina's Ph.D. was to provide a first evidence base to inform and support agri-environment schemes for effective conservation of farmland birds in Cyprus, as a case study for the eastern Mediterranean. Christina carried out extensive field work across the island, surveying birds, habitats and land uses, to understand the relative importance of different habitat and landscape elements to farmland bird communities. Christina went on to describe the methods used to develop separate models of habitat association for 24 priority species for conservation, and illustrated the results from one example. She explained that across all species, a wide range of habitats and land uses were important and that habitat diversity was of key value. Farmland habitats, particularly viticulture and groves, and remnant scrub, were the most important, demonstrating the high value of heterogeneous farmland mosaics to breeding and wintering avian biodiversity on Cyprus.

The final part of the presentation focused on land-use changes that have affected the Cyprus countryside over the last 35 years. Christina demonstrated that land under agriculture has decreased substantially, with much of this attributable to declines in marginal low-intensity crops on which much avian biodiversity depends. Christina ended by emphasising that the complex farmland mosaic of Cyprus was created by traditional farming practices that are usually economically marginal today, and that, for effective conservation of priority species and bird diversity, agri-environment mechanisms are necessary to support this heterogeneity.

The 976th meeting of the Club was held on Tuesday 25 February 2014 in the upstairs room of the Barley Mow, 104 Horseferry Road, London, SW1P 2EE. Twenty-one members and ten non-members were present. Members attending were: Miss H. BAKER, Mr K. F. BETTON, Cdr. M. B. CASEMENT, RN, Mr S. CHAPMAN, Prof. R. CHEKE, Mr D. J. FISHER, Mr M. GAUNTLETT, MR G. M. KIRWAN, Mr R. R. LANGLEY, Dr C. F. MANN, Mr D. J. MONTIER, Mr R. F. PORTER (*Speaker*), Mr R. PRICE, Dr R. P. PRŶS-JONES, Mr N. J. REDMAN, Dr S. RUDGE, MR P. SELLAR, Mr S. A. H. STATHAM, Mr C. W. R. STOREY (*Chairman*) and Mr M. J. WALTON.

Non-members attending were: Mr J. BOORMAN, Mr R. BORELLO, Mrs W. BORELLO, Admiral Sir D. DOBSON, Mrs M. GAUNTLETT, Miss B. HARRISON, Mr R. W. MALIN, Mrs M. MONTIER, Mr D. OWEN, Mr A. RANDALL and Miss J. WHITE.

Richard Porter spoke on *Birds of Socotra: populations and distribution*. A detached part of Yemen situated in the north-west Indian Ocean, the Socotra archipelago is rich in endemism: ten species of birds, 307 plants, 27 reptiles and 60 butterflies and moths, for example, make it one of the Middle East's biodiversity hotspots. A total of 221 birds has been recorded. Forty-four regularly breed (plus five probably do so), of which five are globally threatened: Socotra Cormorant *Phalacrocorax nigrogularis*, Egyptian Vulture *Neophron percnopterus*, Socotra Buzzard *Buteo socotraensis*, Abd Al Kuri Sparrow *Passer hemileucus* and Socotra Bunting *Emberiza socotrana*. Only Egyptian Vulture is globally Endangered, but Socotra probably supports the highest concentration of this species in the world. Of the 175 or so migrants and winter visitors, most are rare or uncommon as Socotra is not on a natural migration route.

Detailed studies since 1999 have mapped the distribution of all breeding species. Surveys, including 384 km of line transects of fixed band-width (throughout all habitats, altitudes and geographic range), have determined their populations. The results were published in *Sandgrouse* (35: 43–81, 2013, and in press). The five commonest landbirds are Socotra Sparrow *Passer insularis*, Black-crowned Sparrow-Lark *Eremopterix nigriceps*, Laughing Dove *Spiloptera senegalensis*, Somali Starling *Onychognathus blythii* and Long-billed Pipit *Anthus similis*. All of the endemics have good populations with the two rarest, Abd Al Kuri Sparrow and Socotra Bunting numbering *c*.1,000 and *c*.3,770 individuals, respectively. Six seabirds have globally important populations, and the first breeding site of Jouanin's Petrel *Bulweria fallax* in the world was discovered on Socotra in 2000.

Socotra's birds have been the subject of several taxonomic studies in recent years, amongst which the naming of the resident buzzard as *Buteo socotraensis*, the splitting of Abd Al Kuri Sparrow from Socotra Sparrow and the confirmation of the resident scops owl as a species *Otus socotranus* represent highlights. The main threats to wildlife are overgrazing, woodland destruction and unplanned development. There is now an active conservation and education programme to help combat these, including the identification of six biodiversity reserves and, in 2008, the establishment of the archipelago as a World Heritage Site. With a large UNDP-GEF conservation programme in the pipeline and the establishment of a branch of the Environment Protection Authority on the island, the overall outlook is optimistic.

Geographical variation in morphology and voice of Three-striped Warbler *Basileuterus tristriatus*

Thomas M. Donegan

Received 3 July 2012; final revision accepted 27 April 2014

Summary.—Plumage and vocal variation were studied in a widespread New World passerine, Three-striped Warbler *Basileuterus tristriatus*. Two parallel north–south clines or step-clines in underparts coloration occur in the Central and East Andes of Colombia, with yellower specimens at northern latitudes in both ranges. In the East Andes, the cline is reversed further north, where paler-bellied birds occur. Most West Andes and west-slope specimens differ from those in the Central and East Andes in their more olivaceous flanks (although some show underparts similar to Central Andes specimens). *B. t. daedalus* can be restricted to the West Andes based on '75%' subspecies concepts but not those requiring diagnosability. Andean *B. tristriatus* possess at least three vocalisation types: (i) a rising song starting with a trill and ending in scratchy notes; (ii) a slow song comprising jumbled notes; and (iii) calls of repeated, simple, single notes. West and Central Andes populations are vocally similar and differ non-diagnosably from East Andes populations in the speed of the trill in rising songs. Specimens from Serranía de San Lucas, Colombia, are morphologically similar to northern Central Andes birds, but the rising song has a shorter introductory trill and neither song attains such low minimum acoustic frequencies. Santa Marta Warbler *B. basilicus* has very different songs comprising low-pitched, slow, incessant, complex notes, is mildly differentiated in biometrics and strongly differentiated in plumage from *B. tristriatus*, supporting its current specific treatment. The rising song of Three-banded Warbler *B. trifasciatus* lacks an initial trill and its slow song has a different note shape to *B. tristriatus* but further research in a potential contact zone in southern Ecuador is required. Within *B. tristriatus*, northernmost populations assigned to *melanotis* and *chitrensis* in Costa Rica and western Panama give only the 'slow song' type, but these are delivered diagnosably faster than in any other population. *B. t. tacarcunae* from eastern Panama and north-western Colombia has a different song, comprising an incessant, long jumble of notes interspersed with short churrs. Populations either side of the Huancabamba depression in Peru show only minor differences in voice, but those either side of the Apurímac show significant but non-diagnosable differences in song speed. Bolivian populations have strikingly different rising songs that are quantitatively diagnosable. The rising song of Venezuelan Three-striped Warblers recalls that of *B. trifasciatus* in its slow delivery. Differences in vocal repertoire and quantitative measures support species rank for Costa Rican Warbler *B. melanotis* and Tacarcuna Warbler *B. tacarcunae*. Bolivian Warbler *B. punctipectus* is also a candidate for species rank.

Three-striped Warbler is widespread and locally common in premontane to montane forests of the Andes and elsewhere, from Costa Rica and northern Venezuela south to Bolivia. Many subspecies are currently recognised, all of them described >60 years ago. These are, from north to south: *melanotis* Lawrence, 1868 (type locality: Cervantes / Birris, Costa Rica), *chitrensis* Griscom, 1927 (Veraguas, western Panama), *tacarcunae* Chapman, 1924 (Tacarcuna


A
B
C
D
E
F
G
H

Legend to plates on facing page and above

Figure 1. Variation in Three-striped Warbler *Basileuterus tristriatus* in the Colombian Andes. Tacarcuna (*tacarcunae*): A. Cerro Tacarcuna, Chocó (© J. M. Ruíz-Ovalle / Fundación Ecotrópico, Colombia). West Andes (*daedalus*): B. RNA Loro Orejiamarillo, Jardín, Antioquia (© G. Suárez / ProAves). C. RNA Eriocnemis, Munchique, Cauca (© ProAves). D. RNA Pangan, Nariño (© J. C. Luna / ProAves). San Lucas (subsp.): E–F. Santa Cecilia, Bolívar (© B. Huertas / Colombian EBA Project) (different individuals). Central Andes (*daedalus*): G. Cay, Ibagué, Tolima (© A. Quevedo / ProAves). H. Cascada, Tolima (© Photographer unknown / ProAves). East Andes (*auricularis*): I. El Talismán, Serranía de los Yariguíes, Santander (© B. Huertas / Colombian EBA Project). J. Virolín, Santander (© N. Silva / ProAves). K. Serranía de los Churumbelos, Cauca (© P. Salaman / Colombian EBA Project). Head of Magdalena Valley (*auricularis*): L. Finca Merenberg, Huila (© P. Salaman / Colombian EBA Project).

Mountains, southernmost Panama), *pariae* Phelps & Phelps Jr., 1949 (Paria Peninsula, Sucre, Venezuela), *bessereri* Hellmayr, 1922 (Caracas, Venezuela), *meridanus* Sharpe, 1885 (Mérida, Venezuela), *auricularis* Sharpe, 1885 ('Bogotá'), *daedalus* Bangs, 1908 (San Antonio, río Cali, Colombia), *baezae* Chapman, 1924 (Baeza, east Ecuador), *tristriatus* (Tschudi, 1844) (Junín, Peru), *inconspicuus* J. T. Zimmer 1949 (Inca Mine, Inambarí Valley, [presumably = Cerro Inca Mina, Puno], southern Peru), *punctipectus* Chapman, 1924 (Cochabamba, Bolivia) and *canens* J. T. Zimmer 1949 (Samaipata, Santa Cruz, Bolivia) (Hellmayr 1935, Dickinson 2003, Curson *et al.* 1994, Restall *et al.* 2006, Curson 2010). Because a useful map of its distribution was published recently by Gutiérrez-Pinto *et al.* (2012), none is given here.

Currently recognised subspecies differ mainly in shade of their underparts and head-stripes, which vary between yellow, orange, buffy and grey, and base colour to the head, which is black, dusky or olivaceous. Some Central American populations also differ in their upperparts coloration, whilst those in southernmost Peru and Bolivia have speckled breasts (Curson *et al.* 1994). Two taxa treated as separate species but which have been considered related are Santa Marta Warbler *B. basilicus* (Todd, 1913) of the Santa Marta Mountains in Colombia and Three-banded Warbler *B. trifasciatus* Taczanowski, 1880, which occurs in drier habitats on the west slope of the Andes in south-west Ecuador (subspecies *nitidior* Chapman, 1924) and north-western Peru (nominate).

Ornithologists have long been puzzled by the phenotype of *B. tristriatus* populations in the northern Central Andes. Chapman (1924) noted that a specimen from La Frijolera, Antioquia, Colombia (AMNH 134101) was an 'interesting exception' due to its bright yellow underparts. He considered '…that our remaining thirty Colombian specimens agree essentially among themselves and that not one closely approaches the Ecuadorean, not to mention Peruvian, bird indicates … that the high colors of the Antioquia specimen are only a striking example of individual variation'. Todd (1929) disagreed, considering that it would be 'odd to find an individual with the characters of another and very different form turning up within the range of an ally". Zimmer (1949) did not assign this specimen to any subspecies, noting that: 'it may be that a series of specimens from the region of La Frijolera would show a resident population with the characters of this unique example. Such a series … should be secured and studied before final disposition of the case is made'. Hellmayr (1935) did not comment on the Frijolera specimen, but confusingly listed it both under nominate *tristriatus* (as per Chapman's comparison) and subspecies *daedalus*.

No-one conducted any study into *B. tristriatus* of the nature proposed by Todd (1929) until Salaman *et al.* (2001a) reached the lower montane slopes of Serranía de San Lucas, an isolated mountain range north of the Central Andes. We trapped several Three-striped Warblers, preparing two specimens, which we considered 'may relate to an undescribed subspecies' with 'bright yellow underparts'. Salaman *et al.* (2002) subsequently considered that birds in San Lucas 'differ from … subspecies of the three Colombian Cordilleras, with brighter and more extensive yellow underparts' and 'represent an undescribed subspecies', but did not provide a name. Curson (2010) also referred to this population as undescribed.

Since Salaman *et al.* (2001a, 2002) rediscovered the northern, yellow-bellied population of *B. tristriatus*, I have been collating data to assess geographical variation in voice and morphology of *B. tristriatus* in Colombia and elsewhere. In January 2010, during another expedition to the San Lucas highlands (see Donegan 2012), six individuals were mist-netted, all of which had bright yellow underparts (Fig. 1E–F). Sound-recordings of all three main vocalisation types were made (Figs. 3A, 5E–F, 7E–F). These materials, together with other recent specimen and mist-net data, facilitate a better understanding of geographical variation in voice and plumage in the group.

In a molecular phylogenetic study of *B. tristriatus*, Gutiérrez-Pinto *et al.* (2012) found that the San Lucas specimens occupy a basal position with respect to other north Andean populations. Morphologically similar birds in the northern Central Andes referred to the same population as the Frijolera specimen clustered with other Central Andean specimens. The molecular study was published after a previous iteration of this manuscript had been submitted for publication and reviewed. This paper was revised to discuss the molecular study. Because Gutiérrez-Pinto *et al.* (2012) have declared their intent to 'present a description of [the San Lucas] new taxon elsewhere', I refrain from making such a designation here.

Methods

Specimens were studied at the following institutions: American Museum of Natural History, New York (AMNH); Natural History Museum, Tring (BMNH); Instituto de Ciencias Naturales, Universidad Nacional, Bogotá (ICN); Universidad Industrial de Santander (UIS); and Smithsonian Institution, National Museum of Natural History, Washington (USNM). Details of studied specimens appear in Appendix 3. Biometric data were taken only at BMNH, AMNH, ICN and UIS. The following measurements were taken: wing-chord and tail length (to nearest mm), tarsus length, culmen length from skull to tip (to nearest 0.5 mm) and, from specimen labels, mass (g), where available. Biometric data from my field work in all three Andean cordilleras with additional mist-net data from ProAves were also analysed.

Biometric and vocal data were subdivided according to currently recognised subspecies, well-known biogeographic divides and the phylogeny of Gutiérrez-Pinto *et al.* (2012). Various diagnosability tests were undertaken for pairs of biometric and vocal variables, following Donegan (2008). For biometrics, three separate analyses were conducted using different datasets: (i) live capture data; (ii) all specimens; and (iii) male specimens.

Sound-recordings assumed to involve *B. basilicus*, *B. trifasciatus* and all described subspecies of *B. tristriatus* except *pariae* were studied (Appendix 3). Recordings were sorted geographically and by vocal type, then compared using subjective criteria (note shape and song structure) and quantitative data using the methodology detailed in Appendix 2.

Most *B. tristriatus* populations possess three different types of vocalisations (Schulenberg *et al.* 2007). The best-known song ('rising song': Figs. 3–4) usually commences with a fast trill ('A' in Fig. 3C), comprising notes of narrow bandwidth, which becomes slower in speed, wider in bandwidth and higher pitched, then usually disintegrates into a series of more scratchy, individually audible notes ('B' in Fig. 3C). A separate vocalisation ('slow song': Fig. 5) is similar in some populations to the last part of rising song, being a series of individually audible, jumbled, scratchy notes of variable acoustic frequency and note shape. In some recordings, the slow song follows shortly after, or is delivered at the same time as a rising song in a duet. As noted by Schulenberg *et al.* (2007), the rising song appears to be given by males and slow song by females, but this is difficult to confirm due to the lack of sexual dichromatism. Finally, all populations give sharp *tsip* notes ('call': Fig. 7). These are given intermittently while foraging but are delivered in more rapid succession in alarm or flight. Other calls with notes similar to individual notes in songs are also sometimes given. Fast, short, high-pitched trills are also particularly prevalent in the East Andes, but were not measured given the small to non-existent samples for most populations. The description by Curson *et al.* (1994) of a *che-weep* call does not relate to any vocalisation in my sample.

Geographical variation in plumage of *B. tristriatus*

Central America.—The northernmost population, *B. t. melanotis*, is restricted to montane Costa Rica. Ridgway (1902) treated it as a separate species. Subspecies *chitrensis* (which is junior to *melanotis*) was described from the same mountain complex but further east. It differs in having darker posterior underparts and flanks. Both subspecies have browner upperparts than other taxa, with a more buffy (almost orange) crown-stripe and supercilium (Curson *et al.* 1994).

B. t. tacarcunae is based on a type collected on the Panamanian side of Mt. Tacarcuna (Chapman 1924) and occurs at higher elevations in the Darién and San Blas region of Panama, as well as just inside Colombia. It has a buffy-yellow crown-stripe, more olivaceous head coloration and darker, greener underparts than Andean birds (Figs. 1A, 2). Compared to *chitrensis*, it has a more olivaceous head, more orange crown-stripe and yellower throat (Curson *et al.* 1994).

Venezuela.—Populations on the Paria Peninsula, in montane Sucre, the Coastal Cordillera and Mérida Andes are mildly differentiated from one another in plumage, but have greyish face-sides, in contrast to the uniform black or dusky head elsewhere in the Andes. They also have dull greyish or cream, not yellow, underparts.

The northern Andes.—In the Colombian Andes, plumage variation in *B. tristriatus* is complex. The main differences are in coloration of the underparts and forecrown, which are concolorous in most populations. There is no consensus concerning the recognition or distribution of subspecies in the region.

The type specimen of *daedalus* was collected along the río Cali, in the West Andes (dpto. Valle del Cauca), so this name is available for westernmost populations. Chapman (1924) treated *daedalus* as a synonym of *auricularis* (a name based on a specimen from the East Andes: see below), and was followed by Meyer de Schauensee (1964) and Hilty & Brown (1986). However, Todd (1929), Hellmayr (1935, 'with considerable reluctance'), Zimmer (1949), Ridgely & Greenfield (2001), Salaman *et al.* (2001b, 2010), Krabbe & Nilsson (2003), Restall *et al.* (2006) and McMullan *et al.* (2010, 2011) all recognised *daedalus* for Colombian West Andes and west Ecuadorian populations. The largest museum collections of Colombian birds are also inconsistent in this respect: in BMNH and ICN, specimens labelled *daedalus* are restricted to the West Andes and west slope, whilst at USNM, specimens from the West and Central Andes bear this name and at AMNH all Colombian material is labelled *auricularis*.

West Andes and west Ecuadorian specimens have a darker and more extensive olivaceous wash to the flanks than those from the Central and East Andes or east slope (Fig. 8). However, a handful of West Andes specimens at ICN and AMNH are indistinguishable in underparts coloration from Central Andes birds from Quindío. Owing to a predominance of specimens with olivaceous flanks, *B. t. daedalus* can be restricted to the West Andes and western slope under 75% subspecies concepts but not under those requiring diagnosability. Fjeldså & Krabbe (1990) and Curson (2010) considered *daedalus* also to occur on the west slope of the Central Andes, with *auricularis* replacing it on the east slope of that range. This hypothesis is not supported, as discussed below. Curson *et al.* (1994) considered *daedalus* to occur broadly over the Central Andes and restricted *auricularis* to the East Andes and east slope.

Striking north / south variation in underparts coloration is evidenced by specimens from both the Central and East Andes and eastern Ecuador (Fig. 2). Various names are available for East Andes and east slope populations. The oldest, *tristriatus*, has its type locality in Junín, Peru, but is widely considered to range north to southern Ecuador (e.g. Ridgely & Greenfield 2001).

According to the original description (Sharpe 1855), *auricularis* has 'paler and duller' underparts than nominate *tristriatus*. The *auricularis* type (and other 'Bogotá' specimens at AMNH) are consistent with more recent East Andes specimens from Cundinamarca to Boyacá, so the null hypothesis of a Colombian East Andes locality for 'Bogotá' specimens is not contradicted. The most junior name for birds in this region, *baezae*, has been applied to populations with rather bright yellow underparts on the Ecuadorian east slope. Topotypical material pertaining to all these names is quite distinct in plumage. However, Ecuadorian specimens with underparts intermediate between 'Ecuadorian *tristriatus*' and '*baezae*' are present in collections and widely reported in the literature (e.g. Ridgely & Greenfield 2001).

A specimen from the southernmost East Andes (Serranía de los Churumbelos) has equally dull underparts as those from Cundinamarca and northern Ecuador (Figs. 1K, 2).

Similar specimens occur at the head of the Magdalena Valley in the southernmost Central Andes of dpto. Huila (Fig. 1L). As is the case for many species in the East Andes, there is a notable lack of specimens (and sound-recordings) from between Churumbelos (dpto. Cauca) and the Picachos depression (dpto. Meta), although little variation is evident between such localities. Further north, from Cundinamarca to Boyacá and southern Santander, there is a gradual but notable increase in yellow underparts saturation with increasing latitude, which peaks in Serranía de las Quinchas (dpto. Boyacá) and the Virolín region (dpto. Santander) (Figs. 1J, 2). North of Virolín, underparts become less intensely yellow in the Yariguíes Mountains and Bucaramanga region. From Bucaramanga north to the Perijá range in Cesar, specimens show little further variation. *B. t. auricularis* is the senior name for east slope and East Andes populations. *B. t. baezae* would be treated as consubspecific with *auricularis* using concepts that require diagnosability or do not recognise points on a cline (e.g. Remsen 2010).

In the Central Andes, specimens and photographs of birds from near the head of the Magdalena Valley in dpto. Huila, in the south of this range, are similar to east-slope birds. More yellowish underparts on average occur in photographed birds from dpto. Tolima (Fig. 1G–H) and specimens from dptos. Valle del Cauca and Quindío (Fig. 2). There is no material available at *c.*02–04°N on the east slope of the Central Andes. Birds in Antioquia and San Lucas have the brightest yellow underparts, these being apparently indistinguishable morphologically. Gutiérrez-Pinto *et al.* (2012) drew attention to similarities between the San Lucas and northern Central Cordillera specimens, but considered them 'phenotypically distinct', citing Salaman *et al.* (2002) and Curson (2010). However, Salaman *et al.* (2002) had no northern Central Andes specimens available for direct comparison[1] and Curson (2010) based his summary on the literature.

It is not currently known if variation in underparts coloration in the Central Andes is clinal or step-clinal owing to the lack of material from southern Antioquia and Caldas (though USNM 436890, 427320 from Hacienda Sofia, río Samaná, are not as intensely yellow as those from Frijolera). The attainment of brighter yellow underparts occurs at similar latitudes to the East Andes cline.

Morphological similarities among birds from Virolín / Quinchas (East Andes) and the northern Central Andes resulted in a hypothesis (reflected, for example, in Donegan & Huertas 2005) that an undescribed subspecies with an upper Magdalena distribution on both Andean slopes could be involved. The subspecies limits suggested by Fjeldså & Krabbe (1990) and Curson (2010) may have been based on a similar understanding. However, specimens and mist-net captures from Serranía de los Yariguíes and Perijá, the nearest localities in the East Andes to Anorí and San Lucas, have duller underparts.

Peruvian and Bolivian Andes.—Plumage variation was discussed by Hellmayr (1935), Zimmer (1949), Fjeldså & Krabbe (1990), Curson *et al.* (1994) and Gutiérrez-Pinto *et al.* (2012). The nominate subspecies is generally treated as occurring over most of Peru. Fjeldså & Krabbe (1990) and Schulenberg *et al.* (2007) considered morphologically different birds (attributed to *B. t. inconspicuus*) to occur only in Puno in southernmost Peru. Curson *et al.* (1994) and Fjeldså & Krabbe (1990) thought that specimens from this region intergrade with Bolivian forms such as *punctipectus*, raising doubts as to the validity of the latter. However, there are no known intermediates between the *tristriatus* and *inconspicuus* groups in Puno.

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[1] No *B. tristriatus* were reported by Salaman *et al.* (1999a) from the northern Central Andes. The earliest modern specimens from the Anorí region are dated 2002, based on Cuervo *et al.* (2008). At the time of their collection, Salaman *et al.* (2002) had already been submitted for publication.

Figure 2. ICN series showing underparts coloration of Three-striped Warbler *Basileuterus tristriatus* in Colombia. Top row, left: West Andes (*daedalus*, south to north, from left to right): Nariño (5), Cauca (1), Valle del Cauca (6), Antioquia (1). Top row, right: Tacarcuna (*tacarcunae*): Chocó (1). Second row: Head of Magdalena Valley (*auricularis*): Huila (1). Central Andes (*daedalus*, south to north from left to right): Quindío (4), Antioquia (10). San Lucas (subsp.) Bolívar (2). Bottom two rows: East Andes (*auricularis*, south to north from bottom to top and left to right). From bottom row: Cauca (1), Meta (1), Cundinamarca (4), Boyacá (Pajarito: 4; Cusiana: 5); second from bottom row: Boyacá (Quinchas: 1), Santander (Virolín: 5, Bucaramanga: 5, Suratá: 1, Yariguíes: 2), Cesar / Perijá (5) (T. M. Donegan)

Biometric data

No population of *B. tristriatus* reaches even Level 2 (50%) diagnosability (Donegan (2008) for any biometric variable when compared with any other population, using any of the three biometric datasets (all specimens, males, mist-net data). Only *B. basilicus* of Santa Marta shows notable deviation from other populations in its biometrics, satisfying the Level 5 test of statistical diagnosability for tail length vis-à-vis *baezae* and *tacarcunae* based on the dataset of all specimens. It also met the Level 2 (50% diagnosability) test from all *tristriatus* populations in tail length based on all data and from some of them in tarsus length based on all specimens and only males.

Vocal differences between *B. tristriatus* and other species

Two populations considered to be related to *B. tristriatus* by previous authors—namely Santa Marta Warbler *B. basilicus* and Three-banded Warbler *B. trifasciatus*—as well as two populations of *B. tristriatus* (*B. t. melanotis* including *chitrensis* and tentatively *B. t. tacarcunae* of Central America) differ in their vocalisations from other populations. The main song of *B. basilicus* (Fig. 6A–B) is broadly equivalent to 'slow song' of *tristriatus*. However, it is delivered as an incessant series of up to 200+ notes, not in short bursts. Moreover, the notes tend to be complex and long, often including multiple 'turning points'. In the quantitative analysis, max. acoustic frequency was diagnosable from most (but not all) other populations, whilst number of notes, song length and min. acoustic frequency displayed substantial but usually not diagnosable (generally Level 2) differentiation. A brief playback study in Santa Marta using the recording in Fig. 6A revealed an aggressive territorial response (Fig. 6B), suggesting that this song is given by males. In contrast, the equivalent 'slow song' appears to be given by females in *B. tristriatus*. Simultaneous with the presumed male song, another individual (presumably female) often duets with a call comprising equally incessant, up-down strokes whose undertone generally is below male song and overtone above it (Fig. 6C). No equivalent type of vocalisation or such closely coordinated duetting occurs in any other populations studied here. Calls of *B. basilicus* (Fig. 7A) are also higher in frequency and of longer duration than *B. tristriatus* (Fig. 7C–N), being more distinct than those of Golden-crowned Warbler *B. culicivorus* (Fig. 7Q), which is often sympatric with *B. tristriatus* in Colombia. These vocal differences support species rank for *B. basilicus*.

The song of *B. trifasciatus* was considered by Ridgely & Greenfield (2001) to be 'similar' to that of *B. tristriatus*. This is borne out by quantitative study, which revealed no significant differences. However, rising song differs structurally in not including any appreciable initial trill (Fig. 4K–L). Venezuelan populations (Fig. 5 C– D) and some Peruvian recordings (Fig. 4G) approach *B. trifasciatus* in lacking a strong or long initial trill to rising song, but always include at least a small number of simple notes that increase in acoustic frequency. Slow song of *B. trifasciatus* is structurally different from all *B. tristriatus*. Although the coordinated duets of *B. basilicus* do not occur, note shape is closer to *B. basilicus*, comprising repeated up-down strokes of broad bandwidth (Fig. 7P), often interspersed with calls.

Ridgely & Greenfield (2001) queried whether *B. tristriatus* and *B. trifasciatus* might overlap in southern Ecuador. A recording identified as *B. tristriatus* from Azuay (ML82620), where *B. tristriatus* occurs, is typical of *B. trifasciatus* in its structure and all variables except song speed (15.5 notes / second vs. 7.6–13.7 for 47 *trifasciatus*). This recording could represent geographical variation and a northernmost record. Notably, the southern (nominate) subspecies has on average slower song. Alternatively, the recording may be of an individual intermediate between *B. trifasciatus* and *B. tristriatus daedalus* (the song speed of which averages 16.9 notes / second for trills (11.1–19.7) or 13.2 notes / second for scratchy notes (8.7–17.9). Further investigation is required into this potential contact zone.

Vocal variation in *B. tristriatus*

Central America.—Central American *B. t. melanotis* and *chitrensis* give rapid jumbled notes (Figs. 6D–F) equivalent structurally to the slow song of other populations. Call notes are also given (Fig. 7B). However, no rising song occurs in any Central American recording,

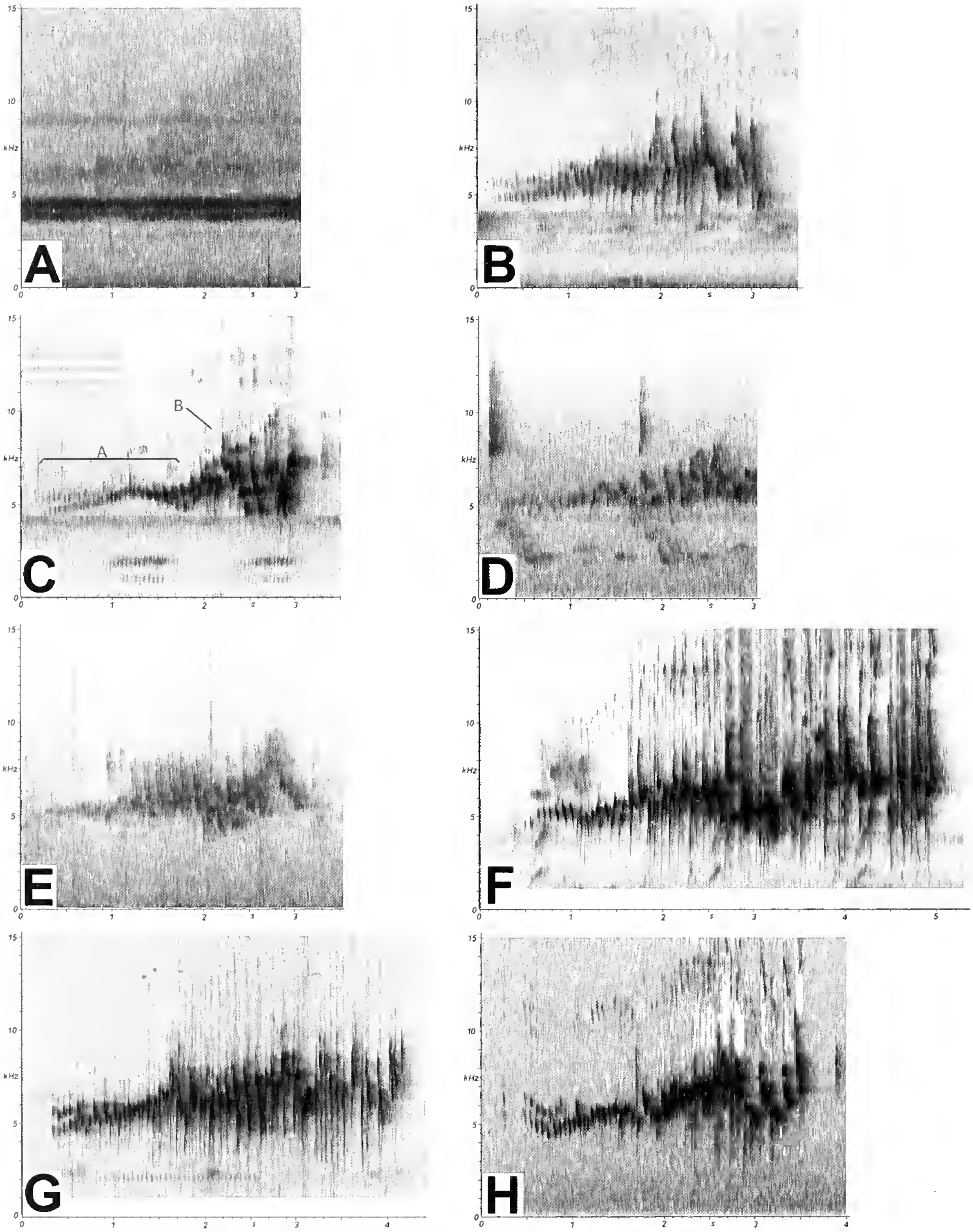

Figure 3. Rising songs of West and Central Andes and west slope populations. San Lucas, Colombia (subsp.): A. Santa Cecilia, Serranía de San Lucas (XC176120: T. M. Donegan). Central Andes, Colombia (*daedalus*): B. Hacienda Termópilas, El Laurel, Neira, Caldas (IAVH 7979: M. Álvarez). C. La Romera, Medellín, Antioquia (Boesman 2012: 3197-4). D. Reserva La Forzosa, Anorí, Antioquia (XC55260: B. López-Lanús). E. Reserva Bremen, Buenavista, Quindío (IAVH 7293: M. Álvarez). West Andes, Colombia (*daedalus*): F. El 18, Valle del Cauca (XC22420: A. Spencer). West slope (*daedalus*): G. Ricaurte, Reserva Natural La Planada, Nariño, Colombia (Álvarez *et al.* 2007, disc 7: 51a). H. Tandayapa Lodge, Pichincha, Ecuador (XC6717: N. Athanas). Sections 'A' and 'B' on 3C denote the 'trill' and 'scratchy' parts, respectively, of the rising song.

suggesting a different vocal repertoire. The song is faster than slow song of any other *B. tristriatus* population, with no overlap and statistical diagnosability from all populations (except *tacarcunae*, for which sample size was small). Songs are also higher pitched on average.

B. t. tacarcunae (of north-westernmost Colombia and southern / eastern Panama) has a different song. The single recording is incessant and scratchy. Although subdivided into two for analyses due to a small break, the sole recording could be considered *c.*300 notes long, greatly exceeding the number of notes and length in any other *B. tristriatus* population. It also has some more complex notes than those in other populations, with low churrs interspersed (Fig. 6G). It is closer to the male song of *B. basilicus* in length and structure than to *B. tristriatus*. However, the song is faster and higher pitched than the former. No other vocalisations are known.

Venezuela.—Recordings from the Mérida Andes and Coastal Cordillera are cohesive but show considerable intra-population variation (Fig. 5A–D). Notably, the distinction between slow and fast songs is less marked than in other Andean populations, with all being similarly (slow) paced with just a few short notes introducing rising songs, which can be considered equivalent to an opening trill. Rising song speed does not change dramatically between the trill and scratchy part. There are notable structural similarities to the rising song of *B. trifasciatus*, which shares a grey ground colour to its head. Songs have variable note shapes, sometimes principally characterised by long downstrokes (e.g. XC65916). Recordings of both song types also often include a falling cadence—a sequence of notes of progressively lower acoustic frequency—towards their middle (Fig. 5A–C), although in rising songs (Fig. 5D) this is weaker. Such cadences occur rarely in some other populations (e.g. XC112289: west Andes of Ecuador) and primarily characterise slow song in Bolivian populations, but are rare in nearby populations. In the quantitative analysis, rising song was found to have diagnosably slower opening trills than nearby East Andes (and various other) populations and significantly slower scratches.

Recordings of rising songs from Tamá National Park (Fig. 4A) are typical of faster-paced East Andes and east-slope recordings, confirming that vocalisations described for Venezuela are restricted to populations north and east of the Tachirá depression. *B. t. auricularis* has been listed for south-west Venezuela (e.g. Fjeldså & Krabbe 1990, Dickinson 2003) and Táchira (Hilty 2003, Restall *et al.* 2006) but only occurs on Tamá (and presumably Perijá) in this country.

No recordings are available from the Paria Peninsula or mountains of Sucre, which support vocally distinctive populations of other species (e.g. Donegan 2008). *B. tristriatus* there is only mildly differentiated in plumage from those in the Coastal Cordillera (Curson *et al.* 1994) and is considered close to other Venezuelan populations (Gutiérrez-Pinto *et al.* 2012).

Northern Andes.—*B. tristriatus* throughout most of the rest of the Andes to southern Peru is vocally fairly uniform, with all populations giving all three vocalisations discussed in the Methods (Figs. 4–5, 7). However, there are some notable differences in quantitative variables. Despite the plumage variation observed in the Colombian East Andes and east slope south to northern Peru, all rising songs, slow songs and calls from this broad region are similar (e.g. Figs. 4A–G, 5I–K, 7J–K). Rising songs in the East Andes usually have faster trills (Level 2) than Central and West Andes populations. The two last-named populations are vocally quite similar, with only small statistically significant differences in a few characters.

Slow song is more or less consistent in quantitative variables throughout the East Andes and east slope south to the Huancabamba depression, with individual notes

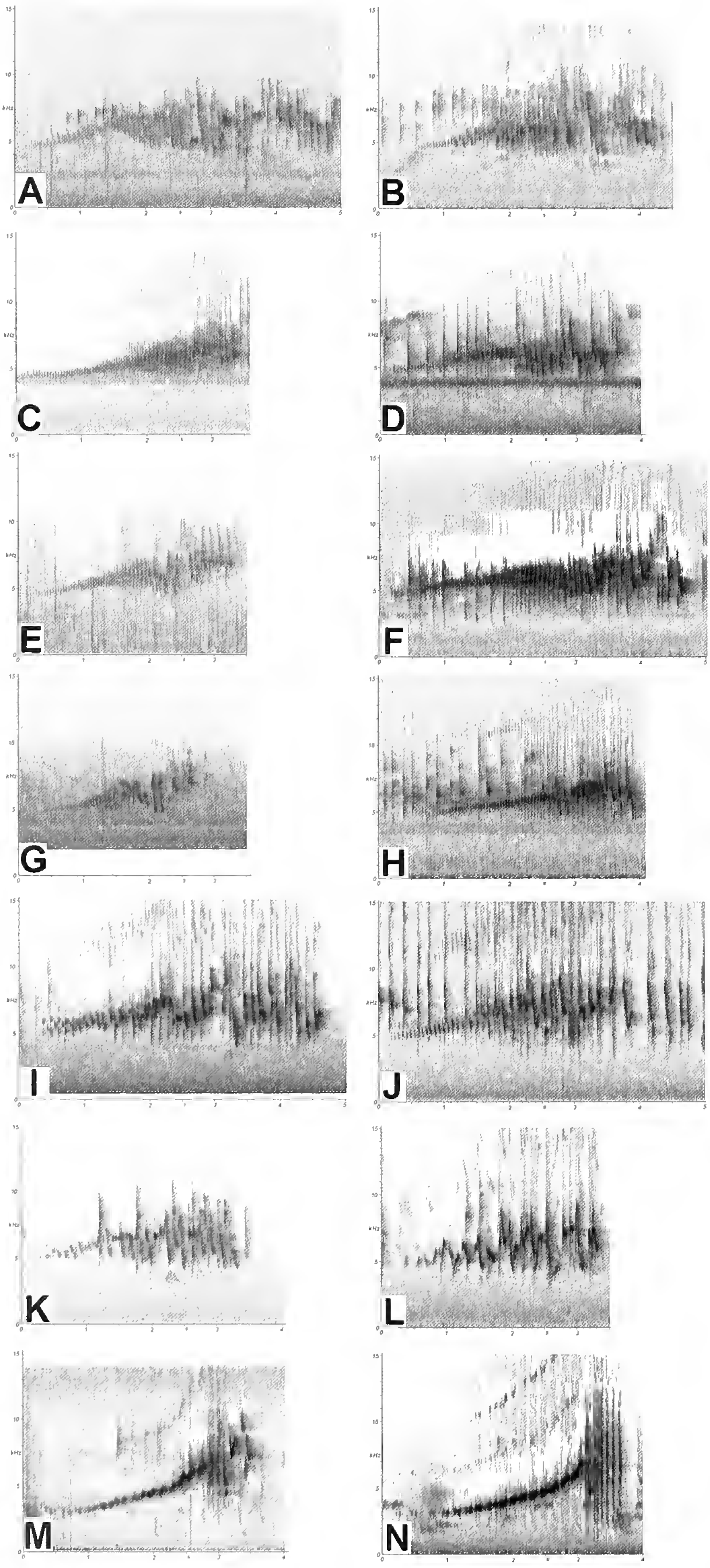

Figure 4. Rising songs of East Andes, east slope and southern populations. Colombia (*auricularis*): A. Sisavita, Carrizal, Cucutilla, Norte de Santander (IAVH 9098: S. Córdoba; also includes calls at start and slow song of second individual towards end). B. La Aurora, above Galán, Serranía de los Yariguíes, Santander (XC25502: T. M. Donegan). C. Medina, Cundinamarca (ML80874: M. Álvarez). D. PNN Los Picachos, Finca Andalucia, Caquetá (ML89242: M. Álvarez). E. PNN Cueva de los Guácharos, Acevedo, Huila (IAVH 7057: M. Álvarez). Ecuador ('*baezae*'): F. Cordillera Guacamayos, Napo (Krabbe & Nilsson 2003: 31-7). Peru north of Huancabamba depression ('*baezae*'): G. East slope of Cerro Chinguela, Lucuma, Cajamarca (ML21713: T. A. Parker). Peru south of Huancabamba depression (*tristriatus*): H. 15 km north-east of Jirillo, San Martín (ML42070: T. S. Schulenberg). I. Below Calabazas, Junín (ML147187: M. B. Robbins). Peru south of Apurímac (subsp.): J. San Pedro, south-west of Pilcopata on Cosñipata Highway, Cusco (ML85067: A. J. Begazo; also includes calls of second individual). West slope of Andes in southern Ecuador (*B. trifasciatus nitidior*): K. Loja, El Cisne–Ambocas road, Ecuador (XC81322: L. Ordóñez-Delgado). West slope of Andes in northern Peru (*B. t. trifasciatus*) L. Bosque Cachil, Cajamarca (XC75966: C. J. Schmitt). Bolivian Andes: M. Urpuma, Sandillani, Cotapata NP, La Paz (XC44438: T. M. Donegan). N. Miguelito, Cochabamba (XC1623: S. Mayer).

appearing rather vertical in sonograms (Fig. 5I–K). Recordings from San Lucas and the West and Central Andes and the west slope are similar quantitatively but all include some notes with a more slanted shape (Fig. 5E–H). The two available recordings of rising song in San Lucas are from the same bird. One is faint and distant but permits analysis (Fig. 3A), whilst in the second only a few variables could be measured. A short trill, early higher note and the sequence of individual scratchy notes thereafter are visible on the sonogram and audible when the volume is increased. These are generally similar to some Central Andes populations (Fig. 3B–D). However, the initial trill has fewer notes than any *B. tristriatus* recording from Colombia, Ecuador or Peru and is shorter than all except the shortest west Ecuadorian recording. The min. frequency of the scratchy part in both San Lucas rising songs is higher than in any Central or West Andes recording (*n* = 67). Without a larger sample, it is impossible to ascertain the extent to which apparent differences are diagnosable, but the lack of any overlap indicates differentiation. Moreover, slow songs in San Lucas (Fig. 5E) also fail to attain such low min. acoustic frequencies as nearby populations. Call notes (Fig. 7E–F) in San Lucas are similar to those of Central and West Andes and west-slope birds (Figs. 5F–H, 7G–I).

In conclusion, the pattern of vocal variation is not always consistent with morphology. West Andes and west-slope populations share vocalisations with Central Andean birds; the morphologically similar Central and East Andes populations differ vocally; no notable vocal variation tracks the dramatic north–south plumage clines in the Central or East Andes or in eastern Ecuador; and San Lucas birds, which are morphologically similar to those in the northern Central Andes, appear to show small vocal differences.

Peruvian Andes.—*B. tristriatus* occurs only on the east slope in Peru (Schulenberg *et al.* 2007), with *B. trifasciatus* replacing it in the west. A rising song from north of the Huancabamba depression (Cajamarca) is essentially identical to Colombian and Ecuadorian east-slope recordings (Fig. 4G). South of the Huancabamba depression to Bolivia rising songs are rather variable (Fig. 4H–J). Quantitative data are similar in northern Peru to eastern Ecuador and Colombia. In contrast, either side of the Apurímac Valley, proposed as a barrier by Gutiérrez-Pinto *et al.* (2012), there is significant but non-diagnosable variation in the speed of scratches and more minor but significant variation in other quantitative variables. Data indicate the presence of two different subspecies in this region of Peru. However, the two northernmost recordings (Boesman 1809-1 and ML42070) from south of the Huancabamba depression attain speeds of >16 notes / second and the slowest 'northern' recording (ML147187 at *c.*10–12 notes / second) is the southernmost of this sample, so clinal variation cannot be discounted without more extensive sampling and additional analyses.

Slow songs throughout most of Peru also differ from those north of the Huancabamba depression, with more slanted note shapes re-appearing (akin to slow song in the Central and West Andes and west slope: Fig. 5L–M). However, quantitative variables for this vocalisation are similar to northern populations and show no major differences within Peru.

Bolivia.—*B. tristriatus* throughout Bolivia (including the ranges of *B. t. punctipectus* and *canens*) possess a strikingly different rising song (Fig. 4M–N) to that in all recordings of this vocalisation north of the border (*cf.* Fig. 4I–J). Bolivian rising songs start with lower pitched notes than any other population, being fully diagnosable (Level 5) from all other *B. tristriatus* populations with sample size of more than two. The trill is also diagnosably slower than in all other populations except Venezuela and the Colombian Central Andes. Some recordings include very rapid scratchy notes at the end (Fig. 4N) but most have only a few scratchy notes, with fewer notes on average (Level 2 vs. most). Slow song also differs from most Andes populations in always including (and usually solely comprising)

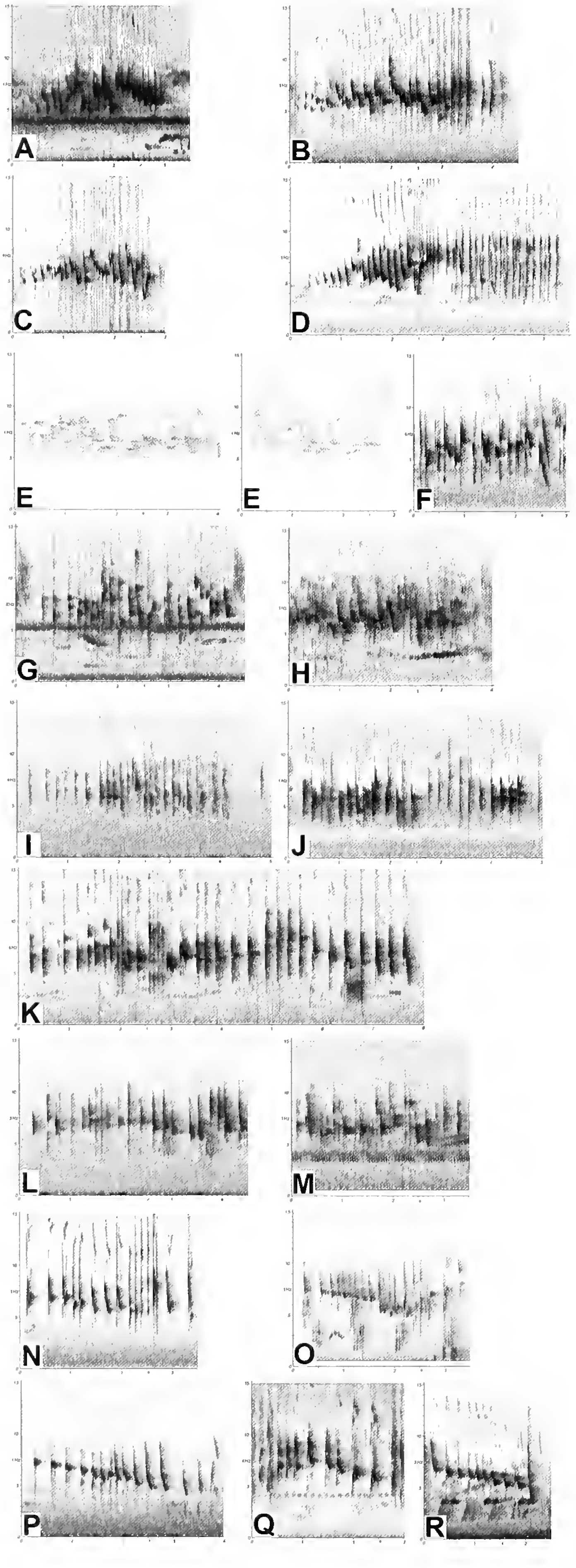

Figure 5. Songs from Venezuela and slow songs of other taxa. Coastal Cordillera, Venezuela (*bessereri*): A. Oripoto, Miranda (ML67198: P. A. Schwartz). B. Colonia Tovar, Aragua (ML53618: L. R. Macaulay). Andes of Venezuela (*meridanus*): C. PN Yacambú, Lara (Boesman 1999: 25-1). D. San Isidro quarry, Barinas (XC65916: D. F. Lane). San Lucas, Colombia (subsp.): E. Santa Cecilia, Serranía de San Lucas (XC176120: T. M. Donegan). Central Andes, Colombia (*daedalus*): F. Amalfi, Antioquia (Álvarez *et al.* 2007, disc 7: 51d). West Andes, Colombia (*daedalus*): G. río Anchicayá, Valle del Cauca (ML83777: S. L. Hilty). West slope, Ecuador (*daedalus*): H. Tandayapa, Pichincha (XC6639: N. Athanas). East Andes, Colombia (*auricularis*): I. La Aurora, above Galán, Serranía de los Yariguíes, Santander (XC25502: T. M. Donegan). East slope, Ecuador ('*baezae*'): J. Cordillera Guacamayos, Napo (Krabbe & Nilsson 2003: 31-7). Peru south of Huancabamba depression (*tristriatus*): K. Abra Patricia–Alto Nieva, San Martín (XC20772: N. Athanas). L. North-east of Tingo María, Loreto (ML28805: A. B. van den Berg). M. 15 km north-east of Jirillo, San Martín (ML42070: T. S. Schulenberg). Peru south of Apurímac (subsp.): N. San Pedro, south-west of Pilcopata on Cosñipata highway, Cusco (ML85067: A. J. Begazo). O. Capiri, Marcapata, Cusco (XC22826: D. Geale). Bolivia (*punctipectus* group): P. Tokoaque, Madidi NP, La Paz (ML121704: A. B. Hennessey). Q. Urpuma, Sandillani, Cotapata NP, La Paz (XC44213: T. M. Donegan). R. Miguelito, Cochabamba (XC1623: S. Mayer).

falling cadences or series of consecutively lower notes (Fig. 5P–R), instead of the jumbled frequency of other populations.

The northern limit of birds with the Bolivian vocal type is unknown. Recent field work in Puno did not produce recordings of rising songs (Robbins *et al.* 2013). No Peruvian rising songs, including examples from the east slope of Cusco (Fig. 4J), approach those of Bolivian birds. However, two recordings of slow song in Cusco (Fig. 5N–O) and one from Puno exhibit unusual note shapes and include falling cadences, like Bolivian recordings. The type locality of *inconspicuus* (considered related to *punctipectus* of Bolivia on account of its morphology by Zimmer 1949) is in Puno, who considered the Urubamba Valley to separate the two groups.

Comparison with molecular data

Gutiérrez-Pinto *et al.* (2012) discussed how their molecular findings were consistent or incongruent with morphological variation. Additional comparisons are now possible including with vocal data.

The molecular and vocal data show some remarkable consistencies. In particular, the most vocally distinctive populations include *basilicus* of Santa Marta, *trifasciatus* of western Peru, *melanotis* of Costa Rica, *tacarcunae* of Panama / Colombia, and Bolivian populations (*punctipectus* group), which coincide with the deepest branches in the molecular phylogeny. Moreover, Gutiérrez-Pinto *et al.* (2012) found *B. basilicus* to be so distantly related as not to be congeneric with *B. tristriatus*. The lack of vocal differentiation along plumage clines in the Central and East Andes is consistent with these birds being more closely related to one another than to populations in other ranges. Moderate differences between the voice of Central and East Andes populations reflects near-monophyletic groups recovered in the molecular phylogeny. Finally, small vocal differences between San Lucas and other Colombian Andean populations, and those either side of the Apurímac in Peru, also reflect the phylogeny.

The molecular phylogeny has west-slope and West Andes populations embedded with those of the Central Andes, which is consistent with their vocal similarities. Most specimens are easily assigned to one population, but a small number of birds whose phenotype is like that of birds from the Central Andes in the Colombian West Andes suggests limited contact.

Some inconsistencies between vocal or morphological and molecular data merit discussion. Most notably, the vocally and morphologically divergent Venezuelan populations represent a relatively young branch of the molecular phylogeny. Another potential point of inconsistency is the unimpressive quantitative vocal differentiation between populations either side of the Marañón or Huancabamba depression in Peru. Specimens from south of the proposed Urubamba Valley divide for subspecies *inconspicuus* (Zimmer 1949) clustered with more northern populations assigned to *tristriatus*. Finally, *tacarcunae* and *trifasciatus* were sister taxa in the phylogeny, but resemble one another little in voice or plumage. Results of mitochondrial and nuclear DNA are often congruent (Zink & Barrowclough 2005) but anomalies may result from differing male and female dispersion rates (Peters *et al.* 2012), including in Parulidae (Gibbs *et al.* 2000). Alternatively, it has been suggested that peripheral populations can differentiate more quickly in vocal characters (Lara *et al.* 2012).

Species limits

Although my core aim was to address subspecific limits of *B. tristriatus* in Colombia, an unprecedented set of materials relevant to species limits was collated. Voice has been widely used to delimit species in suboscine passerines (in which vocalisations are considered

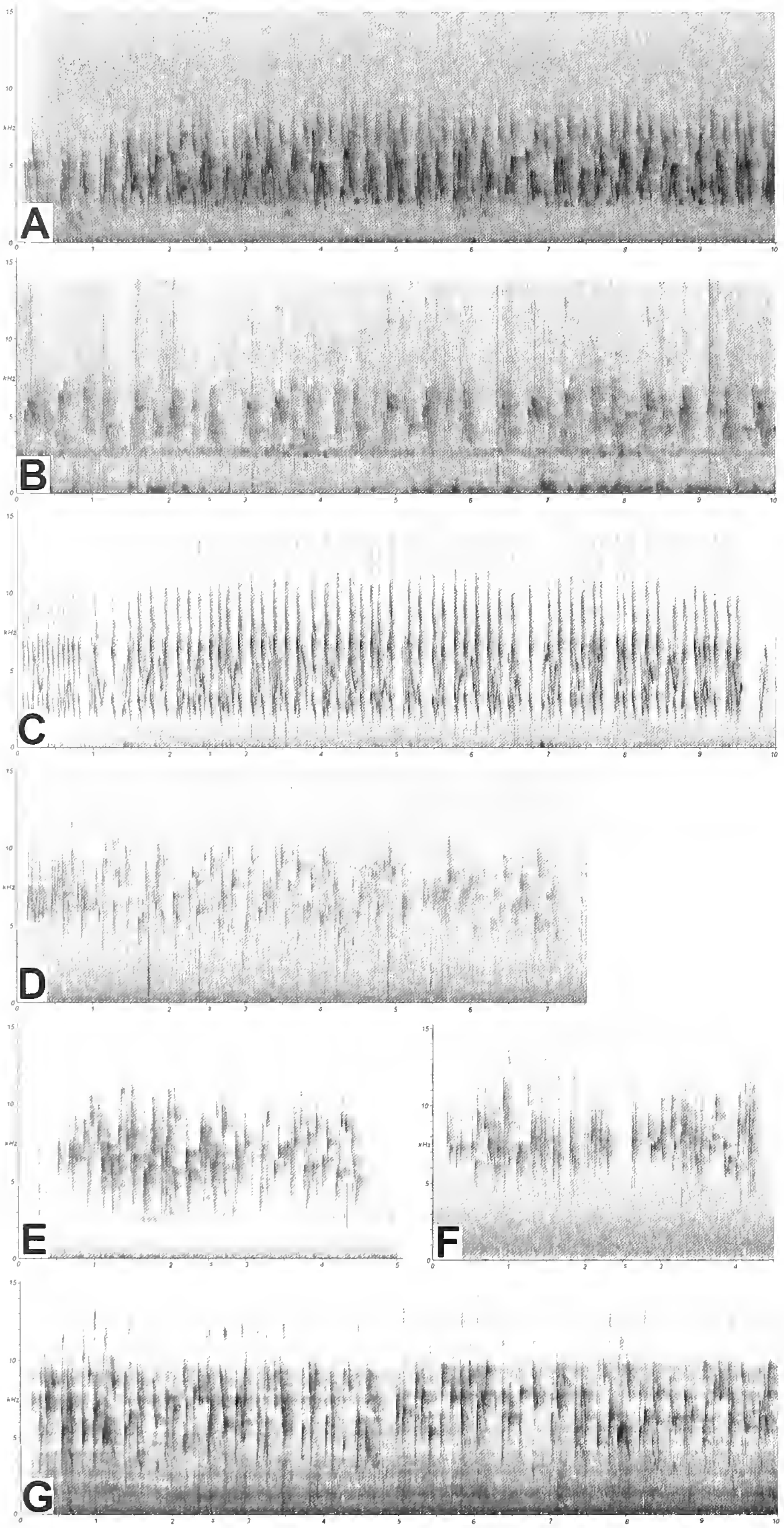

Figure 6. Vocally different populations from most Three-striped Warbler *Basileuterus tristriatus*. Santa Marta Warbler *B. basilicus*: A. RNA El Dorado or San Lorenzo ridge, Santa Marta, Magdalena, Colombia (Krabbe 2008, disc 2: 62). B. Idem (XC43566: T. M. Donegan). C. Idem, duet (XC117717: M. Álvarez). Costa Rica (*melanotis*): D. 90 km north-west of San José, Monteverde, Puntarenas (ML32713: L. F. Kibler). E. Monteverde Cloudforest Preserve, Guanacaste (ML32284: T. A. Parker). Eastern Panama (*chitrensis*): F. Cerro Colorado, Comarca Ngobe-Bugle (XC145616: W. Adsett). Panama (*tacarcunae*): G. Chagres National Park, Panama (XC145623: W Adsett).

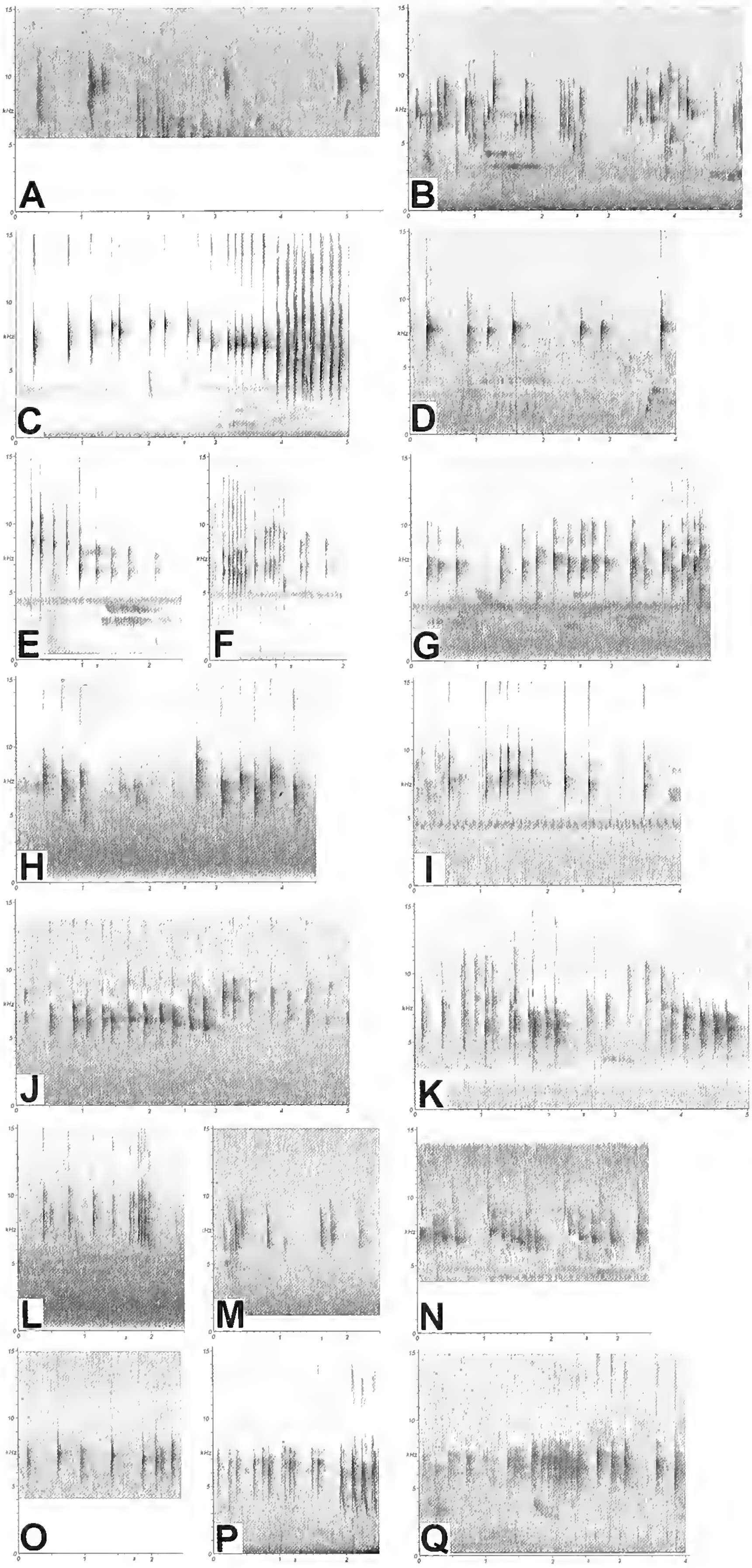

Figure 7. Calls. Santa Marta Warbler *Basileuterus basilicus*: A. RNA El Dorado or San Lorenzo ridge, Santa Marta, Magdalena, Colombia (Krabbe 2008, disc 2: 62). Costa Rica (*melanotis*): B. Monteverde Cloudforest Preserve, Guanacaste (ML39207: T. A. Parker). Coastal Cordillera, Venezuela (*bessereri*): C. PN El Ávila, Distrito Federal (ML127798: C. A. Marantz). Venezuelan Andes (*meridanus*): D. 13 km east of Santo Domingo, Barinas (ML52699: S. L. Hilty). San Lucas, Colombia (subsp.): E–F. Santa Cecilia, Serranía de San Lucas (XC172116, 172118: T. M. Donegan). Central Andes, Colombia (*daedalus*): G. Amalfi, Antioquia (Álvarez *et al.* 2007, disc 7: 51d). West Andes, Colombia (*daedalus*): H. El Cairo, Serranía de los Paraguas, Valle del Cauca (Álvarez *et al.* 2007, disc 7: 51b). West slope, Ecuador (*daedalus*): I. Reserva Maquipacuna, Pichincha (ML80985: D. Ross). East Andes, Colombia (*auricularis*): J. La Aurora, above Galán, Serranía de los Yariguíes, Santander (XC25881: T. M. Donegan). East slope, Ecuador ('*baezae*'): K. Cordillera Guacamayos, Napo (Krabbe & Nilsson 2003: 31-7). Peru south of Huancabamba depression (*tristriatus*): L. 15 km north-east of Villa Rica, Pasco (XC105613: D. F. Lane). Peru south of Apurímac (subsp.): M. San Pedro, south-west of Pilcopata on Cosñipata highway, Cusco (ML85067: A. J. Begazo). Bolivia (*punctipectus* group): N. Urpuma, Sandillani, Cotapata NP, La Paz (XC442216: T. M. Donegan). Southern Ecuador (*B. trifasciatus nitidior*): O. Loja–Catamayo road, Loja (ML68185: P. Coopmans). P. Tierra Colorada, Loja (Krabbe & Nilsson 2003: 30.1), with last four notes an example of 'slow song'. Northern Colombia (Golden-crowned Warbler *B. culicivorus indignus*): Q. Agua de la Virgen, Ocaña, Norte de Santander (XC20538: T. M. Donegan).

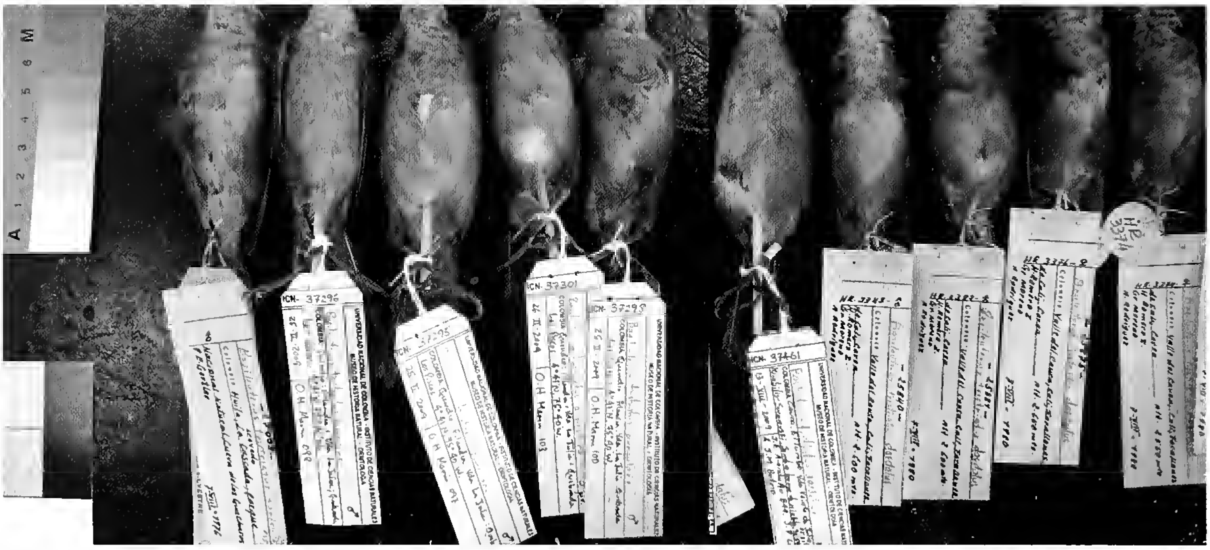

Figure 8. Close-up extracts of two sequences of birds in Fig. 2 showing (left) five head of Magdalena Valley and Central Andes specimens from part of its distribution with dullest underparts: Huila (ICN 37008) and Quindío (ICN 37296, 37295, 37301, 37298); right: five West Andes specimens from Cauca (ICN 37461) and Valle del Cauca (ICN 25840, 25881, 25875, 25873) and Antioquia (ICN 35684). Note darker and more olivaceous flanks of West Andes birds (T. M. Donegan)

innate: Kroodsma 1984, Isler *et al.* 1998), but is relatively little used for Neotropical oscines. Vocal differences are nonetheless evident between allopatric oscine populations (e.g. Cadena *et al.* 2007, Donegan & Avendaño 2010). Gape muscle strength and bill mass must influence the vocal repertoire of oscines, e.g. their ability to trill at given speeds or deliver notes of certain lengths or frequencies (e.g. Podos *et al.* 2004), and vocal differentiation is considered relevant to species limits in all birds (e.g. Helbig *et al.* 2002, Tobias *et al.* 2010).

It is unclear whether all vocal variables found here to be differentiated reflect physiological or innate differences between populations. For example, from this study it appears that most *B. tristriatus* populations avoid acoustic frequencies used by crickets, cicadas or other insects, by singing at a higher pitch. It is perhaps no coincidence that the 'highest frequency' population (in San Lucas) has some of the highest frequency insects (max. 4.9–6.1 kHz vs. 4.2–4.6 kHz for Central Andes populations in a sample of slow songs) or that the lowest frequency songs (in Bolivia) rarely have insect calls vocalising together (and when insect calls are present, the rising song 'crosses the insect line': ML132723). It is unclear whether differences in usage of low frequencies are learned / behavioural or innate. Other differences, in repertoire, song structure, song speed and max. frequencies (which are unconstrained by insects) are probably reflective of physiological or innate differences.

Gutiérrez-Pinto *et al.* (2012) recommended that, within *B. tristriatus*, three species could be recognised to maintain monophyly, i.e. *melanotis*, *tacarcunae* and *tristriatus*. They also proposed maintaining *B. trifasciatus* (which is embedded in the *tristriatus* tree) as a species. Geographical variation in vocalisations supports treating *melanotis* and *tacarcunae* as separate species from the rest of *B. tristriatus* given diagnosable, quantitative differences and differences in repertoire. The Bolivian population, for which *punctipectus* is the oldest name, emerges as another strong candidate for species rank based on voice and occupies the next most basal position in the phylogeny. These three forms (*melanotis*, *tacarcunae* and *punctipectus*) are mutually diagnosable and from remaining *tristriatus* in plumage.

Venezuelan populations are also quite distinctive in their rising song and dull plumage. However, splitting them would render *B. tristriatus* highly paraphyletic without broader separation of Andean group members that display non-diagnosable vocal differences and more minor plumage differences.

Various geographical gaps in sound-recordings render novel arrangements provisional. In particular, *tacarcunae* and San Lucas rising songs are known from just one recording each, and there are no recordings of songs from the Paria Peninsula in Venezuela or Puno, Peru. Gutiérrez-Pinto *et al.* (2012) suggested that an 'integrative study of species delimitation … including an expanded genetic sampling, as well as behavioral, phenotypic, and ecological information' is necessary before formally evaluating further changes to current taxonomy. The present paper does not address additional genetic sampling, behaviour (other than vocal) or ecology. However, with the near-contemporaneous publication of two detailed, independent studies, it seems appropriate to re-evaluate species limits. The following sequence is more consistent with vocal and plumage variation:

Costa Rican Warbler *B. melanotis* (including *B. m. chitrensis*).

Tacarcuna Warbler *B. tacarcunae* monotypic.

Three-striped Warbler *B. tristriatus* (including *B. t. pariae, bessereri, meridanus, auricularis, daedalus, 'baezae'* and the undescribed San Lucas and south Peruvian populations).

Bolivian Warbler *B. punctipectus* (including dubious *B. p. inconspicuus* and *canens*).

All meet the Tobias *et al.* (2010) scoring tests, acquiring at least six points for voice and two for plumage (typically more). The only exception is Bolivian with just four for voice, but it scores three for speckling on the breast and one for underparts coloration. Interaction between *B. trifasciatus* and *B. tristriatus* in southern Azuay, Ecuador, requires further research, but they appear to have maintained vocal, molecular and morphological differences despite potential for contact, so no change to present taxonomy is proposed.

Some populations emerge as high priorities for research and conservation. In particular, *B.* (*t.*) *tacarcunae* is a rare and apparently declining taxon with a tiny geographical range, at high elevations in eastern Panama and extreme north-west Colombia. It formerly occurred on the Cerro Jefe ridge above Cerro Azul (Ridgely & Gwynne 1989), but has not been seen there recently and is apparently absent from Cerro Pirre and other drier localities (K. Allaire & W. Adsett *in litt.* 2012). There are no records from Chucantí (M. Miller & G. Berguido *in litt.* 2012) but it should occur in more humid forest nearby. *B.* (*t.*) *tacarcunae* has been observed at Cerro Guagaral and Cerro Brewster (W. Adsett *in litt.* 2012) and was recently collected on the Colombian side of Cerro Tacarcuna (J. Avendaño pers. comm.; Fig. 1A). Conservation is currently complicated due to several of the few known localities for *tacarcunae* being threatened with habitat modification or coinciding with the Darién Gap, a region notoriously largely outside government control. Taxonomy should be based solely on relevant characters, but resolving the species limits discussed here could have practical implications for conservation.

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Appendix 1: Biometric data

Data presented as: mean ± standard deviation (lowest value–highest recorded value) (*n* = no. of specimens or individuals). Live capture data from: *West Andes and west slope*: Reserva Natural Tambito, Cauca (L. M. Dávalos, TMD). Río Ñambí, Nariño (P. Salaman); Reserva Natural de Aves (RNA) Eriocnemis, Cauca (L. F. Barrera, J. Sandoval / ProAves). RNA Pangan, Nariño (H. Arias / ProAves); RNA Jardín, Antioquia (G. Suárez / ProAves). *San Lucas*: La Punta, Bolívar (P. Salaman, A. Cuervo, TMD); Santa Cecilia, Bolívar (TMD). *Central Andes*: RNA Arrierito Antioqueño, Antioquia (C. Olaciregui, D. Velasco, A. Tovar / ProAves), La Floresta and Aguas Frías, Caldas (F. Guerrero / ProAves). Reserva Ibanasca, Tolima (A. González / ProAves). *East Andes*: Serranía de los Yariguíes, Santander: El Talismán, Honduras Alto, La Luchata, La Aurora, Cerro de la Paz (E. Briceño, J. Avendaño, B, Huertas, TMD); RNA Reinita Cerulea, Santander and RNA Pauxi pauxi, Santander (R. Parra, J. C. Luna / ProAves); Reserva Natural Cachalú, Santander (S. Vaillmarin, A. Daza. A. Magaly); Serranía de los Churumbelos, Cauca: Alto Cagadero and Nabú (P. Salaman, A. Cuervo, TMD). For coordinates and details of localities, see Donegan & Dávalos (1999), Donegan *et al.* (2007), Donegan (2012) and Salaman *et al.* (1999b, 2002, 2010).

Population	Wing-chord (mm)	Tail (mm)	Tarsus (mm)	Culmen to base of bill (mm)	Body mass (g)
			SPECIMEN DATA		
B. basilicus	65.4 ± 2.94 (61–70) (*n* = 7)	63.9 ± 3.54 (58.5–69.4) (*n* = 7)	23.1 ± 0.82 (22.2–24.3) (*n* = 7)	14.3 ± 0.83 (13.2–15.4) (*n* = 7)	/
Males	69.0 ± 1.41 (68–70) (*n* = 2)	68.0 ± 2.05 (66.5–69.4) (*n* = 2)	24.2 ± 0.21 (24.0–24.3) (*n* = 2)	14.1 ± 1.27 (13.2–15.0) (*n* = 2)	/
Females	64.0 ± 1.87 (61–66) (*n* = 5)	62.3 ± 2.52 (58.5–65.2) (*n* = 5)	22.7 ± 0.53 (22.2–23.5) (*n* = 5)	14.4 ± 0.77 (13.3–15.4) (*n* = 5)	/
B. melanotis					
B. m. melanotis Costa Rica and westernmost Panama	60.53 ± 2.68 (55.0–64.5) (*n* = 18)	51.69 ± 1.90 (49–55) (*n* = 18)	21.11 ± 1.12 (19.0–24.5) (*n* = 18)	12.47 ± 0.67 (11.0–13.5) (*n* = 17)	/
Males	62.07 ± 1.30 (61.0–64.5) (*n* = 7)	52.50 ± 1.32 (51.0–55.0) (*n* = 7)	21.29 ± 1.60 (19.5–24.5) (*n* = 7)	12.71 ± 0.64 (11.5–13.5) (*n* = 7)	/
Females	57.5 ± 2.07 (55–60) (*n* = 6)	50.50 ± 1.52 (49–53) (*n* = 6)	20.75 ± 0.88 (19.0–21.5) (*n* = 6)	12.08 ± 0.74 (11–13) (*n* = 6)	/
B. m. chitrensis west Panama	59.29 ± 2.59 (54.5–66.0) (*n* = 19)	50.85 ± 2.36 (47–55) (*n* = 20)	21.15 ± 1.04 (19–23) (*n* = 20)	12.88 ± 0.53 (12.0–14.0) (*n* = 20)	/
Males	59.85 ± 3.23 (54.5–66.0) (*n* = 10)	52.1 ± 2.37 (48–55) (*n* = 10)	21.35 ± 0.97 (19.5–22.5) (*n* = 10)	12.95 ± 0.6 (12.0–13.5) (*n* = 10)	/
Females	58.57 ± 1.72 (56–61) (*n* = 7)	49.88 ± 1.55 (47–52) (*n* = 8)	20.94 ± 1.27 (19–23) (*n* = 8)	12.81 ± 0.53 (12.5–14.0) (*n* = 8)	/
B. tacarcunae east Panama & north-west Colombia	59.93 ± 2.86 (56–64) (*n* = 14)	50.32 ± 2.22 (47–54) (*n* = 14)	20.11 ± 0.71 (19.0–21.5) (*n* = 14)	12.61 ± 0.49 (11.5–13.5) (*n* = 14)	13.25 (*n* = 1)
Males	60.63 ± 2.86 (57–64) (*n* = 8)	51.19 ± 1.65 (48–53) (*n* = 8)	20.0 ± 0.65 (19–21) (*n* = 8)	12.81 ± 0.37 (12.5–13.5) (*n* = 8)	13.25 (*n* = 1)
Females	57.50 ± 1.91 (56.0–60.0) (*n* = 4)	48.00 ± 0.82 (47.0–49.0) (*n* = 4)	20.25 ± 1.04 (19.0–21.5) (*n* = 4)	12.13 ± 0.48 (11.5–12.5) (*n* = 4)	/
B. tristriatus					
B. t. pariae Paria Peninsula, Venezuela	58.67 ± 2.52 (56–61) (*n* = 3)	53.33 ± 2.52 (51–56) (*n* = 3)	20.33 ± 0.29 (20.0–20.5) (*n* = 3)	12.5 ± 0.50 (12–13) (*n* = 3)	/

Population	Wing-chord (mm)	Tail (mm)	Tarsus (mm)	Culmen to base of bill (mm)	Body mass (g)
Males	60.00 ± 1.41 (59–61) (*n* = 2)	54.50 ± 2.12 (53–56) (*n* = 2)	20.25 ± 0.35 (20.0–20.5) (*n* = 2)	12.25 ± 0.35 (12.0–12.5) (*n* = 2)	/
B. t. meridanus type Mérida Andes, Venezuela	63.0 (*n* = 1)	51.0 (*n* = 1)	20.0 (*n* = 1)	12.5 (*n* = 1)	/
B. t. subsp. Serranía de San Lucas, Colombia	60.0 ± 2.32 (59–61) (*n* = 2)	52.5 ± 0.71 (52–53) (*n* = 2)	19.3 ± 1.77 (18.0–20.5) (*n* = 2)	13.5 ± 0.00 (13.5) (*n* = 2)	13.0 ± 1.41 (12–14) (*n* = 2)
Male	61.0 (*n* = 1)	53.0 (*n* = 1)	20.5 (*n* = 1)	13.5 (*n* = 1)	14.0 (*n* = 1)
Female	59.0 (*n* = 1)	52.0 (*n* = 1)	18.0 (*n* = 1)	13.5 (*n* = 1)	12.0 (*n* = 1)
B. t. daedalus Central Andes, Colombia	62.07 ± 2.22 (59–66) (*n* = 15)	54.4 ± 2.16 (51–58) (*n* = 15)	21.1 ± 1.09 (19–23) (*n* = 15)	12.97 ± 0.35 (12.5–13.5) (*n* = 15)	13.15 ± 1.28 (10.5–15.5) (*n* = 15)
Males	62.82 ± 2.09 (60–66) (*n* = 11)	55.27 ± 1.79 (53–58) (*n* = 11)	21.41 ± 1.02 (20–23) (*n* = 11)	12.95 ± 0.35 (12.5–13.5) (*n* = 11)	13.35 ± 1.04 (12.0–15.5) (*n* = 11)
Females	60.33 ± 0.58 (60–61) (*n* = 3)	51.67 ± 0.58 (51–52) (*n* = 3)	20.17 ± 1.04 (19–21) (*n* = 3)	13.0 ± 0.5 (12.5–13.5) (*n* = 3)	11.83 ± 1.26 (10.5–13.0) (*n* = 3)
B. t. daedalus West Andes and west slope, Colombia & Ecuador	61.57 ± 3.48 (56–69) (*n* = 20)	51.55 ± 2.35 (47.0–55.0) (*n* = 20)	20.43 ± 0.93 (19.0–22.5) (*n* = 22)	12.82 ± 0.33 (12.0–13.5) (*n* = 23)	12.18 ± 1.18 (10.5–13.0) (*n* = 4)
Males	64.18 ± 2.64 (61–69) (*n* = 11)	52.70 ± 2.41 (48–55) (*n* = 10)	21.05 ± 0.76 (20.0–22.5) (*n* = 11)	12.91 ± 0.20 (12.5–13.0) (*n* = 11)	13.0 ± 0.00 (13.0) (*n* = 2)
Females	58.72 ± 1.92 (56–61) (*n* = 9)	50.63 ± 1.69 (47–52) (*n* = 8)	19.72 ± 0.67 (19.0–20.5) (*n* = 9)	12.72 ± 0.44 (12.0–13.5) (*n* = 9)	11.35 ± 1.20 (10.5–12.2) (*n* = 2)
B. t. auricularis East Andes, east slope and head of Magdalena Valley, Colombia	61.45 ± 2.77 (54–65) (*n* = 42)	54.29 ± 2.72 (47–60) (*n* = 41)	20.51 ± 0.83 (19–22) (*n* = 40)	12.56 ± 0.70 (10.5–14.0) (*n* = 42)	12.52 ± 1.61 (10–15) (*n* = 17)
Males	62.77 ± 1.47 (60–65) (*n* = 24)	55.38 ± 1.84 (52–60) (*n* = 24)	20.92 ± 0.75 (19.5–22.0) (*n* = 24)	12.83 ± 0.58 (11.5–14.0) (*n* = 24)	12.32 ± 1.50 (10.5–15.0) (*n* = 9)
Females	59.00 ± 2.65 (54–63) (*n* = 13)	53.38 ± 2.81 (49–58) (*n* = 13)	20.08 ± 0.64 (19.0–21.5) (*n* = 13)	12.46 ± 0.43 (11.5–13.0) (*n* = 13)	10.97 ± 0.79 (10–12) (*n* = 7)
B. t. '*baezae*' east slope, Ecuador	63.80 ± 1.75 (62.0–65.5) (*n* = 5)	51.42 ± 1.02 (50–53) (*n* = 6)	20.17 ± 1.08 (18.5–21.5) (*n* = 6)	12.52 ± 0.58 (11.5–13.0) (*n* = 6)	/
Males	63.0 ± 1.41 (62–64) (*n* = 2)	50.75 ± 1.06 (50.0–51.5) (*n* = 2)	20.25 ± 1.06 (19.5–21.0) (*n* = 2)	12.75 ± 0.35 (12.5–13.0) (*n* = 2)	/
Female	65.5 (*n* = 1)	53.0 (*n* = 1)	20.0 (*n* = 1)	12.5 (*n* = 1)	/
B. t. tristriatus Peru	59.0 (*n* = 1)	53.0 (*n* = 1)	19.5 (*n* = 1)	12.0 (*n* = 1)	/
B. punctipectus group Bolivia	59.5 ± 2.12 (58–61) (*n* = 2)	55.0 (*n* = 1)	20.25 ± 0.35 (20.0–20.5) (*n* = 2)	12.25 ± 0.35 (12.0–12.5) (*n* = 2)	/
			LIVE CAPTURE DATA		
B. tristriatus					
B. t. subsp. Serranía de San Lucas, Colombia	65.11 ± 3.10 (61–70) (*n* = 9)	54.80 ± 3.16 (49.0–60.7) (*n* = 9)	20.83 ± 0.95 (19.5–22.9) (*n* = 9)	12.31 ± 0.90 (10.2–13.4) (*n* = 9)	12.29 ± 0.83 (11.3–14.0) (*n* = 9)
B. t. auricularis East Andes and east slope, Colombia	63.79 ± 3.01 (58–71) (*n* = 84)	55.96 ± 3.25 (50.7–65.1) (*n* = 32)	20.53 ± 0.69 (19.5–22.4) (*n* = 35)	12.4 ± 0.77 (10.0–13.6) (*n* = 35)	12.86 ± 1.14 (10.7–16.5) (*n* = 79)

Population	Wing-chord (mm)	Tail (mm)	Tarsus (mm)	Culmen to base of bill (mm)	Body mass (g)
B. t. daedalus Central Andes, Colombia	62.08 ± 2.87 (56–66) (*n* = 30)	60.2 (*n* = 1)	20.0 (*n* = 1)	11.82 (*n* = 1)	12.80 ± 1.11 (10.9–14.9) (*n* = 26)
B. t. daedalus West Andes and west slope, Colombia	62.62 ± 3.09 (55–70) (*n* = 119)	51.50 ± 3.11 (47.7–56.6) (*n* = 9)	20.69 ± 0.96 (19.3–22.5) (*n* = 9)	/	13.02 ± 1.03 (10.3–15.5) (*n* = 150)

Appendix 2: Vocal data

For songs of *B. basilicus*, Central American populations and slow songs of Andean *B. tristriatus* taxa, the following variables were measured (with bracketed capitalised codes used in tables below): (i) number of notes in song (NN); (ii) total song duration (seconds) (SL); (iii) song speed (dividing i by ii) (SS); (iv) max. acoustic frequency of highest note (kHz) (MF); (v) min. acoustic frequency of lowest note (kHz) (mF); (vi) frequency variation (subtracting iv from v) (FV). For rising songs of Andean *B. tristriatus* and *B. trifasciatus,* song was considered to comprise two parts for analyses: (A) initial rising trill, from start of vocalisation until point at which either note shape first changes significantly following initial increase in frequency or point at which max. frequency ceases to increase or is broadly stable; and (B) subsequent 'scratchy part', starting at end of trill and ending at the vocalisation's terminus. The following vocal variables were measured: (i) number of notes in trill (NNT); (ii) number of notes in scratchy part (NNS); (iii) duration of trill (seconds) (SLT); (iv) duration of scratchy part (seconds) (SLS); (v) total song duration (seconds) (SL); (vi) speed of trill (dividing i by iii) (SST); (vii) speed of scratchy part (dividing ii by iv) (SSS); (viii) max. acoustic frequency of lowest note in trill (kHz) (mFT); (ix) max. acoustic frequency of highest note in trill (kHz) (MFT); (x) frequency variation of trill (subtracting viii from ix) (FVT); (xi) min. acoustic frequency of lowest note in scratchy part (kHz) (mFS); (xii) max. acoustic frequency of highest note in scratchy part (kHz) (MFS). Frequency variation of scratchy part (subtracting xi from xii) was also measured in rising songs but data are not presented here as substantial overlap was found for most taxa. For rising songs of *B. trifasciatus,* no clear initial trill was evident although the first few notes are always lower pitched. For such vocalisations, a dataset was taken of 'short songs', plus variable (viii) as for rising songs (based on max. acoustic frequency of the lowest of first four notes). Data for such vocalisations are given alongside rising song data as if all notes were in scratchy part of songs. Calls were not measured for any taxon, nor were short fast trills sometimes given by northern *B. tristriatus* populations or non-comparable apparent female calls of *B. basilicus.*

As vocalisations sometimes included a combination of frequencies delivered simultaneously, all main (loud) tones were included. Harmonic overtones were ignored. Overtones at start of trills were often given but always ignored for purposes of determining mFT. Up to three different examples of each vocalisation type were measured from each recording. Recordings probably of same individual, even on different archived recordings, were treated together, with later recordings excluded from analyses. Additional recordings were ignored if involving consecutive or near-consecutive original tracks, or made within two hours by same recordist at same locality and if recordings had similar mensural variables. On most recordings, the first three vocalisations (where available) of each kind were analysed, but in some recordings if the individual approached closer permitting greater definition on sonograms, later recordings were used. In a handful of recordings with two individuals vocalising, additional datasets were taken per vocalisation type per individual. As many recordings from as many localities as possible were included, to determine the full range of variables. All recordings under natural conditions and after playback were included. The highest- and lowest-recorded values for each variable for each vocalisation for each taxon were double-checked. Songs of *B. basilicus* and Central American taxa were only compared with the structurally most similar slow songs of other *B. tristriatus* (notwithstanding the different sexes that appear to give relevant vocalisations) as a conservative approach to assess differentiation. Various tests were applied to pairs of vocal and biometric variables to assess if postulated statistical tests considered relevant to species or subspecies rank had been passed, following Donegan (2008, 2012). Vocal data from applying these methods are as follows.

Songs of *B. basilicus* and Central American populations.

Taxon	NN	SL (s)	SS (notes/s)	mF (kHz)	MF (kHz)	FV (kHz)
B. basilicus Santa Marta, Colombia (n_{ai} = 7)	125.22 ± 59.06 (63–267) (*n* = 9)	30.52 ± 18.63 (18.62–76.83) (*n* = 9)	4.34 ± 1.03 (3.20–5.98) (*n* = 9)	1.70 ± 0.52 (0.54–2.30) (*n* = 9)	7.67 ± 0.34 (6.97–8.08) (*n* = 9)	5.97 ± 0.67 (5.29–7.49) (*n* = 9)
B. m. melanotis Costa Rica (n_{ai} = 7)	30.87 ± 16.77 (7–56) (*n* = 16)	2.20 ± 1.33 (0.40–4.01) (*n* = 16)	14.86 ± 1.75 (12.76–17.56) (*n* = 16)	3.18 ± 0.69 (2.28–4.35) (*n* = 16)	11.91 ± 0.69 (10.67–13.26) (*n* = 16)	8.73 ± 1.05 (7.26–10.42) (*n* = 16)

B. m. chitrensis Panama (n_{ai} = 2)	31.67 ± 2.08 (30–56) (*n* = 3)	2.07 ± 0.39 (1.65–2.41) (*n* = 3)	15.63 ± 2.67 (12.86–18.19) (*n* = 3)	4.02 ± 0.51 (3.49–4.52) (*n* = 3)	13.05 ± 0.94 (12.86–18.19) (*n* = 3)	9.03 ± 0.75 (8.58–9.89) (*n* = 3)
B. melanotis combined (n_{ai} = 9)	31.0 ± 15.32 (7–56) (*n* = 19)	2.18 ± 1.22 (0.40–4.01) (*n* = 19)	14.98 ± 1.86 (12.76–18.19) (*n* = 19)	3.31 ± 0.73 (2.28–4.52) (*n* = 19)	12.09 ± 0.82 (10.67–13.94) (*n* = 19)	8.78 ± 1.00 (7.26–10.42) (*n* = 19)
B. tacarcunae Panama (n_{ai} = 1)	164.0 ± 26.87 (145–183) (*n* = 2)	21.22 ± 2.74 (19.28–23.15) (*n* = 2)	7.71 ± 0.27 (7.52–7.90) (*n* = 2)	2.22 ± 0.08 (2.16–2.28) (*n* = 2)	10.83 ± 0.12 (10.74–10.92) (*n* = 2)	8.61 ± 0.03 (8.58–8.64) (*n* = 2)

Slow songs

Taxon	NN	SL (s)	SS (notes/s)	mF (kHz)	MF (kHz)	FV (kHz)
B. t. bessereri Coastal Cordillera, Venezuela (n_{ai} = 2)	26.2 ± 26.37 (12–73) (*n* = 5)	3.23 ± 3.36 (1.30–9.16) (*n* = 5)	8.39 ± 0.74 (7.71–9.20) (*n* = 5)	3.02 ± 0.25 (2.84–3.46) (*n* = 5)	11.44 ± 1.32 (10.3–12.9) (*n* = 5)	8.42 ± 1.46 (6.83–9.97) (*n* = 5)
B. t. meridanus Mérida, Venezuela (n_{ai} = 4)	17.71 ± 8.20 (6–31) (*n* = 7)	2.09 ± 1.01 (0.78–3.70) (*n* = 7)	8.56 ± 0.74 (7.67–10.06) (*n* = 7)	3.30 ± 0.43 (2.76–3.99) (*n* = 7)	10.32 ± 0.35 (9.85–10.98) (*n* = 7)	7.02 ± 0.70 (6.27–8.22) (*n* = 7)
B. t. subsp. San Lucas (n_{ai} = 3)	14.5 ± 5.51 (9–21) (*n* = 4)	2.28 ± 1.10 (1.17–3.62) (*n* = 4)	6.64 ± 0.80 (5.80–7.67) (*n* = 4)	5.39 ± 0.32 (5.12–5.74) (*n* = 4)	9.94 ± 0.84 (9.02–10.98) (*n* = 4)	4.55 ± 1.15 (3.28–5.86) (*n* = 4)
B. t. daedalus Central Andes (n_{ai} = 16)	15.88 ± 10.63 (8–62) (*n* = 25)	2.26 ± 1.23 (0.80–7.26) (*n* = 28)	7.06 ± 1.23 (5.41–10.06) (*n* = 25)	3.98 ± 0.68 (1.78–4.72) (*n* = 25)	10.20 ± 0.80 (8.79–11.93) (*n* = 28)	6.32 ± 0.74 (4.97–7.66) (*n* = 5)
B. t. daedalus West Andes, Colombia, and west slope, Colombia and Ecuador (n_{ai} = 34)	21.33 ± 10.44 (10–54) (*n* = 39)	3.21 ± 1.92 (0.91–9.43) (*n* = 39)	7.08 ± 1.62 (4.69–12.05) (*n* = 39)	3.68 ± 0.73 (2.52–5.36) (*n* = 38)	10.78 ± 0.66 (9.70–12.84) (*n* = 38)	7.12 ± 1.14 (5.27–10.33) (*n* = 36)
B. t. auricularis East Andes, Colombia (n_{ai} = 22)	20.32 ± 8.38 (10–54) (*n* = 37)	3.23 ± 1.85 (1.34–11.46) (*n* = 38)	6.55 ± 1.07 (4.71–9.42) (*n* = 37)	3.62 ± 0.53 (2.71–4.83) (*n* = 37)	10.06 ± 0.97 (7.62–12.07) (*n* = 38)	6.42 ± 1.21 (4.21–8.61) (*n* = 37)
B. t. 'baezae' eastern Ecuador and north Peru (n_{ai} = 9)	17.61 ± 5.99 (8–29) (*n* = 18)	3.38 ± 1.26 (1.77–6.35) (*n* = 18)	5.32 ± 0.88 (3.72–7.11) (*n* = 18)	2.72 ± 0.86 (1.53–4.29) (*n* = 18)	10.31 ± 0.49 (9.73–11.42) (*n* = 15)	7.66 ± 0.94 (5.70–9.33) (*n* = 15)
B. t. tristriatus Peru south of Marañón to Apurímac (n_{ai} = 5)	22.15 ± 7.79 (11–36) (*n* = 13)	3.78 ± 1.79 (2.16–7.99) (*n* = 13)	6.30 ± 1.93 (4.43–10.99) (*n* = 13)	3.15 ± 0.70 (2.16–4.11) (*n* = 13)	11.01 ± 0.55 (9.79–11.76) (*n* = 13)	7.86 ± 0.83 (6.59–9.31) (*n* = 13)
B. t. subsp. Peru, Apurímac south (n_{ai} = 4)	15.63 ± 9.02 (8–34) (*n* = 8)	2.90 ± 1.61 (1.42–6.37) (*n* = 8)	5.35 ± 0.86 (4.28–7.09) (*n* = 8)	3.36 ± 0.60 (2.39–4.20) (*n* = 8)	10.87 ± 0.65 (9.85–11.63) (*n* = 8)	7.51 ± 0.93 (6.12–9.24) (*n* = 8)
B. punctipectus group Bolivia (n_{ai} = 21)	12.75 ± 6.66 (3–31) (*n* = 36)	2.73 ± 1.31 (0.54–6.52) (*n* = 36)	4.63 ± 0.92 (2.67–6.08) (*n* = 36)	4.01 ± 1.04 (1.66–5.68) (*n* = 36)	9.11 ± 1.27 (6.95–5.68) (*n* = 36)	5.10 ± 2.11 (2.31–9.70) (*n* = 36)
B.. trifasciatus nitidior Ecuador (n_{ai} = 8)	7.29 ± 3.31 (3–14) (*n* = 17)	1.11 ± 0.49 (0.55–2.29) (*n* = 17)	6.59 ± 1.67 (4.77–11.82) (*n* = 17)	2.52 ± 0.68 (1.63–4.66) (*n* = 16)	7.85 ± 0.63 (6.32–9.18) (*n* = 17)	5.43 ± 0.89 (3.06–6.63) (*n* = 16)
B. t. trifasciatus Peru (n_{ai} = 6)	7.68 ± 7.68 (2–28) (*n* = 15)	1.04 ± 0.97 (0.29–3.70) (*n* = 15)	6.61 ± 1.73 (3.91–10.29) (*n* = 15)	1.92 ± 0.56 (1.04–2.99) (*n* = 15)	7.83 ± 0.78 (6.78.–9.87) (*n* = 15)	5.90 ± 0.86 (4.68–8.10) (*n* = 15)

Rising songs

Taxon	NNT	NNS	SLT (s)	SLS (s)	SL (s)	SST (notes/s)
B. t. bessereri Coastal Cordillera, Venezuela (n_{ai} = 6)	10.72 ± 4.61 (6–20) (*n* = 18)	19.89 ± 5.43 (10–30) (*n* = 18)	1.33 ± 0.51 (0.77–2.34) (*n* = 18)	2.21 ± 0.60 (1.14–3.49) (*n* = 18)	3.54 ± 0.72 (2.73–5.32) (*n* = 18)	7.96 ± 0.80 (6.26–9.95) (*n* = 18)

B. t. meridanus Mérida, Venezuela (n_{ai} = 4)	12.40 ± 4.38 (6–17) (*n* = 10)	13.70 ± 5.96 (6–23) (*n* = 10)	1.44 ± 0.54 (0.80–2.22) (*n* = 10)	1.39 ± 0.62 (0.57–2.46) (*n* = 10)	2.83 ± 0.31 (2.39–3.34) (*n* = 10)	8.71 ± 1.58 (7.27–12.45) (*n* = 10)
B. t. subsp. San Lucas (n_{ai} = 1)	8 (*n* = 1)	18 (*n* = 1)	0.76 (*n* = 1)	2.28 (*n* = 1)	3.04 (*n* = 1)	10.51 (*n* = 1)
B. t. daedalus Central Andes (n_{ai} = 16)	17.91 ± 4.66 (11–28) (*n* = 23)	19.96 ± 3.07 (16–25) (*n* = 27)	1.39 ± 0.28 (0.92–1.74) (*n* = 28)	2.06 ± 0.56 (1.09–3.14) (*n* = 27)	3.45 ± 0.68 (2.66–4.81) (*n* = 27)	13.13 ± 1.93 (10.18–16.93) (*n* = 24)
B. t. daedalus West Andes, Colombia, and west slope, Colombia and Ecuador (n_{ai} = 18)	18.03 ± 3.74 (12–26) (*n* = 37)	27.74 ± 6.19 (14–42) (*n* = 38)	1.20 ± 0.26 (0.71–1.70) (*n* = 37)	2.22 ± 0.57 (1.22–3.42) (*n* = 38)	3.34 ± 0.64 (2.04–4.63) (*n* = 38)	16.36 ± 2.31 (11.08–19.69) (*n* = 37)
B. t. auricularis East Andes, Colombia (n_{ai} = 26)	37.18 ± 8.03 (16–53) (*n* = 38)	20.78 ± 5.36 (6–33) (*n* = 45)	1.63 ± 0.42 (0.99–2.60) (*n* = 49)	1.56 ± 0.43 (0.39–3.32) (*n* = 48)	3.19 ± 0.42 (2.35–4.39) (*n* = 48)	21.24 ± 2.92 (14.13–27.96) (*n* = 18)
B. t. 'baezae' eastern Ecuador and north Peru (n_{ai} = 13)	37.20 ± 6.46 (24–47) (*n* = 25)	18.12 ± 5.89 (0–29) (*n* = 26)	1.81 ± 0.30 (1.23–2.31) (*n* = 27)	1.52 ± 0.41 (0.00–2.72) (*n* = 26)	3.31 ± 0.48 (2.11–4.32) (*n* = 27)	20.76 ± 1.28 (18.77–23.81) (*n* = 26)
B. t. tristriatus Peru south of Marañón to Apurímac (n_{ai} = 7)	28.0 ± 8.52 (18–44) (*n* = 17)	24.94 ± 7.28 (11–39) (*n* = 16)	1.38 ± 0.35 (0.89–2.10) (*n* = 19)	1.72 ± 0.64 (1.00–3.26) (*n* = 20)	3.11 ± 0.66 (2.39–4.54) (*n* = 19)	19.20 ± 2.15 (15.81–23.78) (*n* = 17)
B. t. subsp. Peru Apurímac south (n_{ai} = 4)	23.1 ± 6.92 (15–33) (*n* = 10)	24.13 ± 5.17 (18–30) (*n* = 8)	1.36 ± 0.38 (0.85–1.91) (*n* = 10)	2.61 ± 0.40 (2.07–3.20) (*n* = 8)	4.03 ± 0.21 (3.69–4.35) (*n* = 8)	16.93 ± 0.78 (15.72–18.32) (*n* = 10)
B. punctipectus group Bolivia (n_{ai} = 36)	19.29 ± 3.46 (12–25) (*n* = 34)	6.81 ± 4.39 (0–19) (*n* = 37)	2.35 ± 0.47 (1.37–3.13) (*n* = 52)	0.91 ± 0.70 (0.00–3.78) (*n* = 46)	3.23 ± 0.92 (1.87–6.67) (*n* = 46)	7.72 ± 1.10 (5.42–9.52) (*n* = 34)
B. trifasciatus nitidior Ecuador (n_{ai} = 13)	/	26.47 ± 5.08 (11–34) (*n* = 32)	/	/	2.57 ± 0.59 (1.14–4.39) (*n* = 33)	/
B. t. trifasciatus Peru (n_{ai} = 8)	/	23.77 ± 5.61 (14–35) (*n* = 13)	/	/	2.71 ± 0.50 (1.76–3.53) (*n* = 14)	/

Taxon	**SSS (s)**	**mFT (kHz)**	**MFT (kHz)**	**FVT (kHz)**	**mFT (kHz)**	**MFT (kHz)**
B. t. bessereri Coastal Cordillera, Venezuela (n_{ai} = 6)	9.03 ± 1.15 (7.58–11.96) (*n* = 18)	5.50 ± 0.46 (4.43–6.33) (*n* = 18)	7.48 ± 0.63 (6.04–8.64) (*n* = 18)	1.98 ± 0.82 (0.71–4.21) (*n* = 18)	3.70 ± 0.63 (2.37–4.18) (*n* = 18)	10.32 ± 0.96 (8.61–12.25) (*n* = 18)
B. t. meridanus Mérida, Venezuela (n_{ai} = 4)	9.94 ± 0.62 (9.35–11.14) (*n* = 10)	5.52 ± 0.15 (5.33–5.84) (*n* = 10)	7.44 ± 0.47 (6.59–8.28) (*n* = 10)	1.92 ± 0.44 (1.13–2.63) (*n* = 10)	4.42 ± 0.69 (3.62–5.59) (*n* = 10)	9.37 ± 0.65 (8.18–10.22) (*n* = 10)
B. t. subsp. San Lucas (n_{ai} = 1)	7.63 ± 0.37 (7.37–7.89) (*n* = 2)	5.93 (*n* = 1)	6.51 (*n* = 1)	0.58 (*n* = 1)	5.10 ± 0.08 (5.05–5.16) (*n* = 2)	9.58 ± 0.10 (9.51–9.66) (*n* = 2)
B. t. daedalus Central Andes (n_{ai} = 16)	10.14 ± 2.22 (7.30–15.60) (*n* = 27)	5.21 ± 0.34 (4.73–6.01) (*n* = 29)	6.78 ± 0.44 (6.01–7.75) (*n* = 29)	1.57 ± 0.22 (1.17–1.92) (*n* = 28)	3.87 ± 0.23 (3.30–4.16) (*n* = 28)	9.87 ± 0.63 (8.98–11.08) (*n* = 28)
B. t. daedalus West Andes, Colombia, and west slope, Colombia and Ecuador (n_{ai} = 18)	12.73 ± 2.0 (8.71–17.96) (*n* = 38)	5.34 ± 0.35 (4.68–5.98) (*n* = 38)	6.74 ± 0.49 (5.65–7.74) (*n* = 37)	1.40 ± 0.35 (0.85–2.16) (*n* = 36)	3.30 ± 0.67 (1.80–4.46) (*n* = 39)	6.70 ± 1.35 (3.29–9.34) (*n* = 39)
B. t. auricularis East Andes, Colombia (n_{ai} = 22)	13.58 ± 2.42 (9.93–20.07) (*n* = 45)	4.96 ± 0.41 (3.05–5.61) (*n* = 49)	6.72 ± 0.42 (5.92–7.66) (*n* = 50)	1.74 ± 0.55 (0.92–3.34) (*n* = 48)	4.09 ± 0.57 (2.72–4.94) (*n* = 47)	9.69 ± 0.76 (7.34–11.15) (*n* = 45)

B. t. 'baezae' eastern Ecuador and north Peru (n_{ai} = 9)	12.15 ± 2.36 (8.77–18.17) (*n* = 26)	5.03 ± 0.20 (4.79–5.61) (*n* = 28)	6.89 ± 0.31 (6.07–7.37) (*n* = 28)	1.86 ± 0.31 (1.28–2.37) (*n* = 28)	3.46 ± 0.61 (1.82–4.67) (*n* = 26)	9.75 ± 0.64 (8.54–10.98) (*n* = 26)
B. t. tristriatus Peru south of Marañón to Apurímac (n_{ai} = 7)	14.81 ± 3.53 (10.66–20.87) (*n* = 16)	5.16 ± 0.16 (4.77–5.41) (*n* = 19)	6.64 ± 0.36 (6.09–7.24) (*n* = 20)	1.46 ± 0.28 (1.03–2.13) (*n* = 19)	3.60 ± 0.46 (2.60–4.20) (*n* = 19)	10.34 ± 0.62 (9.06–11.12) (*n* = 20)
B. t. subsp. Peru Apurímac south (n_{ai} = 4)	9.23 ± 1.24 (7.55–11.10) (*n* = 8)	5.23 ± 0.16 (5.01–5.53) (*n* = 11)	6.94 ± 0.43 (6.49–7.55) (*n* = 11)	1.71 ± 0.38 (1.28–2.28) (*n* = 11)	3.62 ± 0.66 (2.93–4.38) (*n* = 9)	9.97 ± 0.48 (9.38–10.98) (*n* = 9)
B. punctipectus group Bolivia (n_{ai} = 21)	7.47 ± 2.45 (4.68–14.04) (*n* = 36)	3.51 ± 0.20 (3.14–4.08) (*n* = 63)	6.40 ± 0.58 (5.19–7.74) (*n* = 62)	2.89 ± 0.62 (1.70–4.29) (*n* = 62)	3.27 ± 1.09 (1.60–5.25) (*n* = 34)	9.59 ± 1.41 (6.97–12.05) (*n* = 34)
B. trifasciatus nitidior Ecuador (n_{ai} = 13)	10.61 ± 1.21 (8.60–13.73) (*n* = 32)	/	/	/	3.63 ± 0.70 (2.19–4.82) (*n* = 33)	9.56 ± 0.82 (8.05–12.43) (*n* = 33)
B. t. trifasciatus Peru (n_{ai} = 8)	8.71 ± 0.97 (7.60–10.31) (*n* = 13)	/	/	/	3.94 ± 0.60 (3.08–5.21) (*n* = 14)	9.98 ± 1.17 (7.95–11.86) (*n* = 14)

Appendix 3: Materials examined

All specimens, sound-recordings and other records used in analyses are cited. For sound-recordings, coordinates are taken from relevant database, publication or recordist.

Specimens.—All were personally examined, as were all *B. basilicus*, *B. trifasciatus* and non-Colombian *B. tristriatus* at AMNH, BMNH and USNM. Some specimen data are based on Biomap Alliance Participants (2012). Other Colombian specimens of *B. tristriatus* are detailed in Biomap Alliance Participants (2012).

***B. basilicus* Santa Marta, Colombia** ICN 23442–447 (San Pedro, Quebrada Cebolleta, Santa Marta, Magdalena). 23448 (San Lorenzo, Santa Marta, Magdalena).

B. melanotis:

***B. m. melanotis* Costa Rica and western Panama** AMNH 131013 (Chiriquí, Panama), 154391, 391969–670, 505641–643 (paratypes, Aquinares, Costa Rica), 505639 (Chiriquí, Panama), 505640 (Costa Rica). BMNH 1885.3.8.667 (Costa Rica), 1898.12.1.826. 1899.12.1.100–103 (all, Azahar de Cartago, Costa Rica), 1900.7.30.46 (La Hondura), 1919.58.807 (Cachí, Costa Rica),

***B. m. chitrensis* Panama** AMNH 187748–749, 246437, 246439–453 (paratypes, Chitrá). BMNH 1885.3.8.668–669 (Cordillera Chucú, Veraguas).

***B. tacarcunae* Panama** AMNH 136199–201, 136204–212 (paratypes, Mt. Tacarcuna, Panama). **Colombia** ICN 37370 (Acandé, Cerro Tacarcuna, Chocó), 38182 (Unguía, Chocó).

B. tristriatus:

***B. t. pariae* Paria Peninsula, Venezuela** AMNH 44323, 44315 (Cerro Humo), 40587 (Cerro Azul).

***B. t.* subsp. Serranía de San Lucas, Colombia** ICN 34167, 34178 (La Punta, Santa Rosa del Sur, Bolívar).

***B. t. auricularis* East Andes and head of Magdalena Valley, Colombia** AMNH 17448–450 (La Candela, Huila), 50630–631 and three others ('Bogotá'), 122666 (Aguadita, Cundinamarca). BMNH 1884.5.15.420 ('Bogotá'), 1885.3.8.666 (co-type, 'vicinity of Bogotá, New Grenada'), 1921.12.29.112 (San Agustín, Huila), 1921.12.29.113, 1921.12.29.168 (La Candela, Huila). ICN 3720, 4221–222 (Aguadita, Fusagasugá, Cundinamarca), 17409–413, 25552, 25620, 25622, 25630 (Corinto, Comijoque, Pajarito or río Cusiana, Boyacá), 25098 (Cañaverales / Virolín, Charalá, Santander), 25390, 25393–394 (Loma del Rayo, Virolín / Charalá, Santander), 27008 (La Cascada, Acevedo, PNN Cueva de los Guacharos, Huila), 30929 (3 km north-east of Monteredondo, Guayabetal, Cundinamarca), 32620 (Aguas Claras, Cubarral, Meta), 32987 (La Grilla, Serranía de las Quinchas, Otanche, Boyacá), 33155 (El Retiro, Campo Hermoso, Ubatá, Boyacá), 33443 (Serranía de los Churumbelos, Cauca), 34365 (El Talismán, San Vicente de Chucurí, Serranía de los Yariguíes, Santander), 34985 (El Mortiño, Floridablanca, Santander), 35218 (Finca La Argentina, Virolín, Charalá, Santander), 35321, 35324, 36447 (La Pajarita, Tona, Bucaramanga), 36323 (Suratá, Bucaramanga), 37067 (El Cinco, Manaure, Serranía de Perijá, Cesar), 37159–160, 37197–198 (San Antonio, Manaure, Serranía de Perijá, Cesar), 37310 (La Aurora, Galán, Serranía de los Yariguíes, Santander), 37325 (Piedecuesta, Santander). UIS unnumbered (2) (Tona, Santander), unnumbered (believed to be near Charalá, Santander). USNM 88398 ('Bogotá'), 369875 (Monte Elias, Fonseca, Guajira), 374780–802 (Laguna de Junco, Jagua del Pilar, Guajira), 374779 (Virolín, Charalá, Santander), 374783–788 (La Africa, Villanueva, Guajira), 398976–987 (Buenos Aires, Bucarasica, Norte de Santander), 412262, 412564 (Hacienda Las Vegas, Piedecuesta, Santander), 403423–425 (Villa Felisa, Cúcuta, Norte de Santander), 447435–436 (Belén, La Plata, Huila).

B. t. daedalus **Central Andes, Colombia** AMNH 109164–168, 109327–330 (east of Palmira, Valle del Cauca), 113257–259 (Salento, Quindío), 113260–262 (El Roble, Circasia, Quindío), 113258 (Páramo de Santa Isabel, Risaralda / Tolima / Caldas), 134101 (La Frijolera, Antioquia). BMNH 1921.12.29.114 (Salento, Quindío). ICN 34376 (Retiro, Antioquia), 34587 (El Encanto, La Secreta, Amalfi, Antioquia), 34531 (Salazar, Finca Bodega Vieja, Amalfi, Antioquia), 34546 (Santa Gertrudis Vereda, Anorí, Antioquia), 34597, 34602, 34624 (Bosque La Escuela, Amalfi, Antioquia), 37295–296, 37298, 37301 (Filandia, Vereda La Julia, Quebrada los Picos, Quindío). USNM 403426–433 (Valdivia, Antioquia), 436884–887 (La Bodega, Antioquia), 436888–891 (Hacienda La Sofia, río Samaná, Caldas).

B. t. daedalus **West Andes and west slope, Colombia** AMNH 108386–390, 108647, 109162–163, 109332, 511391 (San Antonio, La Cumbre, Valle del Cauca), 108391–392 (Lomitas, La Cumbre, Valle del Cauca), 109976 (Cocal, El Tambo, Cauca), 109977, 110288–290 (Cerro Munchique, El Tambo, Cauca), 110291–293, 109973–735 (Gallera, west of Popayán, Cauca). ICN 17522–223, 32286 (Almaguer, Barbacoas, Nariño), 27284 (Reserva Natural La Planada, Ricaurte, Nariño), 25840, 25873, 25875–876, 25881, 25891 (Corea, PNN Farallones de Cali, Valle del Cauca), 35684 (La Messania, Finca Primavera, Jardín, Antioquia), 37461 (20 de Julio, El Tambo, Cauca), 37487 (Reserva Natural Río Ñambí, Nariño). USNM 427317–320, 427324 (Hacienda Potreros, Frontino, Antioquia). **Ecuador** BMNH 1884.5.15.418, 1884.5.15.419, 1885.3.8.672 (Pallatanya) 1901.4.25.44–45 (Posvenio, Bolívar), 1916.8.24.79 (Mindo, Pichincha), 1925.12.24.451 (Tandapi), 1938.12.20.94 (río Saloya), 1953.68.595 (Guayupe, Imbabura, 1,250 m), 1953.68.808 (Chaspé).

B. t. 'baezae' **Ecuador** AMNH series examined but not measured. BMNH 1884.12.9.1–2 ('Trisbrunfoncé cllachay'), 1885.2.8.7 (Machay), 1901.4.25.46 (Mirandar, Baños), 1925.12.24.450 (Baeza), 1953.68.809 (Abanico Oriente, 1,600 m).

B. t. tristriatus **Peru** AMNH 820244 (Cordillera Vilcabamba, Cusco), 82087–096 (Cerros de Sira, Huánuco). BMNH 1903.10.17.12 (Cusco).

B. punctipectus group **Bolivia** AMNH 823900 (15 km north of Monte Punco, Totora, Cochabamba), 823901–902 (río Vanimayo, Yungas de Totora, 30 km north of Monte Punco, Cochabamba). BMNH 1885.3.8.664, 1885.3.8.666 (Simacu).

Sound recordings.—Acronyms as follows: XC = www.xeno-canto.org; IAVH = Instituto Alexander von Humboldt's Colección de Sonidos Ambientales; ML = Macaulay Library, Cornell Lab of Orn.; AV = AVoCet www.avocet.zoology.msu.edu. Localities are listed north to south by taxon and then by country.

B. basilicus *Songs.*—RNA El Dorado or San Lorenzo ridge, Santa Marta, Magdalena (11°06'N, 74°03'W) (Krabbe 2008, disc 2: 62(1–4); XC43566: T. M. Donegan; XC165599, 165611: A. Spencer; XC117717–718: M. Álvarez; XC102579: F. Schmitt). *Calls.*—Krabbe (2008, disc 2: 62(3–5) (as 62(1–4)).

B. m. melanotis **Costa Rica** *Songs.*—90 km north-west of San José, Monteverde, Puntarenas (10°18'N, 84°05'W; 1,600 m) (ML32713: L. F. Kibler). Bosque de Paz Biological Reserve (10°12'N, 84°21'W) (XC107255–257: M. Nelson). Monteverde Cloudforest Preserve, Guanacaste (ML32284: T. A. Parker; ML76716: C. A. Marantz; Ross & Whitney 1995, disc 2: 74). *Calls.*—AV13925 (as ML32284 but P. C. Rasmussen). ML39207 (as ML32284). ML76707 (as ML76717). ML72827 (as ML76716 but D. Ross). ML32713 (as above). XC107255–257 (as above).

B. m. chitrensis **Panama** *Songs.*—Cerro Colorado, Comarca Ngobe-Bugle (formerly Chiriquí) (08°32'N, 81°48'W; 1,600 m) (XC145616–617: W. Adsett).

B. tacarcunae **Panama** *Song.*—Sitio de Guillen, Chagres National Park (09°19'N, 79°18'W, 750 m) (XC145623: W. Adsett).

B. tristriatus

B. t. bessereri **Venezuela, Coastal Cordillera** *Rising songs.*—Oripoto, Miranda (10°26'N, 66°50'W; 1,200 m) (ML67198–99: P. A. Schwartz). Colonia Tovar, Aragua (10°24'N, 67°20'W; 1,800–2,200 m) (ML53618: L. R. Macaulay; Boesman 1999: 25.2 = Boesman 2012: 3197-3). Rancho Grande, km 20.5, Aragua (10°22'N, 67°41'W; 1,100 m) (ML67202: P. A. Schwartz). Sierra de Aroa, Yaracuy, Venezuela (10°20'N, 68°50'W) (Boesman 2012 track 3197-6). *Slow songs.*—Boesman 1999: 25.2, ML67202 (see above). *Calls.*—Parque Nacional El Ávila, Camino de los Españoles, Distrito Federal (10°33'N, 66°56'W) (ML127798: C. A. Marantz). ML67200 (as ML67198). Boesman (1999: 25.2) (as above). Boesman (2012: 3197-6) (as above).

B. t. meridanus **Venezuela** *Songs.*—Parque Nacional Yacambú, Lara (09°43'N, 69°35'W; 1,300–1,750 m) (Boesman 1999: 25-1 = Boesman 2012: 3197-1). San Isidro quarry, Barinas (08°50'N, 70°35'W; 1,500 m) (XC65916: D. F. Lane). South of Santo Domingo Valley, Barinas (08°32'N, 70°30'W; 1,355 m) (ML102505: L.

R. Macaulay). 13 km east of Santo Domingo, Barinas (08°32′N, 70°30′W; 550 m) (ML52699: S. L. Hilty). *Slow songs.*—Boesman (1999: 25-1), XC65916, ML52699, 102505 (as above). *Calls.*—ML52699 (as above). Boesman (1999: 25.3) = Boesman (2012: 3197-7) (as 25.1).

***B. t.* subsp. Serranía de San Lucas, Colombia** *Rising song.*—Santa Cecilia, Santa Rosa del Sur, Bolívar (07°58′33″N, 74°12′55″W; 1,550 m) (XC176120: T. M. Donegan). *Slow songs.*—XC176120 (as above), XC92160, 176116 (both as XC176120). *Calls.*—XC92160, 104230, 176116, 176118, 176119 (all as XC176120).

***B. t. daedalus* Central Andes, Colombia** *Rising songs.*—Vereda Corcovado, Finca Villa Nueva, Antioquia (07°03′N, 75°27′W; 2,100 m) (XC131770: O. H. Marín-Gómez). Reserva La Forzosa, Anorí, Antioquia (07°00′N, 75°09′W; 1,550 m) (XC55260: B. López-Lanús). La Romera, Medellín, Antioquia (Boesman 2012: 1696-1, 3197-4–5). Hacienda Termópilas, Neira, Caldas (05°14′N, 75°29′W; 2,250 m) (IAVH7905: S. Córdoba; IAVH7979: M. Álvarez). Campo Alegrito, Santa Rosa de Cabal, Risaralda (04°52′N, 75°33′W; 2,380 m) (IAVH 15356–357: S. Córdoba). SFF Otún Quimbaya, Risaralda (04°44′N, 75°35′W; 1,875 m) (XC105650, 105659: E. de Fonso). AICA La Patasola, Salento, Quindío (04°41′N, 75°33′W, 2,300 m) (XC128598: O. H. Marín-Gómez). Reserva Bremen, Buenavista, Quindío (04°20′N, 75°44′W) (IAVH 7293: M. Álvarez; XC128994–997, 128999 (all treated as same recording), 130016, 130020, 130032 (all treated as same recording), 131163 (apparent subsong): O. H. Marín-Gómez). *Slow songs.*—Amalfi, verada Guayabito, Antioquia (06°59′N, 75°04′W) (Álvarez *et al.* 2007, disc 7: 51d). Boesman (2012: 1696-1, 3197-4–5, as above). IAVH 7905, 15356–357 as above). XC55262 (as XC55260), XC105654 (as XC105650). XC128531 (as XC128994). XC105650, 128994–995, 130016, 130020, 130032 (latter three same recording but multiple individuals), 131770 (as above). *Calls.*—La Suiza, SFF Otún-Quimbaya, Risaralda (1,700 m) (XC53954: B. López-Lanús). XC128553 (as XC128994). Álvarez *et al.* (2007, disc 7: 51d) (as above). IAVH 7979, 15357 (both, as above). XC102559 (as XC105659, J. Minns). XC130440, XC130714 (both as XC128994), XC105654, 105659, 128531, 128598, 130016, 130020, 130032 (all as above). Boesman (2012: 1696-1, 3197-5, as above). *Juvenile calls.*—XC131767–768 (as XC131770).

***B. t. daedalus* West Andes / west slope** *Rising songs.*—**Colombia** Reserva Natural Mesenia (05°29′N, 75°54′W; 2,000 m) (XC96010: O. Cortes). Apía, Risaralda (05°10′N, 76°19′W; 2,200–2,360 m) (IAVH 15899: S. Córdoba). Near RNA Las Tangaras, Chocó (05°43′N, 76°15′W; 1,800 m) (ML165277: M. J. Sarver). El 18, Valle del Cauca (03°29′N, 76°37′W) (XC22420 = Boesman 2012: 3197-2: A. Spencer). Altaquer, Reserva Natural Río Ñambí, Nariño (01°18′N, 78°05′W; 1,100–1,600 m) (XC12378, 12755–556, 13152; latter three treated as same recording: O. Laverde). Ricaurte, Reserva Natural La Planada, Nariño (01°05′N, 77°53′W; 2,000 m) (XC12747: O. Laverde; Álvarez *et al.* 2007, disc 7: 51a). **Ecuador** Maldonado Road, Carchi (00°57′N, 78°12′W; 1,550 m) (Krabbe & Nilsson 2003: 31-1). Hacienda la Florida, Imbabura (00°22′N, 78°29′W; 2,000 m) (Krabbe & Nilsson 2003: 31-2). Barcelona, Cordillera Toisan, Imbabura 00°20′N, 78°36′W; 1,850 m) (Krabbe & Nilsson 2003: 31-4). Reserva Maquipacuna, Pichincha (00°05′N, 78°37′W; 1,600 m) (ML58048–049, treated as same recording: P. Coopmans). Tandayapa Lodge, Pichincha (00°00′N–00°06′N, 78°40′W; 1,820–1,850 m) (XC6717, 16092: N. Athanas; Krabbe & Nilsson 2003: 31-3). Reserva Las Tangaras, Mindo, Pichincha (00°05′S, 78°47′W; 1,400 m) (XC164158, 165091: M. St. Michel). Tandayapa Valley, Pichincha (00°01′S, 78°41′W; 1,200 m) (XC112289: T. Brooks). Mindo, Pichincha (00°00′S, 78°47′W; 1,200 m) (XC118021, 118023–024: E. de Fonso). Calacalí–Nanegalito road, Pichincha (Moore *et al.* 1999, disc 3: 17-1). *Slow songs.*—**Colombia** Anchicayá Valley, Valle del Cauca (03°32′N, 76°48′W; 1,000 m) (ML83777: S. L. Hilty). Alto de Pisones, Risaralda (05°18′N, 75°56′W) (IAVH11193 / XC148264: F. G. Stiles). ML165277 (as above). XC96010 (as above). **Ecuador** Mashpi Road, Pichincha (00°10′N, 78°51′W; 1,200 m) (XC58007: C. Vogt). Old Chiriboga Road, Pichincha (00°15′S, 78°45′W; 1,800 m) (XC4000: D. Jones; Moore *et al.* 1999, disc 3: 17-3). Krabbe & Nilsson (2003: 31-2) (as above). ML58048 (as above). XC5061, 6639, 32031 (all as XC6717), XC112289, 118023–024, 164518, 165091 (all, as above). XC163525, 168841 (both as XC164518). *Calls.*—**Colombia** PNN Tatamá, Pueblo Rico, Risaralda (05°14′N, 76°05′N; 1,600 m) (Boesman 2012: 3197-8). Reserva Natural Cerro el Inglés, Valle del Cauca (04°44′N, 76°18′W; 1,900 m) (XC22422: A. Spencer). El Cairo, Serranía de los Paraguas, Valle del Cauca (04°18′N, 76°13′W) (Álvarez *et al.* 2007, disc 7: 51a–b) (as above). Territorio Kofán, Ipiales, Nariño (00°28′N, 77°17′W, 800–1,450 m) (XC117226 = IAVH137: M. Álvarez). ML83777, 165277 (both as above). XC12377, 13153 (both as XC12755). XC24421 (as XC24420). XC96010 (as above). XC95883 (as XC96010). IAVH11193 / XC148264 (as above). IAVH11192 (= XC148263), IAVH11202 (=XC148272) (both as IAVH11193 / XC148264). **Ecuador** Cabañas San Isidro, Napo (00°35′S, 77°53′W; 2,130 m) (XC95024: D. F. Lane). Krabbe & Nilsson (2003: 31-2) (as above). Moore *et al.* (1999, disc 3: 17-1-2) (both, as 17-1). ML80985 (as ML58048 but D. Ross). ML58048-049 (as above). XC6632, 9860 (as XC 6717). XC118039 (as XC118023). XC4000, 112289, 163525, 168841 (all as above). *Juvenile begging call.*—XC58002 (as XC58007).

***B. t. auricularis* East Andes and head of Magdalena Valley, Colombia** *Rising songs.*—Sisavita, Carrizal, Cucutilla, Norte de Santander (07°29′N, 72°50′W; 2,150 m) (XC117539 (= IAVH9044), IAVH9098: S. Córdoba). RNA Reinita Cielo Azul, San Vicente de Chucurí, Santander (as 'El Talismán' below, but 1,900 m) (Boesman 2012: 151-2, 625-4, 1252-4). La Luchata, above Galán, Serranía de los Yariguíes, Santander (06°38′N, 73°19′W; 2000 m) (XC30819, 30821, 30823, treated as same recording, 30850–852, treated as same recording, 31694: T. M. Donegan). La Aurora, above Galán, Serranía de los Yariguíes, Santander (06°38′N, 73°23′W; 2,700 m) (XC25497, 25501–502, 25508–509, 25511–514, 25518, 25530, 25533–335 [from 25501 on treated as same recording]: T. M. Donegan). Medina, Cundinamarca (04°35′N, 73°26′W; 1,480–1,800 m) (ML80870, 80874, 80876, latter two treated as same recording, 80923–924 = Álvarez *et al.* 2007, disc 7: 51c; XC117282 = IAVH287: M. Álvarez). PNN Los Picachos, Finca Andalucia, Caquetá (02°48'N, 74°51'W; 1,400 m) (ML89242, 89258 = IAVH455–456: M. Álvarez). PNN Cueva de los Guacharos, Acevedo, Huila (01°37'N, 76°06'W; 1,810–2,100 m) (IAVH6949, 6990, 6991, all treated as same recording, 7006, 7048–49, treated as same recording, 7057, 7162, 7163, 7166, latter four treated as same recording: M. Álvarez; XC117930 [= IAVH16113]: J. E. Parra). *Slow songs.*—El Talismán, San Vicente, Yariguíes, Santander (06°51'N, 73°22'W; 2,000 m) (XC24162: T. M. Donegan). Boesman (2012: 151-2, as above). IAVH8641 (as IAVH9098), IAVH6990, 7057, 9098 (all as above). ML80870, 80923–924, 89242, 89258 (all as above). ML80940 (as ML80870). XC25476, 25501–503 (treated as same recording), 25508, 25512, 25514 (all as XC25497). XC30821, 30850, 31694, 117539 (all as above). *Calls.*—SFF Iguaque, Chiquiza, Boyacá (05°38'N, 73°829'W, 3,000 m) (XC117231 = IAVH 1175: M. Álvarez). Río Yurayaco, San José de la Fragua, Caquetá (01°21'N, 76°08'W, 1,000–1,500 m) (IAVH 4306: M. Álvarez). IAVH 6990, 6991, 7006, 7166 (all as above). IAVH 9087 (as IAVH 9098). IAVH9098. ML89385 = IAVH457 (as ML89242). ML80870, 80876, 80923–234, 80940 (all as above). XC34943 (as XC30819). XC24289 (as XC24162). XC25417 (as XC25418), XC117933–334 (as XC117930). XC25501–502, 25880–881, 117539 (as above).

***B. t. 'baezae'* Ecuador, east slope, and Peru, east slope south to Huancabamba depression** *Rising songs.*—**Ecuador** Hacienda San Isidro, 2 km south-west of Cosanga, Napo (00°35'S, 77°53'W; 2,100 m) (Krabbe & Nilsson 2003: 31-5). San Isidro Lodge, Napo (00°40'S, 77°55'W) (Boesman 2012: 1809-2). Cordillera Guacamayos, Napo (00°37'S, 77°49'W; 1,700–2,150 m) (Krabbe & Nilsson 2003: 31-7). Quebrada las Ollas, Santa Barbara–La Bonita road, Sucumbíos (00°33'N, 77°32'W; 2,150 m) (Krabbe & Nilsson 2003: 31-6). Cordillera Cutucú, Morona-Santiago (02°39'S, 78°08'W; 1,550 m) (ML36050: T. S. Schulenberg). Cordillera de Cutucú, Morona-Santiago (02°43'S, 78°05'W; 2,012 m) (ML41278: M. B. Robbins). Cordillera del Condor, Morona-Santiago (03°29'S, 78°14'W; 1,500 m) (ML72789, 78023, 78027–028, 78030, 78035, 78050 [all treated as same recording], 78058, 79600, 79619: T. A. Parker). Chinapintza, Cordillera del Condor, Zamora-Chinchipe (04°02'S, 78°38'W; 1,700 m) (XC93378–379, treated as same recording: R. Ahlman). **Peru** East slope of Cerro Chinguela, Lucuma, Cajamarca (05°07'S, 79°23'W) (ML21713: T. A. Parker). *Slow songs.*—**Ecuador** Krabbe & Nilsson (2003: 31-7, as above). ML36050, 78023, 78028, 78030, 78035, 78058 (all as above). XC93378-379 (as above). *Calls.*—**Ecuador** La Sofia road, Sucumbíos (00°26'N, 77°35'W; 2,440 m) (XC93158–159: C. Vogt). West of Cutucú, Morona-Santiago (02°26'S, 78°03'W; 1,900–1,950 m) Krabbe & Nilsson (2003: 31-8). Boesman (2009: 1809-1-2). ML41253 (as ML41278). ML79627 (as ML72789). ML36050, 41278, 72789, 78023, 78027-8, 78030, 78035, 78050, 78058, 79619, 82620 (all as above). Krabbe & Nilsson (2003: 31-7) (as above).

***B. t. tristriatus* Peru, south of Huancabamba depression to Apurímac** *Rising songs.*—Abra Patricia, San Martín (05°50'S, 77°46'W) (Boesman 2009: 1809-1; Boesman 2012: 2005-4). 15 km north-east of Jirillo, San Martín (06°03'S, 76°44'W; 1,350 m) (ML42070: T. S. Schulenberg). Afluente, San Martin (05°40'S, 77°42'W; 1,400 m) (XC141786: D. F. Lane). Camp Utter Solitude, Alto Mayo, San Martin (05°43'S, 77°45'W; 2,150 m) (XC132704: D. F. Lane). North-east of Tingo María, Loreto (09°00'S, 75°00'W) (ML28805: A. B. van den Berg). Cordillera Divisoria, Huánuco (09°10'S, 75°29'W; 1,219 m) (ML31886: T. A. Parker). Below Calabazas, Junín (11°27'S, 74°47'W; 1,400 m) (ML147187: M. B. Robbins). *Slow songs.*—Abra Patricia–Alto Nieva, San Martín (05°42'S, 77°49'W; 2,040 m) (XC20772: N. Athanas). ML28805, 42070 (both as above). XC141786 (as above). *Calls.*—Below Alto Mayo, San Martín (05°34'S, 77°44'W; 1,700 m) (XC141785: D. F. Lane). 15 km north-east of Villa Rica, Pasco (10°43'S, 75°09'W; 1,250 m) (XC105613: D. F. Lane). ML42070 (as above). ML147174 (as ML147187). XC141786 (as above).

***B. t.* subsp. Peru, from Apurímac south** *Rising songs.*—San Pedro, Manu Road, Cusco (13°03'S, 71°33'W; 1,400 m) (XC63185: J. Tobias & N. Seddon; XC88623: D. F. Lane). San Pedro, south-west of Pilcopata on Cosñipata highway, Cusco (13°09'S, 71°20'W; 1,300 m) (ML85067: A. J. Begazo). Manu, Cusco (13°10'S, 71°30'W) (Boesman 2009: 1809-3). *Slow songs.*—Suiza, Manu Road (2,120 m) (XC10973: C. Hesse). Capiri, Marcapata, Cusco (13°25'S, 70°55'W, 1,900 m) (XC22826: D. Geale). Rocotal, Manu Road, Cusco (13°07'S, 71°34'W; 1,800 m) (XC39704: D. Geale). ML85067 (as above). *Calls.*—Boesman (2012: 1809-2, as above). XC22826 (as above). XC57236 (as XC63185 but D. Geale). XC91046 (as XC88623 but O. Cortes). XC85953–954 (as XC85953). ML85067, 147174 (both as above). XC63185 (as above).

***B. punctipectus* group Bolivia** *Rising songs.*—Pilón Lajas Biosphere Reserve, La Paz (15°06'S, 67°32'W; 750–1,450 m) (XC3104, 3116: A. B. Hennessey). Serranía Bellavista, north of Caranaví, La Paz (15°39'S, 67°30'W) (ML13815, 13852, 17128, 17154, 33726: T. A. Parker). As previous (15°41'S, 67°30'W; 1,250–1,650 m) (XC4094: S. K. Herzog). Yungas, La Paz (16°14'S, 67°48'W; 1,600 m) (XC145038, 150560: D. F. Lane). Tunquini Biological Station, Cotapata NP, La Paz (16°12'S, 67°52'W; 1,500–2,000 m) (XC4744: S. K. Herzog). Urpuma, Sandillani, Cotapata NP, La Paz (16°13'S, 67°53'W; 1,950 m) (XC43916, 44231–232, 44395, 44438: T. M. Donegan). Laguna Carachupa, Cordillera Mosetenes, Cochabamba (16°14'S, 66°25'W; 1,200–1,600 m) (XC4732: S. K. Herzog). Apa, near Chulumani (16°18'S, 67°50'W) (XC454: J. van der Woude). Bosque Apa Apa, La Paz (16°21'S, 67°30'W; 1,800 m) (ML132723: P. A. Hosner). West of Villa Tunari, Cochabamba (16°59'S, 65°24'W; 1,524 m) (ML33704: T. A. Parker). Carrasco National Park, Cochabamba (17°09'S, 65°37'W; 1,755 m) (ML87653: A. B. Hennessey). Chapare (Colomi–Villa Tunari road), Cochabamba (17°09'S, 65°42'W; 1,850 m) (ML50610: P. Coopmans). Old road from Cochabamba to Villa Tunari, Carrasco NP, Cochabamba (17°10'S, 65°35'W; 1,500–2,000 m) (XC3433, 3468, 3475–78, 3480–81, 3484, 3538–40, 3546–47, 3561, 3583: S. K. Herzog; note only sample of best recordings of this long series analysed). Miguelito Pipeline Road, Cochabamba (17°10'S, 65°46'W; 1,700 m) (XC145025, 149120, 155976: D. F. Lane). Miguelito, Cochabamba (17°10'S, 65°47'W; 1,400–1,600 m) (XC1618–19, treated as same recording), 1623, 1625: S. Mayer). *Slow songs.*—Tokoaque, Madidi NP, La Paz (14°37'S, 68°57'W; 2,400 m) (ML121704, 121718: A. B. Hennessey). XC3431 (as XC3433), XC44216, 44234 (both as XC43916). ML13815, 13852, 17128, 17154, 33704, 33726, 50610, 87653, 132723 (all as above). XC1618, 1623, 4732, 43916, 145025, 145038 (all as above). *Calls.*—ML13815, 13852, 17128, 17154, 33704, 33726 (all as above). XC44213, 44216, 44387 (all as XC43916). XC3431, 149120 (both as above). **Peru** *Calls.*—Maruncunca, Puno (14°10'S, 69°14'W; 2,160 m) (XC85953: D. F. Lane) (identification tentative; as discussed in text, some southern Cusco call or slow song recordings listed above may also belong here).

B. trifasciatus nitidior *Rising songs.*—**Ecuador** Manta Real, Azuay (02°34'S, 79°21'W) (ML82620: T. A. Parker; identified as *tristriatus*, possible intermediate with *B. t. daedalus*; not included in analyses). Piñas (03°43'S, 79°41'W; 1,100 m) (XC55829: M. Sánchez). Loja, El Cisne–Ambocas road (03°49'S, 79°30'W; 1,600 m) (XC81322: L. Ordóñez-Delgado). Loja (03°55'S, 79°40'W; 1,250 m) (ML130400: L. Macaulay). Loja–Catamayo road, Loja (03°57'S, 79°16'W) (ML68185: P. Coopmans). San Pedro de la Bendita, Loja (03°57'S, 79°27'W; 1,850 m) (XC86557: D. F. Lane). Tierra Colorada, Loja (04°02'S, 79°56'W; 1,650 m) (Krabbe & Nilsson 2003: 30.1). Loja (04°02'S, 79°11'W, 2,300 m) (XC136043: L. Ordóñez-Delgado). Between Celica and Guachanamá, Loja (04°05'S, 79°57'W; 2,450 m) (Krabbe & Nilsson 2003: 30.2). Celica, Loja (04°06'S, 79°56'W; 1,700 m) (XC6543: N Athanas). Celica Mountains, Loja (04°07'S, 79°59'W) (XC67696–697: F. Lambert). Bosque Protector El Tundo, Sozoranga, Loja (04°20'S, 79°49'W; 1,700 m) (XC9269: N. Athanas). Sozoranga, Loja (04°20'S, 79°48'W; 1,600 m) (XC20260: C Vogt). Parroquia El Airo, Espindola, Loja (04°29'S, 79°23'W, 1,800 m) (XC118557: L. Ordóñez-Delgado). *Slow songs.*—**Ecuador** Krabbe & Nilsson (2003: 30.1, as above). XC55829, 67696, 81322, 118557, 118562, 136043 (all as above). ML130400 (as above). *Calls.*—**Ecuador** Krabbe & Nilsson (2003: 30.1–2, as above). ML68185, 130400 (both, as above). XC118562 (as XC118557). XC6543, 67696, 55829, 81322 (all as above).

B. trifasciatus trifasciatus *Rising songs.*—**Peru** Abra Porculla, Piura (05°50'S, 79°30'W) (Boesman 2009: 1808-1–2). Zona Reservada Laquipampa, Lambayeque (06°18'S, 79°28'W; 1,400 m) (XC5177, 5568, 8633, 8646, 8648: W.-P. Vellinga). Bosque Cachil, Cajamarca (07°24'S, 78°47'W, 2,500 m) (XC75966: C. J. Schmitt). *Slow songs.*—**Peru** Abra Porculla, Piura (05°51'S, 79°31'W, 2,100 m) (XC8551: H. van Oosten). Boesman (2009: 1808-2–3) (as 1808-1). XC75965–967 (as XC75966). *Calls.*—**Peru** Huancabamba (05°20'S, 79°32'W, 2,240–3,050 m) (ML21862: T. A. Parker). Boesman (2009: 1808-1-3) (as 1808-1). XC5186-7 (as XC5177). XC75965–967 (as XC75966). XC8551, 8648 (both as above).

On the status of Crowned Eagle *Buteogallus coronatus* in Uruguay

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Summary.—Crowned Eagle *Buteogallus coronatus* inhabits open country in eastern and southern Brazil, Bolivia, Paraguay, and northern and central Argentina. Several authors have included Uruguay within the species' range, many of them indicating that it is presumably extinct in the country. Here we evaluate the available evidence concerning its presence in Uruguay by considering all original reports together with the species' past and current distribution and its habitat requirements. We conclude that unambiguous records in Uruguay are still lacking. Given that the species has recently been observed at several localities in nearby Argentina and Brazil, individuals may reach Uruguay sporadically, probably dispersing juveniles. Effective conservation measures targeted at Crowned Eagle habitat will increase the chances that this threatened raptor may yet colonise Uruguay.

Crowned Eagle *Buteogallus coronatus* occurs in south-central South America in eastern and southern Brazil, Bolivia, Paraguay, and northern and central Argentina (Collar *et al.* 1992, Bierregaard 1994). In the south of its range, the species inhabits grasslands, shrublands, steppes and croplands in the Monte, Espinal, Campos and Pampas eco-regions (Bellocq *et al.* 2002, Maceda 2007, Chebez *et al.* 2008). Within these open areas the presence of large trees (including several *Prosopis* spp.), either alone or in small forest islands (used for nesting and as roosts) has been highlighted as a key habitat feature (Bellocq *et al.* 1998, Maceda 2007). The Algarrobo (within the Espinal region) in eastern Argentina was identified as one of those zones with high frequency of Crowned Eagle records in a recent (1981–2000) compilation of observations (Bellocq *et al.* 2002). Here, open woodlands of *Prosopis* spp. and *Geoffroea decorticans* dominate the landscape (Bellocq *et al.* 2002). This same forest type extends to western Uruguay (Brussa & Grela 2007).

Unfortunately, human activities have drastically altered and fragmented xerophytic woodlands and other habitats used by Crowned Eagles (Collar *et al.* 1992, Carrete *et al.* 2009). Apart from habitat loss, direct persecution, collisions with powerlines and drowning in water tanks also affect this eagle's populations (Sarasola & Maceda 2006, Maceda 2007, Chebez *et al.* 2008, BirdLife International 2013). Although trends are particularly difficult to detect in low-density populations, a significant reduction in size has been

Figure 1. Larrañaga's Crowned Eagle *Buteogallus coronatus* illustration in Pl. XLIV of his Atlas (Larrañaga 1930). Overall colour is grey; the cere and feet are yellow.

estimated throughout the species' range (BirdLife International 2013). Thus, it is no surprise that the species is currently classified as Endangered globally (BirdLife International 2013), and Endangered and Critically Endangered in Argentina (López-Lanús *et al.* 2008) and Rio Grande do Sul, Brazil (Bencke *et al.* 2003), respectively.

Several authors have included Uruguay within this eagle's range (e.g., Barattini & Escalante 1958, Collar *et al.* 1992), whereas others have questioned this (Hellmayr & Conover 1949, Cuello & Gerzenstein 1962, Meyer de Schauensee 1966). Alvarez (1911, 1933, 1934) provided details of a specimen from southern Uruguay. Kothe (1912) reported two specimens from Montevideo taken by Sellow. Larrañaga (1930) included a plate of a Crowned Eagle in his atlas. Finally, Arredondo (1953) commented on its status in Uruguay with emphasis on Rocha department. Despite these references, Crowned Eagle has been excluded from most recent national avifaunas (Arballo & Cravino 1999, Azpiroz 2001, Azpiroz *et al.* 2012). According to Cuello (1985) its presence in Uruguay should be confirmed with specimens. In addition, several other sources have suggested that the species is presumably extinct in Uruguay (e.g., Claramunt & Cuello 2004, Maceda 2007, Capdevielle *et al.* 2010, Sarasola *et al.* 2010, BirdLife International 2013). Our objective here is to evaluate the available evidence concerning the presence of Crowned Eagle in Uruguay by considering all original reports in conjunction with the species' past and current distribution patterns as well as its habitat requirements.

Larrañaga's plate

Dámaso Antonio Larrañaga (1771–1848) was a Uruguayan priest and naturalist. He produced a series of writings and plates of birds before 1825 (Escalante 1998). After being poorly conserved and neglected for more than a century (Escalante 1998), these materials were finally published in the 1920s and 1930s. Pl. XLIV of his Atlas (Larrañaga 1930) depicts a Crowned Eagle (Fig. 1), but the illustration lacks any additional data. Escalante (1998) conducted an exhaustive analysis of Larrañaga's ornithological work and found no details of this species in any of the priest's writings (1922, 1923a,b). Due to carelessness, however, some of Larrañaga's materials were lost well before publication (Escalante 1998). Thus, whether or not the original materials included any data concerning the Crowned Eagle plate is unknown.

Most of Larrañaga's collecting and observations were made in Montevideo and its environs (Escalante 1998 provided a tentative list of localities). In June 1815, however, he travelled from Montevideo to Paysandú, through the west of the country. In early June he was at Mercedes (Soriano department) for a few days. There he surveyed the city surroundings, and on 9 June he walked east for a mile or so (Vidal 1930) and commented 'Observé unas aves de rapiña para mí nuevas (Talas Linnei)' ['I observed some birds of prey new to me (Talas Linnei)']. Unable to tie this genus to any particular bird species, 'Talas' was replaced by 'Falco' in some versions of Larrañaga's writings (e.g., Larrañaga 1923b). The next day, Larrañaga mentioned that the landscape of this region included forest islands of 'algarrobos', a characteristic feature of Crowned Eagle habitat in its southern range (Bellocq *et al.* 2002, Maceda 2007).

Sellow's specimens

Friedrich Sellow (1789–1831) was a Prussian naturalist who collected extensively in southern Brazil and adjacent Uruguay and Argentina (Rego *et al.* 2013). He visited the Banda Oriental (currently Uruguay and part of Rio Grande do Sul) in 1821–23 (Escalante 1998). Sellow collected three Crowned Eagles that he sent to the Berlin museum (Kothe

1912). The locality attached to two of these (a young female and an immature male) is Montevideo (Kothe 1912). Because Crowned Eagle was never subsequently observed in Uruguay, their provenance was questioned by Hellmayr & Conover (1949). Alternatively, Claramunt & Cuello (2004) considered Kothe's article as the first report of Crowned Eagle for the country (i.e., the first publication that included a scientific name for the species with reference to Uruguay).

Several unfortunate procedures have contributed to the loss or substitution of key data pertaining to Sellow's specimens. These have included the naturalist's own data-recording practices as well as inappropriate curation at the Berlin museum (Rego *et al.* 2013). Thus, serious limitations restrict analyses of Sellow's specimens and localities (Rego *et al.* 2013). Despite such problems, the possibility that Sellow's eagle specimens were taken in Uruguay cannot be disregarded. During his time in Uruguay, Sellow passed through appropriate Crowned Eagle habitat in the west of the country. This can be inferred from approximate travel routes (Rego *et al.* 2013) and other available information about specific localities he visited in Uruguay (Hackethal 1995). Recent study of archival information relating to these specimens in the Berlin museum has provided no new details (S. Frahnert *in litt.* 2014). All of the specimens Sellow collected in Uruguay may have been labelled 'Montevideo' prior to their being accessioned in the museum, but there is no definitive evidence to support this assumption (S. Frahnert *in litt.* 2014).

During his visits to Montevideo, Sellow met Larrañaga. If he did collect the two Crowned Eagles in Uruguay and shipped them to Europe from Montevideo, it is plausible that Larrañaga saw these specimens. Sellow's specimens are immature while Larrañaga's plate depicts an adult. This suggests that he did not use Sellow's specimens as models for his drawing.

Álvarez's record

Teodoro Álvarez was a Uruguayan agronomist who produced a series of publications about birds (Álvarez 1911, 1933, 1934, 1937). In these he principally highlighted useful and harmful feeding habits of species in terms of their consequences for crops and agriculture in general. Álvarez's (1933) report of a Crowned Eagle taken in the forests of the río Santa Lucía Grande has been cited repeatedly as evidence of the species' presence in Uruguay (e.g., Collar *et al.* 1992, Bencke *et al.* 2003, Maceda 2007, BirdLife International 2013). Several others (e.g., Barattini & Escalante 1958, Cuello & Gerzenstein 1962, Arballo & Cravino 1999), however, have ignored this record.

Analysis of Álvarez's works reveals several inconsistencies. These include inaccurate taxonomic assignments (i.e., some species have incorrect scientific names; e.g., White-spotted Woodpecker *Veniliornis spilogaster*, Narrow-billed Woodcreeper *Lepidocolaptes angustirostris*) and confusion surrounding species identity (e.g., Tropical Screech Owl *Megascops choliba* is confused with Ferruginous Pygmy Owl *Glaucidium brasilianum*). Considering the general lack of bibliographic material at the time, such mistakes are unsurprising.

The Crowned Eagle record is first mentioned in Álvarez (1911) as 'Águila Cenicienta Gen. *Harpyhaliaetus* (Lafr). Esp. *coronatus* (Vieill]'. The species account was reproduced, fully or in part, in subsequent publications by the author. Apart from comments on habits and status, the original account also included a detailed plumage description and range data. Álvarez (1933) only presented the former. In the description (Álvarez 1911, 1934) an occipital crest ('copete en la región occipital'), a distinctive feature of Crowned Eagles, is mentioned. Several other details in the account, however, do not match adults or juveniles of the species: wingtips that extend beyond the tail tip; dark chestnut rectrices with white tips; white underparts, including thighs; bluish mandible and pale purple cere. In addition, the species' range mentioned by Álvarez (South America and part of Central America) do not correspond to Crowned Eagle. We are unable to determine with certainty to which species Alvarez referred in his account. Some features match Osprey (occipital crest, underparts and cere coloration), but others do not.

Arredondo's comments

Horacio Arredondo (1888–1967) was a Uruguayan historian, researcher and naturalist. Arredondo's (1953) observations of Crowned Eagle ('Aguila Mora o Cenicienta *Harpyhaliaetus Coronatus*' sic.) were published in his *Ornitología del Uruguay*. Many of the details were based on Álvarez's publications, but Arredondo made explicit his doubts about the taxonomic assignment. He argued that the species concerned might be Bicoloured Hawk *Accipiter b. bicolor*. Arredondo's description of the bird is almost identical to that of Álvarez. At the end of his account he stated that he had seen the bird throughout most of the country and that it was particularly abundant at Santa Teresa, in Rocha department. Given the clear inconsistencies, this text is wholly unreliable as evidence of Crowned Eagle's presence in Uruguay.

Current status in neighbouring countries

Crowned Eagle has recently been recorded at several localities in adjacent Argentina and Brazil. In north-east Argentina it occurs in Corrientes and Entre Ríos provinces. In Corrientes it has been observed in the following Important Bird Areas (IBAs): Rincón del Socorro (Giraudo & Di Giacomo 2007), Espinal de Mercedes (Di Giacomo 2007) and Felipe Jofre (Fraga 2007). In south-eastern Entre Ríos it has been found at another IBA, Las Ceibas, which is very close (*c*.30 km) to Uruguay. Landscape characteristics at the latter site (open woodland of *Prosopis affinis* and *Acacia caven* within a mosaic of grasslands and wetlands; Veiga 2007) are very similar to those in neighbouring south-west Uruguay. In southern Brazil, Crowned Eagle has recently been found at several localities in Rio Grande do Sul (Albuquerque *et al*. 2006, Barcellos & Accordi 2006). One observation was made at São Gabriel, just *c*.115 km from the Uruguayan border (Dias 2011). These records, together with the fact that juvenile eagles perform significant dispersal movements (up to 400 km from their natal site; Sarasola 2011), suggest that individuals may reach Uruguay. The most promising areas to search are probably the 'forests of the western plains' (*sensu* Brussa & Grela 2008) along the middle and lower Uruguay River and the grassland-dominated landscapes of northern Uruguay.

Conclusions

Unambiguous records of Crowned Eagle in Uruguay remain elusive. Although Alvarez's (1933) observation has been cited as evidence, his record is unreliable. The bird described by Álvarez (1911, 1934) was not a Crowned Eagle. Arredondo's comments also include major inconsistencies. Both Larrañaga and Sellow visited western Uruguay in the early 19th century when this region harboured suitable habitat for the species as evidenced by a confirmed historical record from nearby Entre Ríos, Argentina (Lee 1873). Two of Sellow's specimens may have been collected in western Uruguay. Larrañaga's pl. XLIV may have been inspired by a bird of prey unknown to him, which he observed in the same region. Unfortunately, both Larrañaga and Sellow's materials have suffered from inadequate care and the connections between contemporary notes and plates or specimens have been lost.

Crowned Eagle may still reach Uruguay sporadically, probably juveniles on dispersal. In western Uruguay, 'algarrobo' forests, one of the habitat types favoured by the species, are threatened by several human-related activities (FMAM 1999, Brussa & Grela 2007). Effective conservation measures targeted at these forests may increase the colonisation prospects of this threatened raptor.

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New avian records along the elevational gradient of Mt. Wilhelm, Papua New Guinea

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Summary.—The north slopes of Mt. Wilhelm, the highest peak in Papua New Guinea, support a complete elevational gradient of relatively undisturbed rainforest, from 200 m to the tree line at 3,700 m. Based on field work in 2010 and 2012 over the Mt. Wilhelm elevational gradient, we report novel distribution data for 43 species, including geographic and elevational range extensions, demographic data, and new records of species poorly known in New Guinea.

The island of New Guinea has a complex geological and tectonic history (Hall 2002) that has impacted modern biogeographic patterns in the island's flora and fauna (e.g. Heads 2002, Deiner *et al.* 2011). Although birds are globally well known taxonomically, field work in New Guinea continues to uncover taxa new to science and complex biogeographic patterns (Diamond 1985, Mayr & Diamond 2001, Beehler *et al.* 2007, Beehler & Prawiradilaga 2010).

The island is divided into southern and northern watersheds by the Central Range (Diamond 1985), whose uplift is estimated to have commenced *c.*4–5 MYA (Pigram & Symonds 1991). Most of the Central Range is ornithologically poorly known. The highest peak in Papua New Guinea, Mt. Wilhelm (4,509 m), is near the centre of the Bismarck Range, which forms part of the northern Central Range. From its summit, the northern slopes fall steeply to the Ramu Valley at 50 m. The slopes of Mt. Wilhelm thus support the full suite of elevational zones, with a large region above the tree line. Mt. Wilhelm experiences high annual precipitation, especially its northern slopes, from 4,660 mm at 1,200 m to *c.*3,000–3,400 mm on the summit ridge at 4,450 m; the northern slopes are more consistently cloud-covered than those in the south and east (Hope 1976). Northern slopes of Mt. Wilhelm support relatively pristine forest, being disturbed only in close proximity to larger villages. In consequence, Mt. Wilhelm is of considerable ornithological interest, given a complete elevational gradient supporting relatively undisturbed forest and a highly diverse avifauna.

Diamond's (1972) monograph, describing the avifauna of the broader region around Mt. Wilhelm, arbitrarily defined the 'Eastern Highlands' as the area between Tari in the west to Kainantu in the east, and from the Schrader Range in the north to Lake Kutubu and Mt. Kirimui in the south. Thus it includes, but is larger than, the political subdivision of Papua New Guinea of the same name. The first systematic collections in this region were made in the early 1950s in the Wahgi Valley and environs (Mayr & Gilliard 1954, Gyldenstolpe 1955). The Schrader Range was surveyed by Stresemann in 1923 (*cf.* Diamond 1972) and by Gilliard & LeCroy (1968), Mt. Giluwe and Lake Kutubu by Schodde & Hitchcock (1968), and the Kubor Range by Hitchcock (1964). Bulmer (1962, 1967) made extensive observations in the Kaironk Valley (Schrader Range) and Kyaka area from the Baiyer River to the northern slopes of Mt. Hagen. Diamond undertook four expeditions (1964–66, 1969) to the south-eastern part of the Eastern Highlands (Diamond 1972).

To our knowledge, there has been no detailed ornithological survey of the north-east slopes of Mt. Wilhelm. The region surveyed by us is delimited by the Wahgi Valley in the north, the Kyaka area in the east, and the area surveyed by Diamond in the west. Usually, only the uppermost elevations are visited by keen birdwatchers, whereas the lower valleys from Kegesugl to Bundi and Brahmin stations are very poorly surveyed due to difficulties of access. In 2010 and 2012, we conducted ornithological surveys with the aim of surveying the avifauna of the entire elevational gradient (see Table 2 for survey dates). Here, we report range extensions and other noteworthy observations made during our field work.

Methods

The study was conducted on the north-east slopes of Mt. Wilhelm (4,509 m) in the northern watershed of the Central Range in Madang and Chimbu provinces (Fig. 1). The forest transect spanned 30 km from the lowland floodplain of the Ramu River (200 m; 05°44′S, 145°20′E) to the treeline (3,700 m; 05°47′S, 145°03′E). The surveyed region (hereafter the region) is in the Bismarck Range and includes: the valleys of Lake Aunde and Piunde, Gwaki and Goe Creeks (to the uppermost Inbrum River in the north), the area between Kegesugl village, Bruno Sawmill and Sinopass (bounded by the range encompassing Bunoni station on its southern slopes, and by the Inbrum River in the north), Bundi station, Bundi station airport (bounded by the Ua River in the south-east), and the Inbrum River valley between Bundi station and Wau (near Brahmin airport). A detailed map is available at: http://tvardikova.weebly.com/uploads/3/8/5/6/3856833/ramu_teriotry_map.jpg.

Quantitative surveys were completed at eight sites (Table 1) evenly spaced at 500-m elevational intervals. Birds were surveyed using three standardised methods at each site—point counts, mist-netting and quantitative area counts—over three surveys in 2010 and 2012 (Table 2). Incidental observations were also recorded at camps and along trails between camps.

Point counts were undertaken at 16 sites over a 2,250-m transect (successive points were 150 ± 5 m apart; one transect per elevational site). Transects were directed at representative and diverse microhabitats within the area (e.g. ridges, valleys, creeks; ≥ 150 m from forest edge) and ± 50 m elevational change was permitted. All birds seen or heard within a radius of 50 m were recorded. Each count lasted 15 minutes, with all 16 points being surveyed prior to 11.00 h. To minimise double-counting, we aimed to accurately track moving birds, and we recorded additional individuals of the same species only if vocalising simultaneously and / or from an obviously different direction within a short time. Each transect (of 16

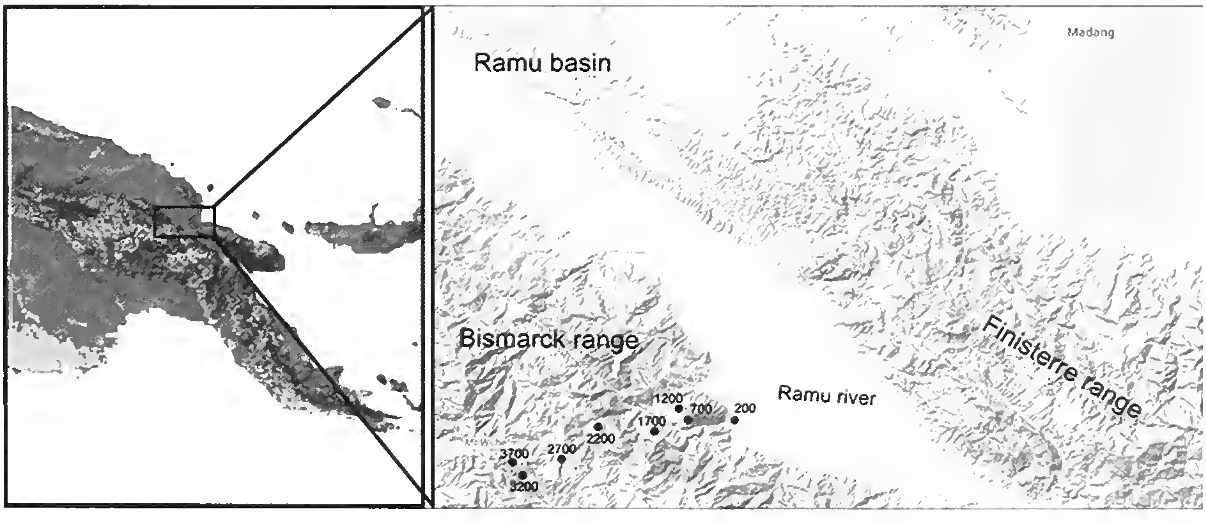

Figure 1. Map of Papua New Guinea showing the location of the Mt. Wilhelm and the elevational gradient that we studied.

TABLE 1
Location of study sites along the Mt. Wilhelm altitudinal gradient surveyed in 2010 and 2012.

Site name	Elevation (m)	Latitude	Longitude
Kausi	200	05°44′33″S	145°20′01″E
Numba	700	05°44′14″S	145°16′12″E
Memeku	1,200	05°43′18″S	145°16′17″E
Bananumbu	1,700	05°45′21″S	145°14′11″E
Sinopass	2,100	05°45′34″S	145°10′49″E
Bruno Sawmill	2,700	05°48′57″S	145°09′02″E
Kombuno Mambuno	3,200	05°48′18″S	145°04′20″E
Lake Aunde	3,700	05°47′10″S	145°03′32″E

TABLE 2
Summary of surveys and methodology used along the Mt. Wilhelm elevational gradient. Each replication of point counts comprised surveys at 16 points evenly spaced over the 2,250-m transect, with mist-netting conducted for 12 hours / day, and each replication of a quantitative area count represents a 2–3-hour survey. The third survey was split into two parts.

Survey number	1	2	3	
Start of survey	9 Apr 2010	26 Jul 2010	15 May 2012	1 Aug 2012
End of survey	31 May 2010	15 Oct 2010	15 Jul 2012	15 Oct 2012
Point counts	three replications	six replications	five replications	
Mist-netting	three days	five days	three days	
Quantitative area counts	three replications	six replications	N.A.	

points) was surveyed 14 times, resulting in 56 hours of data along each transect (i.e. each elevation). In total, we completed 1,792 point counts representing 448 hours.

We mist-netted birds along a 200 m-line of nets placed end to end (each net 2.5 m high × 12–18 m long, mesh 16 mm), from 05.30 h to 17.30 h daily, for 11 days at each site. On the first three days, the nets were placed between the first three points of the point count transect, then transferred to the last three points for the next three days of mist-netting, whenever possible (see Table 2). We identified all mist-netted birds, marked them individually with colour rings and released them within ten minutes. All recaptured birds were identified from colour ring combinations.

Area counts commenced at 15.00 h and lasted until 17.00 h or 18.00 h, during which we randomly walked (*c.*2 km^{-h}) the surrounding area (*c.*80 ha) recording all birds seen or heard. All species recorded during our expeditions are listed in Appendix 1. Photographs, sound-recordings and observation data are deposited online (e.g. Global Biodiversity Information Facility, www.xeno-canto.org (XC), and New Guinea Birds Online: pngbirds.myspecies.info). We used a Marantz PMD 620 digital recorder and Sennheiser ME67 microphone to record vocalisations. We follow IOC World Bird List (version 4.1.; www.worldbirdnames.org/) species-level taxonomy and nomenclature.

In total, our dataset for each site included 14 replications of point count surveys, 11 mist-netting days and 20 hours of quantitative area counts. The point counts and quantitative area counts were performed by both authors and by S. Jeppy, in teams of two with rotating membership. Mist-netting was performed by the authors with help of local villagers.

Results

We recorded 260 species at eight elevational sites (and from trails between them) on Mt. Wilhelm, mist-netted 1,490 birds and censused >34,000 individual birds during the three field surveys. Here we report novel distributional data for 43 species, including range extensions (for at least five species), new elevational ranges (at least 18 species), demographic data and records of species poorly known in New Guinea. We also provide a complete list of species recorded with their observed elevational ranges (Appendix 1).

SALVADORI'S TEAL *Salvadorina waigiuensis*
Endemic to montane New Guinea, rare and local at lower elevations but occurs across the island in suitable habitat. Previously unknown above 4,100 m (Coates & Peckover 2001), we observed two at a small waterbody at 4,300 m on five occasions in April and July 2010.

GREAT-BILLED HERON *Ardea sumatrana*
Scarce resident throughout New Guinea's lowlands, with one record at 550 m (Coates 1985). Mainly in coastal areas, but reported to occasionally follow rivers inland. Previously unreported from the middle Ramu River (but expected to occur in Sepik–Ramu River region: BirdLife International 2013a), we observed it at *c.*300 m on the river near Brahmin station, representing a south-easterly range extension.

FOREST BITTERN *Zonerodius heliosylus*
Occurs at 100–300 m, occasionally to 1,430 m (Coates 1985) or 1,450 m (Beehler *et al.* 1986). Three records of singles at *c.*1,600–1,650 m, near Bundi Station, apparently south of the known range (Martínez-Vilalta & Motis 1992), although the relative lack of recent records compromises efforts to accurately delineate the species' distribution. Those we observed were under the cover of shrubs at the river edge, once in swampy vegetation. One that flushed perched on a tree *c.*3 m high. Observed to take a lizard and twice small fish.

BLACK-WINGED KITE *Elanus caeruleus*
Twice observed in mid-August 2012 above shrub and grassland habitat below Lake Piunde (at 3,200–3,600 m), which is higher than previously reported for New Guinea (2,300 m: Beehler *et al.* 1986; 1,830 m: Coates 1985).

BLACK-MANTLED GOSHAWK *Accipiter melanochlamys*
Previously unrecorded above 3,000 m (Coates & Peckover 2001). We observed it regularly at *c.*3,200 m and 3,500 m below Lake Piunde (*c.*05°47′45″S, 145°03′53″E) in 2010 and 2012.

MEYER'S GOSHAWK *Accipiter meyerianus*
Regularly observed in May 2010, August 2010 and August 2012 at 1,700–2,200 m, always in forest interior along rivers. Never observed soaring or gliding. Pairs repeatedly encountered on exposed branches of tall trees at 2,200 m, and observed hunting for large lizards on a tree at 1,700 m and for a large honeyeater in the canopy at 2,200 m. Ours are possibly the first records of this uncommon species in the Bismarck Range (Ferguson-Lees & Christie 2001), although it is expected to occur throughout the eastern Central Range.

FORBES'S FOREST RAIL *Rallicula forbesi*
Previously recorded at 1,000–3,000 m (Coates & Peckover 2001). We found it to be quite common between 2,200 m (six records) and 3,200 m (five), especially at 2,700 m (seven seen,

three heard) where we mist-netted two individuals. We observed a pair near their roost on three consecutive days at 2,700 m, foraging on the forest floor in the morning.

BARE-EYED RAIL *Gymnocrex plumbeiventris*
Previously reported from sea level to 1,200 m (Beehler *et al.* 1986), max. 1,600 m in east New Guinea (Taylor 1996). We observed one foraging in a grassy area beside a river at 1,400 m on 20 September 2012. Local people informed us that the species occurs in this area year-round.

NEW GUINEA WOODCOCK *Scolopax saturata*
Recorded at 1,500–3,000 m (Beehler *et al.* 1986) even up to 3,800 m (Coates 1985). Our two observations at 2,700 m are from a region lacking previous records, although the species was expected to occur (Beehler *et al.* 1986). One was observed foraging in dense understorey near our camp in primary forest at *c.*20.00 h. What was presumably another was seen *c.*1.5 km away in dense vegetation at dawn.

METALLIC PIGEON *Columba vitiensis*
Regularly observed (12 records of at least seven birds on six days) at 2,700 m in 2010, rarely ($n = 2$) in 2012; less common (four in six days) at 2,200 m. Peckover & Filewood (1976) mist-netted one at 2,700 m, whilst Mayr (1941) considered it a lowland species found below 1,400 m. We did not encounter it at lower elevations. Two sound-recorded at 2,700 m (XC165214; pngbirds.myspecies.info/species/columba-vitiensis). Observed alone, in pairs or groups of three, usually on very tall emergents, although one was perched *c.*4 m above ground, just before dusk, near our camp at 2,200 m.

SLENDER-BILLED CUCKOO-DOVE *Macropygia amboinensis* / **BAR-TAILED CUCKOO-DOVE** *M. nigrirostris*
M. amboinensis occurs in mainland New Guinea from sea level to 1,800 m, locally to 2,100 m (Beehler *et al.* 1986). We found it to be very common (5–7 birds per day) at all elevations 200–2,200 m, and similarly abundant throughout, albeit slightly more numerous at 200 m. *M. nigrirostris* is also well known in the region, and expected from sea level to 2,600 m (Beehler *et al.* 1986). However, we found it only at 2,700 m, never at lower elevations.

THICK-BILLED GROUND PIGEON *Trugon terrestris*
Inhabits rainforest and monsoon forest in lowlands and hills below 640 m (Baptista *et al.* 1997, Coates & Peckover 2001). Villagers killed one at *c.*1,100 m and brought it to our camp at 1,200 m in July 2010. Observed regularly only at our 700 m site.

PHEASANT PIGEON *Otidiphaps nobilis*
We observed what was presumably the same bird (in the same tree) at 2,600 m on 15–17 August 2012, with another at 1,700 m in 2010 and three at 2,200 m in 2010 and 2012. Our observations are higher than previously reported (to 1,900 m; Beehler *et al.* 1986, and heard at 2,050 m on Huon Peninsula; Freeman *et al.* 2013).

CORONETED FRUIT DOVE *Ptilinopus coronulatus quadrigeminus*
Previously known to 1,200 m (Beehler *et al.* 1986), but we recorded it at 200–1,700 m.

ORNATE FRUIT DOVE *Ptilinopus ornatus*
Found primarily at 200–1,350 m, but apparently nomadic up to 2,500 m (Beehler *et al.* 1986). We observed a flock of five in the canopy of a fig tree, one perched at dusk *c.*2 m above

ground in a tree near our camp at 2,200 m, and we disturbed another two in a fig tree at 2,200 m in 2010. Interestingly, we did not record it at lower elevations.

PESQUET'S PARROT *Psittrichas fulgidus*
Threatened by hunting; recorded to 2,000 m in Central Range (Beehler *et al.* 1986) and at 600–2,420 on the Huon Peninsula (Freeman *et al.* 2013). Just one observation involving two birds at 2,200 m. Usually reported as rare and in small numbers, with recent rapid declines recorded locally (BirdLife International 2013b).

PAPUAN KING PARROT *Alisterus chloropterus*
Reported to be mainly a hill forest species ranging from sea level to 2,300 m, occasionally to 2,600 m (Coates 1985). We made 100 records at 2,700 m and 128 records at 2,200 m, while it was less abundant at 700 m and 1,700 m (two and three observations, respectively), and we did not encounter it at 200 m. Our other surveys in the Madang lowlands found the species to be quite abundant at 50–250 m.

DUSKY LORY *Pseudeos fuscata*
Common at 2,200–2,700 m, and also present at 200 m and 1,700 m. Previously reported only to 2,400 m (Beehler *et al.* 1986, Collar 1997).

PYGMY LORIKEET *Charmosyna wilhelminae*
Uncommon, possibly overlooked (Beehler *et al.* 1986), in montane forest, mainly at 1,000–2,200 m (Collar 1997). Also descends to lowlands, even to sea level. Surprisingly, most of our records were at 1,200 m ($n = 43$) with many fewer ($n = 19$) at 700 m, lower than expected.

RED-FRONTED LORIKEET *Charmosyna rubronotata*
Reported by Coates (1985) at 0–850 m, from the Vogelkop east to the Ramu River in Madang province, whereas Collar (1997) listed it only from Vogelkop east to the Adelbert Mountains on mainland New Guinea. We observed it at 200 m, at least 60 km up the Ramu River from the range in Coates (1985) and at least 150 km from that reported by Collar (1997). Identification was based on the distinct red forehead and blue ear-coverts, not blue ear-coverts and red lores, cheeks and upper throat like Red-flanked Lorikeet *C. placentis*. Never observed in flocks with *C. placentis* but once with Black-capped Lory *Lorius lory*. We mostly observed *C. placentis* at 700 m (17 records), rarely at 200 m (five), while we recorded eight *C. rubronotata* at 200 m (two flocks on separate surveys). Photographed and sound-recorded (XC164011; pngbirds.myspecies.info/species/charmosyna-rubronotata).

CHESTNUT-BREASTED CUCKOO *Cacomantis castaneiventris* / **FAN-TAILED CUCKOO** *C. flabelliformis*
We observed *C. castaneiventris* at 200–1,200 m and *C. flabelliformis* at 1,200–3,700 m, within their known ranges. Surprisingly, we mist-netted them in syntopy at 1,200 m. In the hand, *C. castaneiventris* is smaller and more richly coloured than *C. flabelliformis*. *C. castaneiventris* has the head-sides and chin dark bluish grey, throat rich chestnut and bill black, whereas *C. flabelliformis* has the head-sides and chin grey with a greenish sheen, throat grey and bill blackish brown. The whistled trill of *C. castaneiventris* is *c.*2 times shorter (and slightly faster) than that of *C. flabelliformis*. *C. castaneiventris* also produces a slow-paced phrase of three mournful notes (*seei-to-saai*) resembling Brush Cuckoo *C. variolosus* (but slower and on an even pitch). Mournful-sounding *C. flabelliformis* has only two notes (*pee-wee*; slow and the second note higher pitched).

BARKING OWL *Ninox connivens*

Commonly heard around Bundi village at *c.*1,500 m. Elevational range on New Guinea unknown, but our observation is higher than all available records from the mainland (up to 500 m), although reported at 1,040 m on Karkar Island (Diamond & LeCroy 1979).

MARBLED FROGMOUTH *Podargus ocellatus*

Mainly in the lowlands, but recorded to 1,500 m on New Guinea (Holyoak 1999, Coates & Peckover 2001). We mist-netted and photographed the species at 1,200 m and 1,700 m, and sound-recorded it at 2,200 m (XC 164007; pngbirds.myspecies.info/species/podargus-ocellatus).

PACIFIC SWIFT *Apus pacificus*

Rare winter visitor to New Guinea, recorded principally in southern New Guinea in October–March (Beehler *et al.* 1986). Coates (1985) mentioned a record from the Huon coast (Wasu Station) in mid November, with another observation on the Huon Peninsula in July (Freeman *et al.* 2013). We recorded it in April and late May 2010 at 200 m and mid June until early July 2012 at the same elevation, suggesting that some (perhaps younger) birds over-summer on New Guinea.

MOUNTAIN KINGFISHER *Syma megarhyncha* / **YELLOW-BILLED KINGFISHER** *S. torotoro*

S. torotoro is common to fairly common in lowlands, mostly below 500 m, locally to 1,100 m (Coates 1985); *S. megarhyncha* occurs at 700–2,200 m (Beehler *et al.* 1986) or 760–2,200 m (Coates 1985). The transition zone in Chimbu province is at 1,100–1,340 m (Diamond 1972). We observed *S. torotoro* only at 200 m and 700 m, and did not record *S. megarhyncha* below 2,200 m, with the highest at 2,700 m (sound-recorded) and one at *c.*2,600 m. Given the difficulty of observing of *Syma* kingfishers in the field and separating the two species' vocalisations, further work is needed to elucidate their true elevational ranges.

RAINBOW BEE-EATER *Merops ornatus*

Widespread throughout New Guinea and Australia, with Australian birds mainly wintering in New Guinea, where migrants are present early March to early October. Present in smaller numbers during the rest of the year in the Port Moresby area where it breeds. Also said to breed in the Sepik–Ramu River Region. The very similar Blue-tailed Bee-eater *M. philippinus* breeds locally throughout New Guinea. We recorded *M. philippinus* at our study sites near Madang town, but not on Mt. Wilhelm. All those observed at our 200 m site had yellow-orange (not greenish) foreheads and a broad black eyestripe bordered narrowly by blue (not white) above, confirming their identity as *M. ornatus*. Observed during all surveys (9 April–15 October 2010) with a few breeding pairs in September 2012, in burrows in flat sandy soil along the Ua River.

PAPUAN TREECREEPER *Cormobates placens*

Widespread in the Central Range but apparently absent from central-eastern New Guinea (Diamond 1972). *C. p. steini* occurs in west and central New Guinea in the Weyland Mountains east through the Hindenburg Range to Tari Gap, with *C. p. meridionalis* in south-east New Guinea east from the Aseki area, Mt. Kaindi and Herzog Mountains (Coates 1990, Noske 2007). Occurs at 1,250–2,600 m (or 3,000 m in Snow Mountains: Coates 1990). Our observation refutes Diamond's contention as to the absence of *C. placens* in this part of the Central Range. We recorded it at 2,630 m, outside its known range, but were unable to identify the subspecies, observing three individuals (two on 25 April and one on 27 April 2010) bark-climbing and searching for food on dry branches and the trunk of a tall tree (*c*.10–15 m above ground). The singleton was with a group of five Large Scrubwrens *Sericornis nouhuysi* and two Friendly Fantails *Rhipidura albolimbata*. Sound-recorded (XC165217; pngbirds.myspecies.info/species/cormobates-placens).

MOUNTAIN HONEYEATER *Meliphaga orientalis*

Occurs mostly at lower and mid elevations, *c*.550–2,100 m, and is the only *Meliphaga* common (or present) above 1,400 m (Beehler *et al*. 1986). We mist-netted it frequently at 1,700–2,700 m (*n* = 7; pngbirds.myspecies.info/species/meliphaga-orientalis).

LONG-BEARDED MELIDECTES *Melidectes princeps*

Endemic to a few valleys on Mt. Giluwe, Mt. Hagen and the Kubor Range, mainly at 3,000–3,800 m (Higgins *et al*. 2008) but recently recorded to 4,200 m and extends to 2,750 m (Coates & Peckover 2001). On Mt. Wilhelm, previously reported mainly above 3,050 m (Coates & Peckover 2001, Higgins *et al*. 2008). Very abundant at 3,200–3,700 m, but none found in denser forest at lower elevations, and the species seems to prefer scattered trees at the tree line. Albeit restricted to small areas (on Mt. Wilhelm *c*.200 ha), it is one of the commonest species in the valley of Lakes Piunde and Aunde.

YELLOWISH-STREAKED HONEYEATER *Ptiloprora meekiana*

Resident of Saruwaged Mountains (Huon Peninsula), Herzog Mountains, the upper Mambare Range and Mt. Tafa-Efogi (Higgins *et al*. 2008). We provide the first record for Mt. Wilhelm, where two were observed foraging in a flowering tree at *c*.2,500 m in May 2012. The species is thought to be nomadic, which fits our lone observation. Call is an easily overlooked *chip* or *ship*.

BICOLOURED MOUSE-WARBLER *Crateroscelis nigrorufa*

Patchily distributed throughout foothill forest of New Guinea, with a very restricted elevational range (Beehler *et al*. 1986). We found it to be quite abundant (2–4 records / 12.6 ha) at 1,700 m, and even commoner at 1,770–1,790 m (but we did not conduct standardised surveys there). The local abundance of this species is surprising, given that just 38 specimens are listed in the ORNIS database (Freeman *et al*. 2013).

BUFF-FACED SCRUBWREN *Sericornis perspicillatus* / **PAPUAN SCRUBWREN** *S. papuensis*

These species differ markedly in their vocalisations and are easily separated if singing. In the hand, local *S. papuensis* has a dark subterminal tail-band (95%, *n* = 64) and a brownish-buff crown and forehead, while *S. perspicillatus* has a grey crown and no subterminal tail-band at least in individuals examined by KS (*c*.70%, *n* = 73). *S. perspicillatus* was very numerous at 1,700–2,200 m with abundance decreasing to 2,700 m, whilst *S. papuensis* appeared at 1,700 m and became more abundant towards its upper range limits at 3,200 m. They overlap broadly at *c*.1,700–2,700 m. Diamond (1972) previously suggested that the presence or lack of a subterminal tail-band is helpful in their separation, confirmed by Freeman *et al*. (2013) and by our data. We disagree with Gregory (2007), who stated that Buff-faced Scrubwren also has a dark subterminal tail-band.

STOUT-BILLED CUCKOOSHRIKE *Coracina caeruleogrisea*
On New Guinea, known mainly in lowlands, hill forest and lower montane regions, from sea level to 1,700 m, rarely 2,450 m (Beehler *et al*. 1986, Taylor 2005). Recorded also at Tari Gap at 2,500 m in 1990 (N. P. Dreyer pers. comm.). We observed four regularly at 2,700 m in September 2012, frequently heard its distinctive voice at all sites 700–2,700 m, and mist-netted a male at 2,200 m.

YELLOW-BREASTED SATINBIRD *Loboparadisea sericea*
We mist-netted a male on 16 June 2012 at 1,700 m, and observed the species three times near our mist-nets (presumably the same male twice, and a female). Once we heard three harsh *sssh* notes, louder than those of Superb Bird-of-paradise *Lophorina superba*, which was abundant at this elevation. The male was observed feeding on berries in the lower forest strata, the female berries and large insects.

GOLDEN CUCKOOSHRIKE *Campochaera sloetii*
Previously known only in the Arfak Mountains east to the Wewak area (Idenburg River and near Holland; *C. s. sloetii*) and the southern New Guinea lowlands from the River Mimika east to Moroka, and foothills of Owen Stanley Range (*C. s. flaviceps*; Rand & Gilliard 1967, Taylor 2005). Previously reported from sea level to 1,100 m (Coates 1990). We recorded it at 200 m and 1,200 m, but made just two sightings and never mist-netted the species, with most records vocal only. The vocalisation we heard was closer to available recordings of *C. s. flaviceps*, which would represent a northerly range extension, if confirmed. Our other surveys in the Madang lowlands confirmed the species to be a rare resident along the Ramu River.

BLACK SICKLEBILL *Epimachus fastuosus* / **BROWN SICKLEBILL** *E. meyeri*
Sicklebills occur in mid-montane primary forest, more rarely in adjacent second growth and garden edges. *E. fastuosus* was previously known at 1,280–2,550 m, mainly 1,800–2,150 m, and predominates at lower elevations over *E. meyeri*. The latter occurs in middle and upper montane forests at 1,500–3,200 m, mainly at 1,900–2,900 m. We suggest that they are not elevational replacements on Mt. Wilhelm, as their ranges overlap broadly: *E. fastuosus* was abundant at 2,200 and 2,700 m (*n* = 21 and 41, respectively) and rare at 1,200 and 1,700 m (*n* = 3 and 5, respectively); *E. meyeri* was most abundant at 2,700 m (*n* = 98), less numerous at 2,200 and 3,200 m (*n* = 45 and 48, respectively), and rare at 1,700 m (*n* = 2). We observed *E. fastuosus* higher than expected and *E. meyeri* within its previously described range.

NORTHERN VARIABLE PITOHUI *Pitohui kirhocephalus* / **HOODED PITOHUI** *P. dichrous*
These sister species (Dumbacher *et al*. 2008) appear to replace each other elevationally over most New Guinean ranges (Beehler *et al*. 1986). On Mt. Wilhelm, *P. kirhocephalus* occurs at lower elevations (200–1,200 m; *n* = 50/1, 68/2 and 54/2, seen + heard/mist-netted, respectively), with *P. dichrous* at higher elevations (700–1,700 m; *n* = 53/2, 231/5 and 105/1, respectively). On the other hand, their ranges are not strictly exclusive as at 700 m and 1,200 m, both were common in syntopy, and the species are possibly widely sympatric. The zone of transition is also much higher than in the Fakfak Mountains (*c*.950–980 m: Rheindt 2012).

Discussion

All of New Guinea is relatively unexplored ornithologically. Our comprehensive surveys along the elevational gradient of Mt. Wilhelm in 2010 and 2012 confirm this, given that our work produced at least five additions to the regional avifauna (*Cormobates placens, Campochaera sloetii, Ptiloprora meekiana, Charmosyna rubronotata, Ardea sumatrana,* and possibly *Zonerodius heliosylus* and *Accipiter meyerianus*). Our observations of *Cormobates placens* are especially interesting as Diamond (1972) considered *C. placens* one of nine 'drop-out' species (i.e. those recorded from the Central Range to the east and west of the Eastern Highlands, but not in the Eastern Highlands despite suitable habitat). The range of *C. placens* was believed to be marked by a gap of *c.*400 km, but our observations confirm its presence there. Nevertheless, we did not record any of the other eight bird species assumed to be missing.

Two other species regularly found along the Ramu River and in the Madang lowlands were not observed: Northern Cassowary *Casuarius unappendiculatus* and Victoria Crowned Pigeon *Goura victoria*. These could be absent due to hunting pressure. Habitats at our 200 m site on the Mt. Wilhelm gradient were flat and swampy, and did not differ obviously from sites in the Madang lowlands where we encountered both species regularly (KS unpubl.). Nearby Brahmin mission (*c.*1.5 hours walk) is one of the largest villages in the region, and local people hunt the surrounding area heavily, perhaps including our study site. Hunting at our 200 m site might also explain the local absence of *Alisterus chloropterus,* which is expected to occur from sea level to 2,600 m, and our surveys of primary forest in the Madang lowlands confirmed it to be abundant there.

Competition between closely related species is believed to play an important role in avian community structure in New Guinea (Diamond 1973, 1986), which hypothesis is supported by distributional patterns of elevational replacements, i.e. closely related species (usually congeners) inhabiting the same habitat type but which possess largely or completely exclusive elevational ranges. However, our observations from Mt. Wilhelm do not support some of Diamond's (1972) conclusions concerning segregation by elevation. For most species-pairs mentioned in Diamond's work, we observed large gaps in their elevational ranges, e.g. Purple-tailed *Ducula rufigaster* (200 m) and Rufescent Imperial Pigeons *D. chalconata* (1,700–2,700 m), *Syma torotoro* (200–700 m) and *S. megarhyncha* (2,200–2,700 m) or Lowland *Peltops blainvillii* (200–700 m) and Mountain Peltops *P. montanus* (1,700–2,700 m). At least some of the apparent gaps between species-pairs might reflect our survey methodology, with field work at closer-spaced elevational sites necessary to confirm their true elevational ranges.

More surprisingly, we observed few sharp elevational transitions or complete mutual exclusions. Diamond (1972) regarded segregation of Rusty *Crateroscelis murina* and Mountain Mouse-warblers *C. robusta* as an example of abrupt elevational segregation. On Mt. Karimui, *C. murina* progressively increased in abundance with elevation until it abruptly disappeared at 1,643 m, to be replaced by *C. robusta* at 1,646 m (Diamond 1972). On Mt. Wilhelm, *C. murina* was present at 200–1,700 m and *C. robusta* at 1,200–3,700 m, with *C. nigrorufa* narrowly present at 1,700–1,790 m. Similarly, we did not confirm a sharp segregation for congeneric species of *Pitohui, Epimachus, Sericornis* (see main text), *Melanocharis, Rhipidura* and *Coracina* (*cf.* Appendix 1). Species from these genera overlapped in their elevational ranges (sometimes broadly).

Diamond (1973) illustrated the phenomenon of interspecific competition by comparing the elevational ranges of species of *Ptiloprora* in the Huon and Central Ranges. Rufous-backed Honeyeater *Ptiloprora guisei* is resident at *c.*1,700–2,500 m (2,900 m: Higgins *et al.* 2008) in the Central Ranges, replaced above 2,500 m by its close relative Grey-streaked Honeyeater *P. perstriata*. On the Huon Peninsula, where *P. perstriata* is absent, *P. guisei* expands its niche, to *c.*1,660–3,500 m. Surprisingly, we observed *P. guisei* at 1,700–3,200 m (*n* = 6, 11, 17 and 1 mist-netted, respectively), with *P. perstriata* at 2,200–3,700 m (*n* = 8, 39, 34 and 12 mist-netted, respectively). Our mist-netting data confirm that the two species overlap broadly, and both are most abundant at 2,200 m and 2,700 m, suggesting a lack of strong competition. *P. guisei* also appears to extend to higher elevations, without any obvious impact on *P. perstriata* (which was observed within its expected range).

We recorded many extensions to upper elevational ranges (≥ 18 species, or 7% of the total), which is especially surprising considering the elevational distance of 500 m between sites, resulting in significant under-estimation of limits at in-between elevations, and that we did not consider potential extensions of < 100 m as significant. However, our main caveat is the absence of historical data for Mt. Wilhelm. Baseline information on the abundance of species over elevational gradients is essential to determine shifts in elevation and their significance (Shoo *et al.* 2006). Ranges reported in the general literature may include mistakes, may lack precision or may be specific to another region. However, it seems unlikely that data on elevational ranges would systematically under-estimate only upper elevational limits.

Shifts in geographic ranges are frequent in temperate regions, where species may respond to climate warming by moving to higher latitudes or elevations. The few studies that have reported elevational range extensions for tropical birds (Pounds *et al.* 1999, Peh 2007) have relied on indirect evidence, derived from community changes in census plots (Pounds *et al.* 1999) or changes inferred from bird lists (Peh 2007). In accordance with a previous study (Forero-Medina *et al.* 2011), we found more elevational shifts for frugivorous birds (ten species) than insectivores (four), while range extensions comprised mainly non-passerines and frugivores. These groups comprise rather mobile species with larger home ranges and lower densities, while many frugivores may seasonally follow resources such as flowering or fruiting trees (Loiselle & Blake 1990). Nevertheless, the observed shifts were repeated across the three surveys, and we repeatedly observed several species higher than expected.

Our new data regarding avian distributions reveal that New Guinea continues to be an excellent theatre to study diversification, competition and community structure. Our new elevational records suggest that some species are expanding upslope in response to climate change. We recommend further biodiversity surveys in all of New Guinea's mountains, and continued monitoring to investigate species distributions in more detail.

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Appendix 1

Recorded bird species and their observed elevational ranges. A single elevation is given if the species concerned was recorded at just one site. Continuous range is entered as lowest–highest, whilst elevational sites separated by commas indicate the species was not observed at all sites between the lowest and highest elevation. Species denoted * are discussed in the text.

English name	**Scientific name**	**Observed range (m)**
Dwarf Cassowary	*Casuarius bennetti*	2,700
Wattled Brushturkey	*Aepypodius arfakianus*	1,700
Collared Brushturkey	*Talegalla jobiensis*	1,200
New Guinea Scrubfowl	*Megapodius decollatus*	200–700
Salvadori's Teal	*Salvadorina waigiuensis*	4,300*
Pacific Black Duck	*Anas superciliosa*	3,500
Forest Bittern	*Zonerodius heliosylus*	1,600–1,650*
Great-billed Heron	*Ardea sumatrana*	300*
Black-winged Kite	*Elanus caeruleus*	3,200–3,600*
Long-tailed Honey Buzzard	*Henicopernis longicauda*	200–700
Grey Goshawk	*Accipiter novaehollandiae*	700
Black-mantled Goshawk	*Accipiter melanochlamys*	3,200–3,500*
Meyer's Goshawk	*Accipiter meyerianus*	1,700–2,200*
Black Kite	*Milvus migrans*	200–1,700
Whistling Kite	*Haliastur sphenurus*	200–700
Brahminy Kite	*Haliastur indus*	200–2200
Pygmy Eagle	*Hieraaetus weiskei*	1,700
Papuan Eagle	*Harpyopsis novaeguineae*	200–1,200, 2,200–3,200
Forbes's Forest Rail	*Rallicula forbesi*	2,200–3,200*
Bare-eyed Rail	*Gymnocrex plumbeiventris*	1,400*
New Guinea Woodcock	*Scolopax saturata*	2,700*
Metallic Pigeon	*Columba vitiensis*	2,700*
Slender-billed Cuckoo-Dove	*Macropygia amboinensis*	200–2,200*
Bar-tailed Cuckoo-Dove	*Macropygia nigrirostris*	2,700*
Great Cuckoo-Dove	*Reinwardtoena reinwardti*	200–3,200
Common Emerald Dove	*Chalcophaps indica*	200–700
Stephan's Emerald Dove	*Chalcophaps stephani*	200–1,200
New Guinea Bronzewing	*Henicophaps albifrons*	200–1,200
Thick-billed Ground Pigeon	*Trugon terrestris*	700–1,100*
White-breasted Ground Dove	*Gallicolumba jobiensis*	2,200
Bronze Ground Dove	*Gallicolumba beccarii*	1,200–1,700

Pheasant Pigeon	*Otidiphaps nobilis*	1,700–2,600*
Wompoo Fruit Dove	*Ptilinopus magnificus*	700–1,200
Pink-spotted Fruit Dove	*Ptilinopus perlatus*	200–700
Ornate Fruit Dove	*Ptilinopus ornatus*	2,200–2,700*
Superb Fruit Dove	*Ptilinopus superbus*	200–2,200
Coroneted Fruit Dove	*Ptilinopus coronulatus*	200–1,700*
Beautiful Fruit Dove	*Ptilinopus pulchellus*	200–1,200
White-bibbed Fruit Dove	*Ptilinopus rivoli*	1,700–3,200
Orange-bellied Fruit Dove	*Ptilinopus iozonus*	200
Purple-tailed Imperial Pigeon	*Ducula rufigaster*	200
Rufescent Imperial Pigeon	*Ducula chalconota*	1,700–2,700
Pinon’s Imperial Pigeon	*Ducula pinon*	200
Zoe’s Imperial Pigeon	*Ducula zoeae*	200–1,200
Papuan Mountain Pigeon	*Gymnophaps albertisii*	1,700–3,700
Palm Cockatoo	*Probosciger aterrimus*	200–1,200
Sulphur-crested Cockatoo	*Cacatua galerita*	200–1,200
Pesquet’s Parrot	*Psittrichas fulgidus*	2,200*
Orange-fronted Hanging Parrot	*Loriculus aurantiifrons*	200
Buff-faced Pygmy Parrot	*Micropsitta pusio*	200–700
Red-breasted Pygmy Parrot	*Micropsitta bruijnii*	700–1,200
Dusky Lory	*Pseudeos fuscata*	200–2,700*
Coconut Lorikeet	*Trichoglossus haematodus*	200–1,200
Goldie’s Lorikeet	*Psitteuteles goldiei*	2,700–3,200
Black-capped Lory	*Lorius lory*	200–1,200
Pygmy Lorikeet	*Charmosyna wilhelminae*	700–1,200*
Red-fronted Lorikeet	*Charmosyna rubronotata*	200*
Red-flanked Lorikeet	*Charmosyna placentis*	200–700
Papuan Lorikeet	*Charmosyna papou*	1,700–3,700
Plum-faced Lorikeet	*Oreopsittacus arfaki*	1,700–3,700
Yellow-billed Lorikeet	*Neopsittacus musschenbroekii*	1,200–3,200
Orange-billed Lorikeet	*Neopsittacus pullicauda*	1,700–3,700
Brehm’s Tiger Parrot	*Psittacella brehmii*	2,200–2,700
Painted Tiger Parrot	*Psittacella picta*	2,700–3,700
Red-cheeked Parrot	*Geoffroyus geoffroyi*	200
Blue-collared Parrot	*Geoffroyus simplex*	700
Eclectus Parrot	*Eclectus roratus*	200–1,200
Papuan King Parrot	*Alisterus chloropterus*	700–2,700*
Orange-breasted Fig Parrot	*Cyclopsitta gulielmitertii*	200
Double-eyed Fig Parrot	*Cyclopsitta diophthalma*	200–1,700
Edwards’s Fig Parrot	*Psittaculirostris edwardsii*	200–1,200
Pheasant-Coucal	*Centropus phasianinus*	200–700
Dwarf Koel	*Microdynamis parva*	200
Asian Koel	*Eudynamys scolopaceus*	200–1,200
Channel-billed Cuckoo	*Scythrops novaehollandiae*	200
Little Bronze Cuckoo	*Chrysococcyx minutillus*	200
Rufous-throated Bronze Cuckoo	*Chrysococcyx ruficollis*	2,700–3,200
Chestnut-breasted Cuckoo	*Cacomantis castaneiventris*	200–1,200*
Fan-tailed Cuckoo	*Cacomantis flabelliformis*	1,200–3,700*
Brush Cuckoo	*Cacomantis variolosus*	200–1,700
White-crowned Cuckoo	*Cacomantis leucolophus*	200–1,200
Rufous Owl	*Ninox rufa*	1,700

Barking Owl	*Ninox connivens*	1,500*
Papuan Boobook	*Ninox theomacha*	200–2,200
Marbled Frogmouth	*Podargus ocellatus*	1,200–2,200*
Large-tailed Nightjar	*Caprimulgus macrurus*	200
Feline Owlet-Nightjar	*Euaegotheles insignis*	2,700
Mountain Owlet-Nightjar	*Aegotheles albertisi*	2,200
Glossy Swiftlet	*Collocalia esculenta*	200, 1,500–2,700
Mountain Swiftlet	*Aerodramus hirundinaceus*	3,700
Pacific Swift	*Apus pacificus*	200*
Oriental Dollarbird	*Eurystomus orientalis*	200–700
Hook-billed Kingfisher	*Melidora macrorrhina*	200–700
Common Paradise Kingfisher	*Tanysiptera galatea*	200–700
Shovel-billed Kookaburra	*Clytoceyx rex*	1,700–2,200
Rufous-bellied Kookaburra	*Dacelo gaudichaud*	200–700
Forest Kingfisher	*Todiramphus macleayii*	1,700
Yellow-billed Kingfisher	*Syma torotoro*	200–700*
Mountain Kingfisher	*Syma megarhyncha*	2,200–2,700*
Azure Kingfisher	*Ceyx azureus*	200–1,200
Little Kingfisher	*Ceyx pusillus*	200
Variable Dwarf Kingfisher	*Ceyx lepidus*	200–1,200
Rainbow Bee-eater	*Merops ornatus*	200*
Blyth's Hornbill	*Rhyticeros plicatus*	200–1,600
Hooded Pitta	*Pitta sordida*	200–700
Red-bellied Pitta	*Erythropitta erythrogaster*	200–700
White-eared Catbird	*Ailuroedus buccoides*	200–1,700
Spotted Catbird	*Ailuroedus melanotis*	2,200
MacGregor's Bowerbird	*Amblyornis macgregoriae*	2,200–3,200
Yellow-breasted Bowerbird	*Chlamydera lauterbachi*	2,200
Papuan Treecreeper	*Cormobates placens*	2,630*
White-shouldered Fairywren	*Malurus alboscapulatus*	1,700–2,200
Orange-crowned Fairywren	*Clytomyias insignis*	2,700–3,200
Red-collared Myzomela	*Myzomela rosenbergii*	1,200–3,700
Rufous-backed Honeyeater	*Ptiloprora guisei*	1,700–3,200
Grey-streaked Honeyeater	*Ptiloprora perstriata*	2,200–3,700
Yellowish-streaked Honeyeater	*Ptiloprora meekiana*	2,500*
Plain Honeyeater	*Pycnopygius ixoides*	200–1,200
Tawny-breasted Honeyeater	*Xanthotis flaviventer*	700–1,200
Meyer's Friarbird	*Philemon meyeri*	200–1,200
Helmeted Friarbird	*Philemon buceroides*	200–700
Long-billed Honeyeater	*Melilestes megarhynchus*	200–2,200
Common Smoky Honeyeater	*Melipotes fumigatus*	1,200–3,700
Olive Straightbill	*Timeliopsis fulvigula*	1,700
Green-backed Honeyeater	*Glycichaera fallax*	700
Black-throated Honeyeater	*Caligavis subfrenata*	1,700–3,700
Obscure Honeyeater	*Caligavis obscura*	1,200
Sooty Melidectes	*Melidectes fuscus*	2,200–3,700
Long-bearded Melidectes	*Melidectes princeps*	3,200–3,700*
Yellow-browed Melidectes	*Melidectes rufocrissalis*	1,700
Belford's Melidectes	*Melidectes belfordi*	2,200–3,700
Forest Honeyeater	*Meliphaga montana*	700–1,200
Mountain Honeyeater	*Meliphaga orientalis*	1,700–2,700*

Mimic Honeyeater	*Meliphaga analoga*	200–1,700
Puff-backed Honeyeater	*Meliphaga aruensis*	200–1,200
Rusty Mouse-warbler	*Crateroscelis murina*	200–1,700
Mountain Mouse-warbler	*Crateroscelis robusta*	1,200–3,700
Bicoloured Mouse-warbler	*Crateroscelis nigrorufa*	1,700–1,790*
Pale-billed Scrubwren	*Sericornis spilodera*	700–1,200
Papuan Scrubwren	*Sericornis papuensis*	1,700–3,200
Grey-green Scrubwren	*Sericornis arfakianus*	1,200–1,700
Large Scrubwren	*Sericornis nouhuysi*	1,700–3,700
Buff-faced Scrubwren	*Sericornis perspicillatus*	1,700–2,700
Yellow-bellied Gerygone	*Gerygone chrysogaster*	200–700
Ashy Gerygone	*Gerygone cinerea*	1,700–3,200
Green-backed Gerygone	*Gerygone chloronota*	200–1,200
Fairy Gerygone	*Gerygone palpebrosa*	200, 1,200
Brown-breasted Gerygone	*Gerygone ruficollis*	1,700–3,200
New Guinea Thornbill	*Acanthiza murina*	2,700–3,700
Goldenface	*Pachycare flavogriseum*	1,200–2,200
Papuan Babbler	*Garritornis isidorei*	200
Loria's Satinbird	*Cnemophilus loriae*	1,700–3,200
Crested Satinbird	*Cnemophilus macgregorii*	2,200–3,700
Yellow-breasted Satinbird	*Loboparadisea sericea*	1,700*
Black Berrypecker	*Melanocharis nigra*	200–1,200
Mid-mountain Berrypecker	*Melanocharis longicauda*	1,700
Fan-tailed Berrypecker	*Melanocharis versteri*	1,700–3,700
Streaked Berrypecker	*Melanocharis striativentris*	1,700, 2,700
Dwarf Longbill	*Oedistoma iliolophus*	700–1,700
Yellow-bellied Longbill	*Toxorhamphus novaeguineae*	200–1,200
Slaty-chinned Longbill	*Toxorhamphus poliopterus*	1,200–2,200
Tit Berrypecker	*Oreocharis arfaki*	2,200–3,700
Crested Berrypecker	*Paramythia montium*	2,700–3,700
Spotted Jewel-babbler	*Ptilorrhoa leucosticta*	1,700–2,700
Blue Jewel-babbler	*Ptilorrhoa caerulescens*	200–1,200
Chestnut-backed Jewel-babbler	*Ptilorrhoa castanonota*	1,200
Yellow-breasted Boatbill	*Machaerirhynchus flaviventer*	200–1,200
Black-breasted Boatbill	*Machaerirhynchus nigripectus*	1,700–3,200
Lowland Peltops	*Peltops blainvillii*	200–700
Mountain Peltops	*Peltops montanus*	1,700–2,700
Black Butcherbird	*Cracticus quoyi*	200
Hooded Butcherbird	*Cracticus cassicus*	200–700
Great Woodswallow	*Artamus maximus*	2,700–3,700
Stout-billed Cuckooshrike	*Coracina caeruleogrisea*	700–2,700*
Boyer's Cuckooshrike	*Coracina boyeri*	200–1,200
White-bellied Cuckooshrike	*Coracina papuensis*	200–1,700
Hooded Cuckooshrike	*Coracina longicauda*	2,700
Common Cicadabird	*Coracina tenuirostris*	200–1,200
Black-shouldered Cicadabird	*Coracina incerta*	200–700
Black Cicadabird	*Coracina melas*	200
Black-bellied Cuckooshrike	*Coracina montana*	1,200–2,700
Golden Cuckooshrike	*Campochaera sloetii*	200–1,200*
Black-browed Triller	*Lalage atrovirens*	200
Black Sittella	*Daphoenositta miranda*	2,700–3,200

Mottled Whistler	*Rhagologus leucostigma*	1,700–2,700
Wattled Ploughbill	*Eulacestoma nigropectus*	2,700
Rufous-naped Whistler	*Aleadryas rufinucha*	1,700–3,700
Crested Pitohui	*Ornorectes cristatus*	1,200
Black Pitohui	*Melanorectes nigrescens*	1,700–2,200
Rusty Whistler	*Pachycephala hyperythra*	200–1,700
Brown-backed Whistler	*Pachycephala modesta*	2,700–3,200
Grey Whistler	*Pachycephala simplex*	700–1,200
Sclater's Whistler	*Pachycephala soror*	1,200–2,200
Regent Whistler	*Pachycephala schlegelii*	1,700–3,700
Rusty Pitohui	*Pseudorectes ferrugineus*	200
Little Shrikethrush	*Colluricincla megarhyncha*	200–2,200
Northern Variable Pitohui	*Pitohui kirhocephalus*	200–1,200*
Hooded Pitohui	*Pitohui dichrous*	700–1,700*
Brown Oriole	*Oriolus szalayi*	200–700
Pygmy Drongo	*Chaetorhynchus papuensis*	200–1,700
Spangled Drongo	*Dicrurus bracteatus*	200–700
Northern Fantail	*Rhipidura rufiventris*	200–1,700
Sooty Thicket Fantail	*Rhipidura threnothorax*	200–1,200
White-bellied Thicket Fantail	*Rhipidura leucothorax*	200–1,200
Black Fantail	*Rhipidura atra*	200–2,700
Friendly Fantail	*Rhipidura albolimbata*	1,700–3,700
Dimorphic Fantail	*Rhipidura brachyrhyncha*	1,200–3,700
Rufous-backed Fantail	*Rhipidura rufidorsa*	200–700
Black Monarch	*Symposiachrus axillaris*	1,200–2,700
Spot-winged Monarch	*Symposiachrus guttula*	200–1,200
Hooded Monarch	*Symposiachrus manadensis*	200
Rufous Monarch	*Monarcha rubiensis*	200
Black-winged Monarch	*Monarcha frater*	200–1,200
Golden Monarch	*Carterornis chrysomela*	200–1,200
Ochre-collared Monarch	*Arses insularis*	200–1,700
Torrent-lark	*Grallina bruijni*	1,200
Shining Flycatcher	*Myiagra alecto*	200–1,700
Grey Crow	*Corvus tristis*	200–1,700
Lesser Melampitta	*Melampitta lugubris*	2,700–3,700
Blue-capped Ifrit	*Ifrita kowaldi*	1,700–3,700
Crinkle-collared Manucode	*Manucodia chalybatus*	700–1,200
Princess Stephanie's Astrapia	*Astrapia stephaniae*	2,700–3,700
Superb Bird-of-Paradise	*Lophorina superba*	1,700
Magnificent Riflebird	*Ptiloris magnificus*	200–700
Black Sicklebill	*Epimachus fastuosus*	1,200–2,700*
Brown Sicklebill	*Epimachus meyeri*	1,700–3,200*
Magnificent Bird-of-Paradise	*Diphyllodes magnificus*	700–1,700
King Bird-of-Paradise	*Cicinnurus regius*	200–700
Lesser Bird-of-Paradise	*Paradisaea minor*	200–1,200
Ashy Robin	*Heteromyias albispecularis*	1,200–1,700
Black-sided Robin	*Poecilodryas hypoleuca*	200–1,200
Black-throated Robin	*Poecilodryas albonotata*	2,200–3,200
White-winged Robin	*Peneothello sigillata*	2,700–3,700
Slaty Robin	*Peneothello cyanus*	1,700–2,700
White-rumped Robin	*Peneothello bimaculata*	700–1,700

White-faced Robin	*Tregellasia leucops*	200–1,700
White-eyed Robin	*Pachycephalopsis poliosoma*	1,200–1,700
Torrent Flyrobin	*Monachella muelleriana*	200
Canary Flyrobin	*Microeca papuana*	1,700–3,200
Yellow-legged Flyrobin	*Microeca griseoceps*	1,200
Olive Flyrobin	*Microeca flavovirescens*	200–1,200
Garnet Robin	*Eugerygone rubra*	1,700–3,700
Lesser Ground Robin	*Amalocichla incerta*	1,700
Pacific Swallow	*Hirundo tahitica*	200–2,200
Island Leaf Warbler	*Phylloscopus maforensis*	1,200–2,200
Black-fronted White-eye	*Zosterops minor*	200–1,200
Papuan White-eye	*Zosterops novaeguineae*	1,700–2,700
Metallic Starling	*Aplonis metallica*	200–700
Singing Starling	*Aplonis cantoroides*	200
Yellow-faced Myna	*Mino dumontii*	200–700
Island Thrush	*Turdus poliocephalus*	2,700–3,700
Pied Bush Chat	*Saxicola caprata*	2,200
Red-capped Flowerpecker	*Dicaeum geelvinkianum*	200–2,200
Black Sunbird	*Leptocoma sericea*	200–1,200
Olive-backed Sunbird	*Cinnyris jugularis*	200–1,700
Streak-headed Mannikin	*Lonchura tristissima*	200
Blue-faced Parrotfinch	*Erythrura trichroa*	1,700–3,700
Hooded Mannikin	*Lonchura spectabilis*	2,200
Alpine Pipit	*Anthus gutturalis*	3,200–3,700
Mountain Firetail	*Oreostruthus fuliginosus*	3,700

Revision of the endemic West Indian genus *Melopyrrha* from Cuba and the Cayman Islands

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Summary.—Hartert described the Grand Cayman population of *Melopyrrha* as separate from the Cuban population, but the two forms were considered conspecific by Bond and later authors. Based on differences in body size, plumage and vocalisations, we recommend the two populations be treated as separate endemic species: Cuban Bullfinch *Melopyrrha nigra* on Cuba, Isla de Pinos and cays of the Cuban archipelago, and Cayman Bullfinch *M. taylori* for Grand Cayman. We present natural history information for both populations.

Cuban Bullfinch *Melopyrrha nigra* occurs in the Cuban archipelago and on Grand Cayman in the Cayman Islands (Garrido & García Montaña 1975, AOU 1998, 2012, Raffaele *et al.* 1998, Bradley & Rey-Millet 2013). Bonaparte described the genus *Melopyrrha* in 1853 based on *Loxia nigra* named by Linnaeus. Cuban Bullfinch, called Negrito in Cuba and Black Sparrow in the Cayman Islands, was described by Linnaeus in 1758 under the name *Loxia nigra*, based on material from Cuba. In his earliest works, Gundlach (1856, 1876) was unaware that the bullfinch's range extended to the Cayman Islands, but mentioned Grand Cayman in a later (1893: 110) publication, as did Cory (1892: 112). The Cayman population was considered the same as the Cuban taxon until Hartert (1896) described the Grand Cayman population as *Melopyrrha taylori*. For several years, both taxa were treated

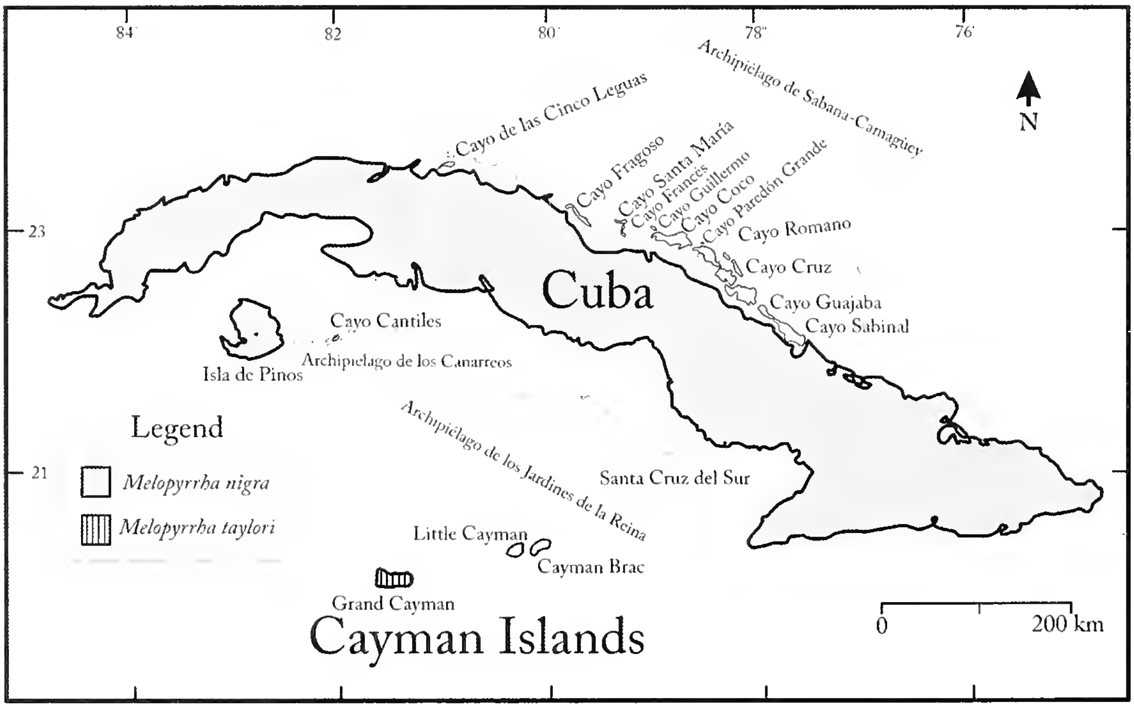

Figure 1. Distribution of Cuban Bullfinch *Melopyrrha nigra* in the Cuban archipelago and Cayman Islands, showing distributions of proposed species *M. nigra* and *M. taylori*.

specifically (Ridgway 1901: 562–563, Lowe 1910, Bond 1936: 388), but since Bond's first check-list (1940: 155) he and others (Hellmayr 1938: 168, Paynter & Storer 1970: 151, Garrido & García Montaña 1975, Sibley & Monroe 1990: 768, AOU 1998: 594, Dickinson 2003: 794) have treated them as conspecific, Cuban Bullfinch *Melopyrrha nigra*, with two subspecies, *M. n. nigra* of Cuba and its satellites and *M. n. taylori* of Grand Cayman (Fig. 1). Hellmayr (1938) recognised that whereas *M. n. taylori* was clearly a geographical race of Cuban Bullfinch, it was easily distinguished from birds in Cuba by being larger and having less glossy plumage.

Our investigation was stimulated by a birdwatcher who informed AK that he had the impression that Cuban and Grand Cayman bullfinches had different songs. His observations were correct, but we learned that not only are the vocalisations different, but the birds are morphologically distinct as well. Here, we describe the distinctions between the two populations and present the conclusions we draw based on those differences.

Methods

We measured Cuban Bullfinch specimens at nine USA and Cuban institutions (Table 1). All specimens were measured using a ruler and dial calipers to the nearest 0.1 mm, following Baldwin *et al.* (1931). Chord measurements were made with the wing flattened against the ruler. Culmen measurements are from the tip to the feathers. Only adults (*n* = 211) were used to compare morphometrics. Mass data were obtained from live (*n* = 64 individuals) and post-mortem (*n* = 6) birds. Descriptive statistics include standard deviation as a measure

TABLE 1

Mean, standard deviation, range and sample size (in brackets) for measurements of wing, tail, culmen, tarsus, and mass from 211 *Melopyrrha nigra* specimens from Cuba and Grand Cayman, examined in nine collections in the USA and Cuba[1] and live mist-netted birds (mass only).

Measurement (mm)						
Wing	Tail	Culmen length	Culmen width	Culmen depth	Tarsus	Mass (g)
			Males			
Cuba						
66.1 ± 2.2 (79)	57.6 ± 2.6 (75)	11.3 ± 0.9 (77)	9.8 ± 1.0 (16)	4.9 ± 0.5 (13)	17.6 ± 1.2 (78)	15.6 ± 1.1 (39)
60.5–73.0	52.0–67.0	9.1–14.9	8.5–11.4	4.6–5.6	15.0–21.4	13.4–17.9
Grand Cayman						
70.4 ± 2.9 (55)	58.0 ± 3.0 (57)	12.9 ± 0.7 (60)	10.8 ± 0.5 (31)	6.2 ± 0.5 (20)	20.4 ± 1 (47)	17.2 ± 0.8 (7)
65.0–79.0	53.–67.0	10.7–15.0	9.7–11.9	5.6–7.1	18.0–22.8	16.1–18.6
			Females			
Cuba						
63.9 ± 2.2 (48)	54.5 ± 3 (49)	10.9 ± 0.6 (48)	8.9 ± 0.6 (10)	4.6 ± 0.5 (6)	17.2 ± 1.1 (49)	14.5 ± 0.6 (31)
59.0–70.0	45.0–63.0	9.6–12.3	8.0–9.9	4.4–4.9	15.0–19.9	13.5–16.0
Grand Cayman						
68.0 ± 2.1 (21)	56.4 ± 2 (23)	12.5 ± 0.8 (21)	10.5 ± 0.5 (8)	5.6 ± 0.5 (7)	20.5 ± 0.6 (20)	15.7 ± 0.3 (4)
64.0–72.0	53.0–61.0	11.0–14.0	10.0–11.2	5.3–6.0	19.1–22.0	15.4–16.0

[1] Collections examined include Louisiana State University Museum of Natural Science, Baton Rouge; Museum of Comparative Zoology, Harvard University, Cambridge, MA; American Museum of Natural History, New York; National Museum of Natural History, Smithsonian Institution, Washington DC; Academy of Natural Sciences of Philadelphia, Philadelphia; Carnegie Museum, Pittsburgh; Field Museum of Natural History, Chicago; and Instituto de Ecología y Sistemática, and Museo Nacional de Historia Natural de Cuba, La Habana.

of variation about the mean. Comparisons of size between sexes were conducted using unpaired t-tests. A parametric test was used if populations showed normal distribution, whereas non-normally distributed data were analysed using Welch's approximate t, which assumes Gaussian populations with different standard deviations. Significance level for all tests was set at 0.05. Data on breeding biology were collected incidental to other studies on Cuba, Isla de Pinos (Isla de la Juventud) and the Caymans. G. B. Reynard provided recordings of bullfinch vocalisations that he made in Cuba using several models of Nagra and Uher reel-to-reel recorders, and a Sony TCM-5000 cassette recorder together with Sony, AKG and Sennheiser microphones, and parabolic reflectors with diameters of 43 cm, 61 cm or 91 cm. On Grand Cayman, AG-C used a portable Sony PCM-D50 96 KHz/24-bit Linear Recorder with two built-in microphones set at 90°. Frequency response was set at 20 HZ–20 KHZ, at high sensitivity (-35.0 dB / Pa 1 kHz). Raven (Ver. 1.0) sound analysis software was used to analyse vocalisations.

Results

Systematics.—We examined 356 bullfinch specimens from Cuba and 83 from Grand Cayman, although a sample of just 211 (all adults) of those was used in our analyses (Table 1). Before comparing populations from Cuba and Grand Cayman, we examined bullfinch populations within Cuban territory. Todd (1916) found no plumage differences between birds from Cuba and Isla de Pinos, a conclusion with which we agree. Further, we could find no differences in size or coloration within populations on the main island of Cuba.

We found some slight differences (non-significant) in size and coloration among birds from different Cuban cays. Garrido & Schwartz (1969: 38) noted: 'birds from [Cayo] Cantiles have the same coloration as Cuba and the Isle of Pines, but seem to be a bit larger. The colour is slightly darker in the females from Cantiles than those from Cuba and the Isle of Pines.' The series from Cayo Cantiles is not large enough for us to determine if these differences are

TABLE 2

Morphometric comparisons between populations of *Melopyrrha nigra* from Cuba and Grand Cayman, Cayman Islands. Comparisons made with unpaired t-test, with significance level set at 0.05. Level of significance: ** = < 0.01, and *** = < 0.001; ns = not significant.

	Measurement (mm)						
Locality	**Wing**	**Tail**	**Culmen length**	**Culmen width**	**Culmen depth**	**Tarsus length**	**Mass (g)**
			Males				
Cuba	66.1 ± 2.2 (79)	57.6 ± 2.6 (75)	11.3 ± 0.90 (77)	9.8 ± 1.0 (16)	4.9 ± 0.5 (13)	17.6 ± 1.2 (78)	15.6 ± 1.1 (39)
vs. (t [df] *P*)	9.755 (132) ***	0.8190 (130) ns	11.350 (135) ***	4.594 (45) ***	7.298 (31) ***	13.427 (123) ***	4.81 (10) ***
Grand Cayman	70.4 ± 2.9 (55)	58.0 ± 3.0 (57)	12.9 ± 0.70 (60)	10.8 ± 0.5 (31)	6.2 ± 0.5 (20)	20.4 ± 1.0 (47)	17.2 ± 0.8 (7)
			Females				
Cuba	63.9 ± 2.2 (48)	54.5 ± 3.0 (49)	10.9 ± 0.6 (48)	8.9 ± 0.6 (10)	4.6 ± 0.5 (6)	17.2 ± 1.1 (49)	14.4 ± 0.6 (31)
vs. (t [df] *P*)	7.219 (67) ***	2.758 (70) **	9.182 (67) ***	6.040 (16) ***	3.595 (11) **	12.634 (67) ***	7.25 (7) ***
Grand Cayman	68.0 ± 2.1 (21)	56.4 ± 2.0 (23)	12.5 ± 0.8 (21)	10.5 ± 0.5 (8)	5.6 ± 0.5 (7)	20.5 ± 0.6 (20)	15.7 ± 0.3 (4)

significant. We observed that wing lengths of specimens from Cayo Paredón Grande were substantially less than those of specimens from Cuba but, again, our sample sizes were too small to statistically confirm this. Adults from Cayo Coco are similar to Cuban adults, although females appear somewhat paler and duller. Therefore, we do not believe that Cuban Bullfinch has differentiated sufficiently within Cuban territory, including Isla de Pinos and the cays, to constitute geographical races.

We analysed size between populations on Cuba and Grand Cayman, examining within-sex measurements because of substantial sexual size dimorphism in both Cuban and Grand Cayman birds, particularly in wing, tail, some bill measurements, and mass (Tables 1, 3). In general, birds from Grand Cayman (*taylori*) were larger than Cuba (*nigra*) in both sexes; i.e., we found significant differences in all seven measurements for females, and all but one (tail length) of seven measurements of males (Table 2). Notably, the bill of *taylori* is substantially bulkier than that of *nigra*, being longer, wider and deeper (Fig. 2).

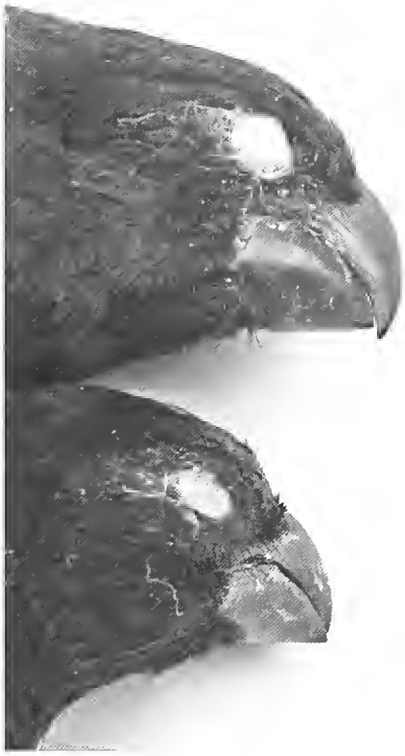

Figure 2. Comparison of bill size between Cuban Bullfinch *Melopyrrha n. nigra* of Cuba (lower bird) and *M. n. taylori* of Grand Cayman (upper bird), United States National Museum, Smithsonian Institution, Washington DC (James W. Wiley)

Although adult males of both forms are essentially uniform black with some white on the primaries, pattern and coloration are inconsistent, and are quite different in females and immatures. Adult male *M. n. nigra* is more lustrous or glossy black overall, with a violet sheen. In contrast, *M. n. taylori* is duller with no gloss. The two populations show differing amounts of white on the primaries. The great majority of *taylori* show more white on the fringes of the outer primaries, in both sexes. This white fringe is usually present in the two outer feathers in *taylori*, whereas in *nigra* it usually occurs in only one outer feather. Also, *taylori* shows considerably more white on the axillaries and underwing-coverts than *nigra* (although we did not quantify this difference morphometrically). Bond (1936: 389) noted that the 'outer rectrices [are] indistinctly tipped with whitish' in male *taylori*. The two populations also show different bill coloration: that of *nigra* is all black whereas that of *taylori* is silvery grey.

Female *nigra* is uniform dull slate-black and less glossy, sometimes almost dark slate, especially on the posterior underparts. The upperparts are almost uniform except the lower neck, back and rump are tinged brownish contrasting with the slate-black head. Female *taylori* is bicoloured, being mostly blackish slate on the head and upperparts, although not as dark as *nigra*, and has dull brownish olive-grey lower abdomen and flanks (Fig. 3). Throat, breast and upper abdomen are not dull black as in *nigra*, but are blackish grey contrasting with a paler lower abdomen and flanks. In Cuban females, the slate-black coloration is practically uniform from throat to undertail-coverts. Immature *nigra* resembles adult females, but have brownish wing feathers and tail, a smaller and less contrasting white wing patch, with no gloss or slate tones. Immature male *taylori* resemble adult females, with an olive-tinged dark head and much paler olive-grey posterior upperparts (Ridgway 1901), brownish fringes to the primaries, and abdomen tinged cinnamon. White in the wing is reduced or absent in both sexes (Bradley & Rey-Millet 2013).

TABLE 3

Sexual size dimorphism in populations of *Melopyrrha nigra* from Cuba and Grand Cayman, Cayman Islands. Comparisons made with unpaired t-test. Parametric test used if populations showed normal distribution; if not, Welch's approximate t is shown, which assumes Gaussian populations with different standard deviations. ns = not significant.

		Mean ± SD (*n*)				
Population	**Measurement**	**Males**	**Females**	t	df	P
Cuba	Wing	66.1 ± 2.2 (79)	63.9 ± 2.2 (48)	5.464	125	<0.0001
	Tail	57.6 ± 2.6 (75)	54.5 ± 3.0 (49)	6.105	122	<0.0001
	Culmen length	11.3 ± 0.9 (77)	10.9 ± 0.6 (48)	2.723	123	0.0074
	Culmen width	9.8 ± 1.0 (16)	8.9 ± 0.6 (10)	2.561	24	0.0171
	Culmen depth	4.9 ± 0.5 (13)	4.6 ± 0.5 (6)	1.216	17	0.2407 ns
	Tarsus length	17.6 ± 1.2 (78)	17.2 ± 1.1 (49)	1.887	125	0.0614 ns
	Mass	15.6 ± 1.1 (39)	14.4 ± 0.6 (31)	5.60	59	<0.0001
Grand Cayman	Wing	70.4 ± 2.9 (55)	68.0 ± 2.1 (21)	3.456	74	0.0009
	Tail	58.0 ± 3.0 (57)	56.4 ± 2.0 (23)	2.351	78	0.0212
	Culmen length	12.9 ± 0.7 (60)	12.5 ± 0.8 (21)	2.171	79	0.0329
	Culmen width	10.8 ± 0.5 (31)	10.5 ± 0.5 (8)	1.513	37	0.1388 ns
	Culmen depth	6.2 ± 0.5 (20)	5.6 ± 0.5 (7)	2.733	25	0.0114
	Tarsus length	20.4 ± 1.0 (47)	20.5 ± 0.6 (20)	0.4154	65	0.6792 ns
	Mass	17.2 ± 0.8 (7)	15.7 ± 0.3 (4)	4.79	7	0.002

Vocalisations.—Males perch atop low trees to sing, repeatedly, a descending and ascending high-pitched melody. The call of Cayman birds is an insect-like *chi-p* and *zee zee*, the first note high-pitched, whereas the song begins as a trill *zee-zee-zee*, falls briefly then rises over 8–30 *tssi* notes, the longest reaching a very high and barely audible pitch, only heard at the onset of the breeding season (Bradley & Rey-Millet 2013). The call of Cuban birds is a staccato *chi-dip*, and thin *tsee*, often repeated (Garrido & Kirkconnell 2000). The song of Cuban birds is a thin, prolonged, melodious warble, *ti-ti-tisissiiiitssiiiitsiiii-toeee* (Garrido & Kirkconnell 2000).

Songs of the Cuban population are distinct from those of Grand Cayman, being typically more complex in structure, longer ($\text{mean}_{\text{Cuba}}$ = 4.54 ± 1.04 seconds [r = 2.32–6.25 seconds, *n* = 10] vs. $\text{mean}_{\text{Grand Cayman}}$ = 2.03 ± 0.71 seconds [r = 1.11–3.98 seconds, *n* = 46]; t = 7.28, $P < 0.001$, df = 10) and comprise more elements ($\text{mean}_{\text{Cuba}}$ = 23.0 ± 5.33 [r = 13–33 elements, *n* = 10] elements / song vs. $\text{mean}_{\text{Grand Cayman}}$ = 13.9 ± 4.19 elements / song [r = 9–23 elements, *n* = 47]; t = 5.08, $P < 0.001$, df = 11) than songs of birds on Grand Cayman (Fig. 4). Songs of Cuban birds reach distinctly higher frequencies than on Grand Cayman during the first two seconds (Fig. 4). Songs of *M. taylori* possess a series of introductory elements with more uniform frequency than Cuban birds, with a duration of *c*.1.5 seconds, followed by a drop then an increase in frequency.

We noted slight variations in vocalisations within Cuba, as there are clearly different dialects in various regions. J. P. Sarracino (pers. comm.), a bird-fancier who has kept up to 500 bullfinches, informed OHG that birds from some parts of Pinar del Río province (western Cuba) possess dialects different from populations in other regions, although in AK's experience the song of Cuban Bullfinch at localities he has sampled in this province is typical of that elsewhere in Cuba (Fig. 6).

Natural history.—Few data have been reported on the ecology and behaviour of Cuban Bullfinch, although more are available for *nigra* than for *taylori*. Race *nigra* is common at most mainland localities (where it has not been harvested excessively for the cagebird trade), including thickets, brushy pastures and forest from sea level to high (1,300 m) elevations (Barbour 1923: 129, Fong *et al.* 2005). It also forages in mangroves, including buttonwood mangrove (*Conocarpus erectus*) on the mainland and cayos. On the Cuban cayos and Isla de Pinos, however, it occurs only at sea level, and is found only in the low coastal southern part of Isla de Pinos, in dry brushland and woods. The bullfinch has long been a favoured target of Cuban 'pájareros' (bird trappers) and Barbour (1943: 128) already suggested it had been trapped excessively. Most harvested birds are males, because non-singing females are released. Captive males are often used in local singing competitions. It is also one of the birds most frequently smuggled out of Cuba to meet international demand for cagebirds, especially to Miami, Florida (Garrido & Kirkconnell 2000). Harvesting for the cagebird trade has resulted in a dramatic decline of populations in many areas where the species was formerly common.

Although formerly considered common on Grand Cayman, the bullfinch's range has been reduced and it is now rare to absent west of Savannah due to urban development and loss of habitat due to forest clearance and hurricanes. East of Savannah, it is a locally common resident breeding mainly in dry forest within the protected Botanic Park and Mastic reserve, and in shrubland and woodland in the north and east where continued development threatens habitats (Bradley 2000, Bradley & Rey-Millet 2013). It bred infrequently in mangroves but since Hurricane Ivan (2004) breeding has not been observed in mature black (*Avicennia germinans*), white

Figure 3. Comparison of plumage coloration between female Cuban Bullfinch *Melopyrrha nigra taylori* of Grand Cayman (left two individuals) and *Melopyrrha n. nigra* of Cuba (right two individuals): (A) upperparts, (B) lateral view, (C) underparts, United States National Museum, Smithsonian Institution, Washington DC (James W. Wiley)

(*Laguncularia racemosa*) and buttonwood mangroves; it was always absent from the interior red mangrove (*Rhizophora mangle*) of the Central Mangrove Wetlands. The only record of breeding in coastal habitat was in 1985. Johnston (1975) reported it was uncommon in sea grape (*Coccoloba uvifera*)-tropical almond (*Terminalia catappa*) woodland, pure logwood (*Haematoxylon campechianum*) forest, pastures and cultivated areas; fairly common (December) to uncommon (April–May) in logwood-silver thatch palm (*Coccothrinax proctorii*)-red birch (*Bursera simaruba*) forest (now called shrubland); common (December) to fairly common (April, May, August) in limestone forest; and fairly common around houses, towns and roadsides. PEB (unpubl. data), however, found that its range is not seasonal.

Grand Cayman adults are shy, staying concealed except when foraging or when males perch on exposed branches to sing. In contrast, Cuban birds are considerably less shy. Immatures of all populations are very tame and curious.

Bullfinches on Grand Cayman forage for seeds and fruit (insects in breeding season) at all levels from the canopy, understorey, to near the ground in woodland and dry shrubland, rough pasture, inland gardens and mangrove edge, but seldom in littoral areas. Cuban birds are similar, foraging at all levels from canopy to near the ground in woodland. In Cuba, bullfinches also tend to forage in small groups (Gundlach 1876: 94, 1893: 110), although Barbour (1923: 129) did not observe the species associating in groups and thought it solitary. In winter, we found that one or two males often forage with several females and immatures of both sexes, and individuals often join mixed-species flocks of warblers (Hamel & Kirkconnell 2005). Grand Cayman males are occasionally solitary. Gálvez & Berovides (1991) noted Cuban birds occurred singly, as pairs or in small groups, with peak densities of individuals within groups in May–June and August–September.

On Isla de Pinos, Todd (1916) recorded it feeding in the blossoms of *Jatropha* (*glaucovirens*) *integerrima*. Gundlach (1876: 94) gave its diet in Cuba as seeds, fruits and occasional insects. Danforth (1935) found small seeds and sand (grit) in the stomachs of eight birds from Cuba. During incidental observations ($n = 54$; all during breeding season) of foraging bullfinches at the Ciénaga de Zapata, Cuba, we recorded birds taking fruit ($n = 17$, 31.5% of observations), seeds (27, 50%) and insects (ten, 18.5%). Of two bullfinches we collected during the breeding season on Cayo Coco, Cuba, the stomach of one contained 32 seeds, whereas the other's contained insects and seeds. Johnston (1975) reported feeding ecology on Grand Cayman, where bullfinches forage on fruits, seeds and arthropods.

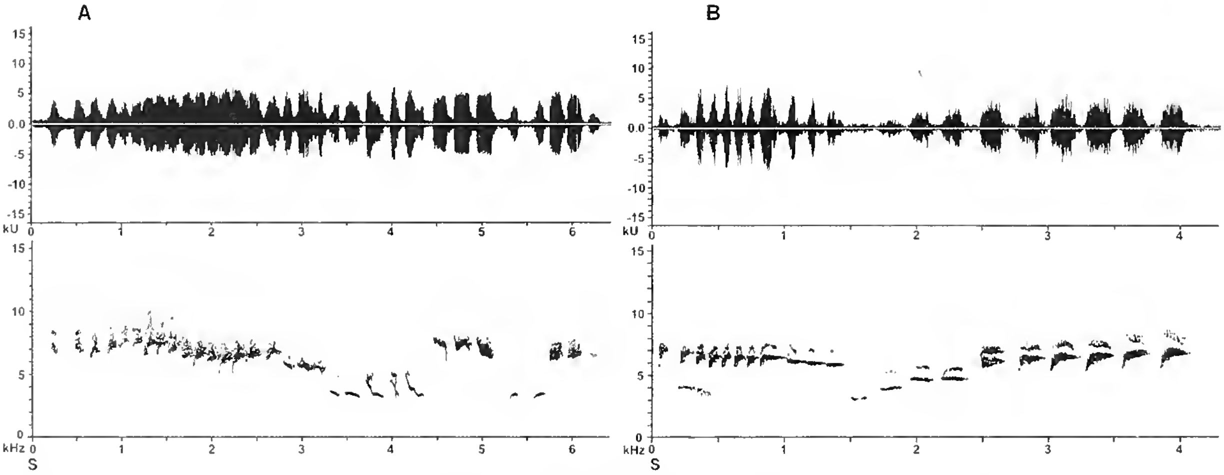

Figure 4. Song of Cuban Bullfinch *Melopyrrha nigra* from Santo Tomás, Ciénaga de Zapata, Cuba, recorded by G. B. Reynard (A) and an adult male at Queen Elizabeth Botanic Park, Grand Cayman, Cayman Islands, 16 May 2010, recorded by Alexandra Günther-Calhoun (B). Upper figure is waveform (kU), lower figure is spectrogram (kHz).

Animal matter (Lepidoptera larvae, Coleoptera and possibly Chrysomelidae) comprised 39% and vegetable matter (unidentified seeds) 61% of items in stomachs of four birds (Johnston 1975). At one nest we watched briefly ($\Sigma = 5.4$ hr) during the late nestling stage, 44 identifiable items were delivered to three chicks, including ten (22.7%) seeds and berries and 34 (77.3%) small insects, at a mean rate of 8.1 items per hour.

Breeding on Grand Cayman starts as early as January, with peak breeding in March–June, and occasional nests with young in July–early August. Onset of breeding is thought to be related to fruiting phenology (Bradley 2000, Bradley & Rey-Millet 2013). Johnston (1975) reported nests with young in May–June on Grand Cayman. In Cuba, Gundlach (1876: 94, 1893: 110) reported nesting in April–July. We have found nests in the Ciénaga de Zapata from late March (eggs) to early June (older chicks). Courtship can be prolonged, with male display involving wing-flashing, exposing the white axillaries, from January. Both sexes participate in nest-building through egg laying. Nest construction occurs mainly in March–August, although it has been observed as early as January on Grand Cayman (Bradley 2000, Bradley & Rey-Millet 2013). Nests are constructed mainly in dry low forest and shrubland, open woodland, rough pasture and gardens on Grand Cayman, where preferred trees include silver thatch palm *Sideroxylon horridum* and *Xylosma bahamense* (Bradley 2000). The majority of nests are of similar construction in Cuba and Grand Cayman: a large, woven, untidy enclosed globular nest, of palm fibres, grasses, twigs, hair and plant fibre, lined with red birch bark and hair, with a side entrance similar to grassquit (*Tiaris* spp.) or Bananaquit *Coereba flaveola* nests, built around vines or dense vegetation on a heavy branch. On Grand Cayman the nest is often in a tangle of *Selenicereus grandiflorus* vines or *Phoradendron rubrum*. A second nest type is occasionally constructed there: an apparently partially constructed nest comprised an open arch of twigs backed by a tree bole with a rough nesting cup (Bradley & Rey-Millet 2013). Nests are also used as roosts. Gundlach (1856) observed two pairs that had their nests destroyed rebuild the structures.

Gundlach (1876: 94; repeated by Bond 1936 and Valdés Miró 1984) noted bullfinches in Cuba lay 3–4 dull white eggs, often with a bluish or greenish tinge, spotted, chiefly at the larger end, with dark reddish brown and umber-brown and, to a much lesser degree, drab or lilac-grey. Eggs (3–4) on Grand Cayman are dull white with a greenish wash and reddish-brown spots. Gundlach (1876: 94) gave the dimensions of eggs from Cuba as 21 × 15 mm. Three clutches collected by C. Ramsden in eastern Cuba each comprised 2–3 eggs (mean = 2.33 ± 0.58). Four clutches we observed at Los Indios, Isla de Pinos were of 2–3 eggs (mean = 2.50 ± 0.58), whereas four clutches at the Ciénaga de Zapata, Cuba, were of 2–4 eggs (mean = 3.00 ± 0.82) ($t = -1.00$, df = 5, $P > 0.05$). We measured 29 eggs from Cuba and Isla de Pinos: eastern Cuba—mean = 21.26 ± 0.44 mm (r = 20.8–22.1 mm; $n = 7$) × 15.44 ± 0.62 mm (14.9–16.7 mm, $n = 7$); central Cuba—mean = 21.17 ± 0.25 mm (20.8–21.5 mm, $n = 12$) × 15.27 ± 0.30 mm (14.7–15.7 mm, $n = 12$); Isla de Pinos—mean = 20.78 ± 0.77 mm (19.0–21.5 mm, $n = 10$) × 15.20 ± 0.30 mm (14.8–15.9 mm, $n = 10$). Sizes of eggs did not vary between eastern and central Cuba ($t = 0.50$, $P = 0.628$, df = 8) or Cuba (east and centre combined) and Isla de Pinos ($t = 0.95$, $P = 0.351$, df = 24). Both parents feed the young in both races, but PEB noted that only females incubated on Grand Cayman.

Discussion

The morphological differences, i.e. coloration of adult males, and especially females and immatures, plus the significant differences in size, particularly in the bill (length, width and depth of culmen), the differences in vocalisations, together with their isolated ranges, clearly suggests that *nigra* and *taylori* constitute separate species rather than subspecies. The AOU (1998) endorses the Biological Species Concept (BSC), in which species are considered to be genetically cohesive groups of populations reproductively isolated from other such groups. According to the BSC, geographic isolation leads to genetic change and potentially to the reproductive isolation of sister taxa, which is the case in the bullfinch populations of the different archipelagos. No evidence of contact exists and therefore a lack of gene flow can be presumed. Reproductive isolation could be maintained via the different vocalisations, despite that these are learnt in oscine passerines. Our taxonomic treatment accords with the Comprehensive Biological Species Concept postulated by Johnson *et al.* (1999), in which an avian species is a series of populations representing an essentially monophyletic, genetically cohesive, and genealogically concordant lineage of individuals that share a common fertilisation system through time and space, present an independent evolutionary trajectory, and exhibit essential but not necessarily complete reproductive isolation from other species.

We found that populations from the Cuban archipelago, especially Isla de Pinos (50 km from the nearest point on the Cuban mainland), have not diverged from mainland populations, whereas the more distantly separated Grand Cayman population (240 km south of Cuba) has deviated substantially. Supporting this evaluation is the discovery of a fossil species of *Melopyrrha*: *M. latirostris* on Cayman Brac (Steadman & Morgan 1985). *M. latirostris* was a larger bird, with a more robust bill than *M. nigra*. Steadman & Morgan's (1985) discovery suggests that a *Melopyrrha* fossil could also be found in Cuba but, until now, palaeontologists there have devoted their attention mainly to large birds, and the passerine palaeofauna has not yet been examined. Undoubtedly the Cuban avifauna has a great affinity with that of the Caymans, because a total of 23 species of landbirds (79% of breeding species) are shared between them. Much landbird colonisation of the Caymans is the result of natural dispersal from Cuba, most probably from the south of the Cuban archipelago. The nearest point of Cuba to the Caymans is Santa Cruz del Sur, Camagüey province, 209 km from Cayman Brac, whereas Cayos de las 12 Leguas, Archipelago Jardines de la Reina, are the closest Cuban satellites to Cayman Brac (147 km).

Melopyrrha nigra formerly occurred on Cayman Brac, where Quaternary remains have been found (Morgan 1994). Steadman & Morgan (1985) reported that *taylori* and *latirostris* co-existed on Cayman Brac, and suggested '*latirostris* may have swamped out *M. n. taylori* through interbreeding.' Plausible or not, they treated *taylori* as a subspecies of *nigra*. Steadman & Morgan (1985) also noted that six of the West Indian emberizid genera (*Melopyrrha, Tiaris, Loxipasser, Loxigilla, Euneornis, Melanospiza*) 'could be accommodated in an expanded genus *Tiaris* Swainson, 1827, on the basis of plumage and osteology.' As we have not compared skeletons of these taxa, we cannot comment on their suggestion, but we can mention an example that may support their opinion. In the early 1960s, Garrido & García Montaña (1975: 117), while collecting around Gibara, near Holguín, visited a 'pájarero' who had kept two sibling hybrid Yellow-faced Grassquit *Tiaris olivaceus* × *Melopyrrha nigra*. Both were slightly larger than *Tiaris*; one had more *Tiaris* features, whereas the other was more *Melopyrrha*-like. The pájarero had monitored the nestlings until they were large enough to be removed from the nest; thereafter he raised them in captivity until they were full grown. The male parent was *Tiaris*, whereas the female was *Melopyrrha*. Despite these observations and other reports, we remain sceptical of such hybridisation under natural conditions.

Based on the evidence we have presented, we propose that Cuba and Cayman forms of *Melopyrrha* should be treated as distinct species (Fig. 1), as follows:

Cuba

Melopyrrha nigra Linnaeus, 1758—Cuban Bullfinch, Negrito

Loxia nigra Linnaeus, *Syst. Nat.*, 10th edn., 1758: 175 (Cuba).

Distribution.—Cuba; Isla de Pinos; Cayo Cantiles and Cayo Arenoso (Archipelago de los Canarreos); Cayo de las Cinco Leguas, Cayo Francés, Cayo Las Brujas, Cayo Santa María, Cayo Ensenachos, Cayo La Aguada, Cayo Lucas, Cayo Aji, Cayo Ajicito, Cayo Caguanes, Cayo Cueva, Cayo Fábrica, Cayo Obispo, Cayo Palma, Cayo Salinas, Cayo Judas, Cayo Guillermo, Cayo Coco, Cayo Paredón Grande, Cayo Romano, Cayo Cruz, Cayo Guajaba, Cayo Sabinal, Cayo Ensenacho del Medio (Archipelago Sabana-Camagüey).

Cayman Islands

Melopyrrha taylori Hartert, 1896—Grand Cayman Bullfinch

Melopyrrha taylori Hartert, *Novit. Zool.* 3(3), 1896: 257 (Grand Cayman).

Distribution.—Grand Cayman. Scattered localities in the eastern half of the island.

Material examined

Localities of *Melopyrrha* from the Cuban archipelago and Cayman Islands.

Cuba.—Península de Guanahacabibes, Artemisa, Los Palacios, Sierra de Guacamaya, San Vicente, Nortey (Pinar del Río province); San Antonio de los Baños (La Habana province); Matanzas, Ciénaga de Zapata, Salinas de Bidos (Matanzas province); Casilda (Sancti-Spíritus province); Jobabo (Camagüey province); Cupeyal (Holguín province); La Munición, Yateritas, Baitiquirí, Guantánamo, Baracoa, Tabajó, Maisí (Guantánamo province). Isla de Pinos. Cuban cayos.—Cayo Coco, Cayo Paredón Grande (Archipélago Sabana-Camagüey); Cayo Cantiles (Archipélago de los Canarreos).

Grand Cayman.—0.8 km north of Bodden Town; 5.6 km north of East End; 3.2 and 5.6 km south of North Side; 3.2 km north-east if West Bay; 3.5 km south of Old Man village.

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Vocal evidence for species rank to *Cercomacra nigrescens fuscicauda* J. T. Zimmer

by Sjoerd Mayer†, Paul Coopmans†, Niels Krabbe & Morton L. Isler

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Summary.—Vocal analysis confirms that male song of the west Amazonian form of Blackish Antbird *Cercomacra nigrescens fuscicauda* differs distinctly from songs of other forms of the species including in areas where their ranges meet, an indication that *fuscicauda* is reproductively isolated from adjacent taxa. Elevating *fuscicauda* to species rank leaves *C. nigrescens* with disjunct but vocally fairly similar populations.

The genus *Cercomacra* P. L. Sclater, 1858, encompasses 25 cryptic taxa presently ranked as 12 species, all medium-sized, fairly long-tailed, often with fairly horizontal posture, and all vocally distinct. Three of the species were only recognised recently (Fitzpatrick & Willard 1990, Bierregaard *et al.* 1997, Graves 1997). The genus has been divided into two major species groups: C. [*tyrannina*] and C. [*nigricans*] each including five species. The remaining two species (Rio de Janeiro *C. brasiliana* and Grey Antbirds *C. cinerascens*) are of uncertain relationships but may be intermediate between the two groups (Zimmer & Isler 2003).

The C. [*tyrannina*] group includes Blackish *C. nigrescens*, Willis's *C. laeta*, Dusky *C. tyrannina*, Parker's *C. parkeri* and Black Antbirds *C. serva*. They occur in secondary undergrowth and river and lake edge habitats from southern Mexico to the Guianas, central Brazil, and northern Bolivia (Zimmer & Isler 2003). The geographical ranges of its component species are largely allo- or parapatric, and where they meet or overlap slightly, the species usually differ in habitat (Zimmer & Isler 2003). The only exception is the range of *C. serva*. It covers almost the entire range of *C. nigrescens fuscicauda* and overlaps slightly with the Andean forms of *C. nigrescens*.

Zimmer (1931) described three new taxa of *Cercomacra* from eastern Ecuador, eastern Peru and northern Bolivia, *aequatorialis* and *notata* from the foothills of the Andes, intergrading in San Martín, Peru, and *fuscicauda* from the adjacent Amazonian lowlands. Despite the distinctive female plumage of *fuscicauda* and its close geographical proximity to the Andean forms, he ranked all three as subspecies of *C. nigrescens* (Cabanis & Heine, 1859), a species otherwise known from populations in the Guianas (*nigrescens*) and central Brazil (*approximans*, *ochrogyna*).

The type locality of *fuscicauda* is Lagarto, on the río Ucayali near the mouth of the Urubamba, Peru (Zimmer 1931). Birds tape-recorded along the river nearby (MLNS 165676; for acronym see Methods) vocalise similarly to lowland birds from throughout eastern Ecuador, eastern Peru and western Brazil. Additionally, a dependent immature male was collected (Academy of Natural Sciences Philadelphia 177794) after its loudsong, similar to that of an adult male, was tape-recorded (MLNS 37541) in Loreto, Peru, establishing that the name *fuscicauda* is correctly assigned to this vocal type.

Males of all six forms of *C. nigrescens* are rather similar, grey above, slightly paler below, with narrow white tips to the wing-coverts, small white shoulder patch and semi-concealed white interscapular patch. Nominate *nigrescens* is darkest, the central Brazilian and Andean taxa palest, while west Amazonian *fuscicauda* is nearly as dark as the nominate, relatively dark below, and usually has a faint 'bluish' bloom (Zimmer 1931). The white interscapular and shoulder patches in *fuscicauda* average smaller than in other forms, and the white tips to the wing-coverts narrower than in the Andean and central Brazilian taxa, but males of all forms are rather variable. Nominate *nigrescens* often lacks white tips to the wing-coverts altogether (Cory & Hellmayr 1924), one male specimen of *fuscicauda* from La Paz, Bolivia, was considered intermediate in plumage between *fuscicauda* and *approximans*, and some *fuscicauda* are noticeably large-billed (Zimmer 1931), rendering it difficult to identify male specimens to subspecies with certainty.

Females, in contrast, are more easily identified to subspecies group. They have greyish-brown upperparts and flanks, ochraceous forehead, lores, superciliary region and most of the underparts, and faintly indicated pale tips or fringes to the wing-coverts (Cory & Hellmayr 1924, Zimmer 1931). The tail is fuscous in the Guianas and Brazil, pale brown in the Andes, blackish fringed olivaceous in *fuscicauda*. Female *fuscicauda* is paler and duller ochraceous than the rest, and has the crown washed tawny, thus showing a markedly less contrasting facial pattern; additionally, its flanks are greyer and wing-coverts more clearly marked with light Dresden Brown (as of Ridgway 1912) than the other forms (Zimmer 1931, Schulenberg *et al.* 2007).

The voices of these taxa were unknown when Zimmer (1931) and Hellmayr (Cory & Hellmayr 1924) wrote. During the 1980s T. A. Parker recorded the voices of all forms of *C. nigrescens* except the nominate (MLNS recordings), but he never published on the different voice of *fuscicauda*. Mayer (1996) presented recordings of *fuscicauda* and *approximans* from north-east Bolivia and suggested that they were not conspecific. Around the same time (early 1990s), P. Coopmans discovered that two vocal types occurred in different habitats and elevations in Ecuador (Ridgely & Greenfield 2001). The distinctive voice of *fuscicauda* was also noted by Zimmer & Isler (2003) and Schulenberg *et al.* (2007), but a comparative analysis was never published.

We present the results of such an analysis and demonstrate that male song of *fuscicauda* differs markedly from the other five subspecies in two vocal characters, with non-overlapping distributions of data for number of notes and pace. According to Isler *et al.* (1998) a member of Thamnophilidae is unlikely to interbreed with other forms if its song differs consistently in at least three characters, but for parapatric taxa fewer than three diagnosable characters can be considered appropriate. With significant difference in two characters, we add the lack of intermediate song types in areas of parapatry as evidence that *fuscicauda* does not interbreed with geographically adjacent forms, and conclude that it should be ranked as a biological species.

Methods

Vocal material obtained during field studies, from published recordings (Isler & Whitney 2002, Krabbe & Nilsson 2003, Lysinger *et al.* 2005, Moore *et al.* 2009), and from the public archives Macaulay Library of Natural Sounds (MLNS) and XenoCanto (XC) were compared using the sound-editing programme CoolEditPro (Syntrillium Software). Recordings of all six subspecies were analysed. The major types of vocalisations and number of recordings examined are specified in Table 1.

We compared 161 recordings of male song, from the majority of known localities: *nigrescens* from French Guiana, Surinam, Guyana, Roraima and northern Amazonas, Brazil, north of the Amazon River; *approximans* from Santa Cruz, Bolivia, Amazonas, Rondônia, Mato Grosso and Pará, Brazil; *ochrogyna* from Pará, Brazil; *aequatorialis* from Napo, Morona-Santiago and Zamora-Chinchipe, Ecuador; possible *aequatorialis* / *notata* intergrades from San Martín and Amazonas, Peru; *notata* from Huánuco, Loreto, Pasco, Ucayali, Junín and Cuzco, Peru. Recordings of *fuscicauda* were obtained from Amazonas, Colombia; Sucumbíos, Orellana, Napo and Pastaza, Ecuador; Loreto, Ucayali, Madre de Dios and Cuzco, Peru;

TABLE 1
Major types of vocalisations and number of recordings examined for each of the six subspecies of Blackish Antbird *Cercomacra nigrescens*.

Taxon	*aequatorialis*	*aequatorialis/ notata*	*notata*	*approximans*	*ochrogyna*	*nigrescens*	*fuscicauda*
Male song	20	9	23	39	8	14	46
Female song	15	2	13	21	6	12	25
Contact call	3	0	4	15	2	9	27
Churred calls	8	0	3	17	3	9	11
Other calls	0	0	0	0	0	0	10

Acre and south-west Amazonas, Brazil; and Beni, Bolivia. The only region of interest from which no tape-recordings were examined is the upper Mamoré drainage in Cochabamba, Bolivia, which is the only part of the range of *fuscicauda* where *C. serva* is absent. All songs comprised an introductory note followed by a rattle. They were measured for total duration and duration of the introductory note, and the rattle was measured for number of notes, duration, mean pace, pace at start and end, and pitch of highest and lowest note.

We compared 94 recordings of female song from most of the same localities. Female songs, comprised of a rising series of notes, were measured for number of notes, duration, and pitch of first and last note. Additionally, we compared 121 recordings of various calls.

Diagnostic differences had to be discrete, non-overlapping character states that have the potential for unambiguous signal recognition (Isler *et al.* 1998). Ranges of samples of continuous variables could not overlap, and the likelihood that ranges would not overlap with larger sample sizes was estimated by tests described in detail in earlier publications (e.g., Isler & Whitney 2011).

Results

Duets of *Cercomacra nigrescens* typically comprised three songs, male-female-male, and the female song usually partly overlapped in time with one or both male songs, and the second male song was often longer, with more notes than the first.

Male song in all forms of *C. nigrescens* was composed of a low-pitched introductory note followed by a rattle of descending notes (Fig. 1). In *fuscicauda* the rattle differed drastically from all other forms in being composed of a much larger number of notes given at a much faster pace. In all other forms there was considerable overlap in pace and number of notes. In *fuscicauda* the pitch usually rose slightly (1.8 ± 1.1 half notes on a chromatic scale, range 0.0–4.2) at the beginning of the rattle (only remaining constant in one of 42 recordings), and always dropped markedly towards the end, whereas in the other forms the pitch descended evenly or occasionally remained constant. On average, *fuscicauda* songs also differed, albeit with overlap, in a longer introductory note, higher max. pitch of the rattle and in decelerating rather than accelerating pace (Table 2). Eight recordings from the tributaries of the Xingu and Tocantins rivers were tentatively referred to *ochrogyna*. While the rattle of male song recorded near the mouth of the rio Xingu resembles *approximans* in all respects, the rattles in recordings from 480 km to the south (middle rio Xingu) and 350 km south-east (upper rio Itacayunas, a tributary of the rio Tocantins) all showed fairly constant pitch and decidedly slower pace (Fig. 2).

The number of notes and mean pace of male loudsongs of *fuscicauda* differed measurably from those of all other populations (Table 2). The ranges of these measurements

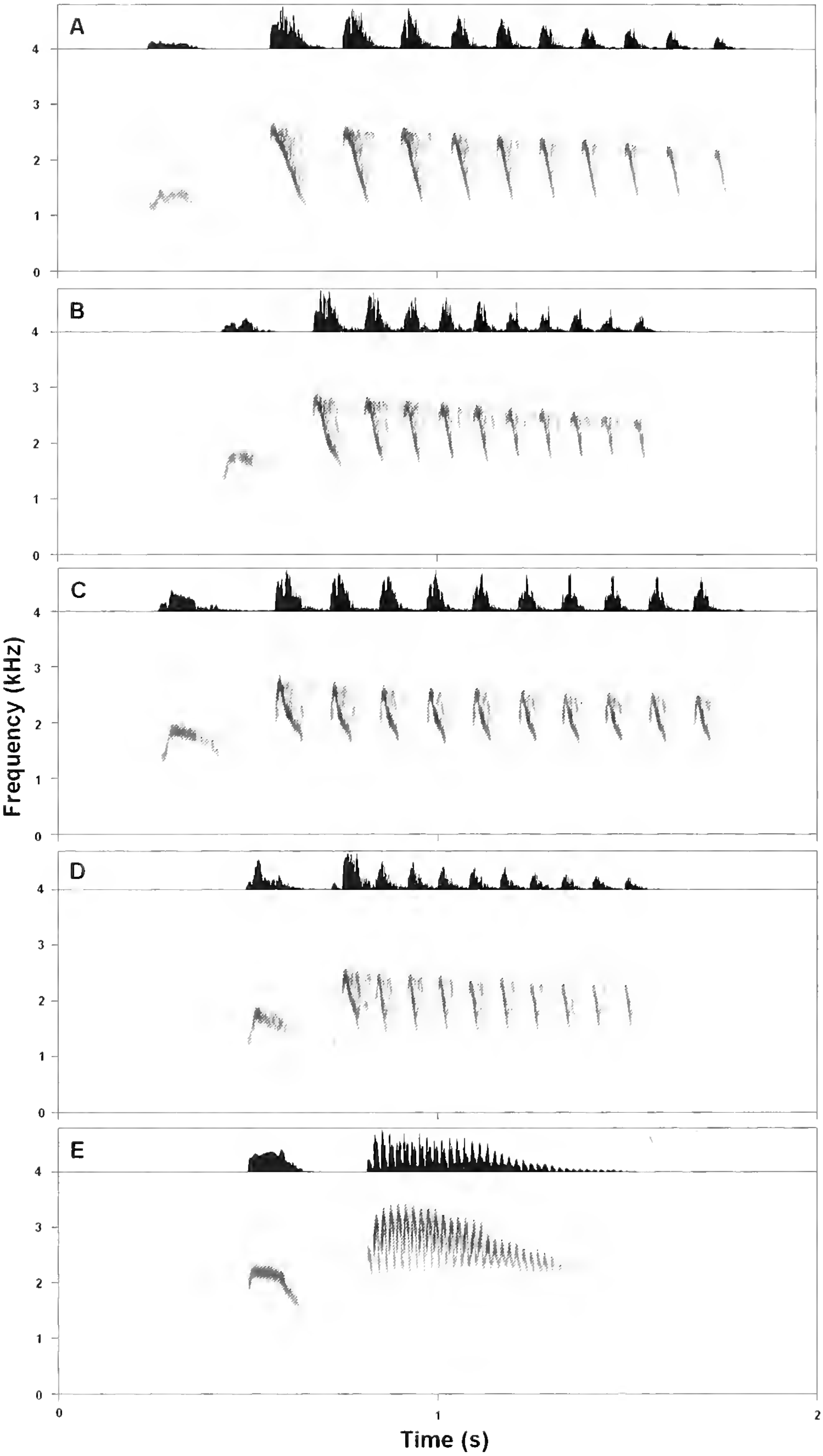

Figure 1. Oscillograms and sonograms of male songs of different taxa referred to Blackish Antbird *Cercomacra nigrescens*. A: *C. n. aequatorialis*; B: *C. n. notata*; C: *C. n. approximans*; D: *C. n. nigrescens*; E: *C. n. fuscicauda*. Note the drastically different song of *fuscicauda*.

TABLE 2

Some properties of male song of different taxa of Blackish Antbird *Cercomacra nigrescens* (mean ± standard deviation, range, sample size). First six rows measure the rattle alone. Change in pitch is measured in half notes on a chromatic scale ((ln(pitch of highest note/pitch of last note))/ln$\sqrt[12]{2}$), change in pace from start of second to start of third, and start of penultimate to start of last note. Note the drastically fast pace in *fuscicauda*, and the slow pace and lack of change in pitch in *ochrogyna*.

Taxon	*aequatorialis*	*notata*	*approximans*	*ochrogyna*	*nigrescens*	*fuscicauda*
No. notes	9 ± 2 (7–13) *n* = 20	12 ± 3 (10–21) *n* = 23	9 ± 2 (7–15) *n* = 39	8 ± 2 (6–11) *n* = 8	13 ± 4 (8–21) *n* = 14	32 ± 6 (23–48) *n* = 38
Duration (seconds)	1.1 ± 0.3 (0.7–1.5) *n* = 20	1.1 ± 0.2 (0.7–1.6) *n* = 23	0.9 ± 0.3 (0.5–1.5) *n* = 39	1.5 ± 0.3 (1.1–2.0) *n* = 8	1.1 ± 0.4 (0.6–1.7) *n* = 14	0.6 ± 0.1 (0.4–0.8) *n* = 46
Mean pace (notes / seconds)	8 ± 1 (6–9) *n* = 20	11 ± 1 (9–14) *n* = 23	10 ± 2 (6–14) *n* = 39	5 ± 1 (3–8) *n* = 8	12 ± 1 (10–13) *n* = 14	53 ± 5 (44–62) *n* = 38
Δ pace	1.32 ± 0.14 (1.15–1.65) *n* = 20	1.16 ± 0.20 (0.91–1.72) *n* = 23	1.09 ± 0.17 (0.89–1.95) *n* = 39	1.19 ± 0.12 (1.03–1.41) *n* = 8	1.09 ± 0.22 (0.86–1.75) *n* =14	0.90 ± 0.14 (0.62–1.13) *n* = 38
Highest pitch (Hz)	2,641 ± 114 (2,482–2,873) *n* = 20	2,598 ± 124 (2,231–2,832) *n* = 23	2,728 ± 225 (2,428–3,292) *n* = 38	2,538 ± 132 (2,313–2,616) *n* = 8	2,275 ± 144 (2,048–2,525) *n* = 14	2,880 ± 209 (2,520–3,377) *n* = 42
Δ pitch (half notes)	2.4 ± 0.8 (0.8–3.9) *n* = 20	3.4 ± 0.7 (2.5–4.9) *n* = 23	2.4 ± 1.1 (0.4–4.7) *n* = 38	0.4 ± 0.4 (0.0–1.1) *n* = 8	2.0 ± 0.9 (0.3–3.4) *n* = 14	6.5 ± 2.9 (0.6–12.4) *n* = 42
Duration of introductory note (seconds)	0.15 ± 0.02 (0.11–0.18) *n* = 20	0.12 ± 0.02 (0.10–0.17) *n* =23	0.14 ± 0.02 (0.09–0.20) *n* = 39	0.15 ± 0.02 (0.12–0.18) *n* = 8	0.12 ± 0.02 (0.10–0.17) *n* = 14	0.17 ± 0.03 (0.13–0.28) *n* = 46

TABLE 3

Some properties of female songs of different taxa of Blackish Antbird *Cercomacra nigrescens* (mean ± standard deviation, range, sample size). Note the similarity.

Taxon	*aequatorialis*	*notata*	*approximans*	*ochrogyna*	*nigrescens*	*fuscicauda*
No. notes	6 ± 1 (5–8) *n* = 15	7 ± 1 (6–10) *n* = 13	6 ± 1 (5–11) *n* = 21	7 ± 1 (6–8) *n* = 6	6 ± 1 (4–9) *n* = 12	5 ± 1 (3–7) *n* = 25
Duration (seconds)	1.9 ± 0.4 (1.4–2.6) *n* = 15	2.3 ± 0.4 (1.8–3.1) *n* = 18	1.9 ± 0.4 (1.4–2.9) *n* = 21	2.2 ± 0.3 (1.7–2.5) *n* = 6	1.9 ± 0.4 (1.2–2.5) *n* = 12	1.7 ± 0.3 (0.9–2.1) *n* = 25
Pitch of first note (Hz)	1,572 ± 203 (1,280–2,019) *n* = 15	1,351 ± 116 (1,172–1,473) *n* = 13	1,578 ± 157 (1,320–1,830) *n* = 21	1,578 ± 118 (1,375–1,676) *n* = 6	1,397 ± 150 (1,236–1,777) *n* = 12	1,624 ± 223 (1,331–2,189) *n* = 25
Pitch of last note (Hz)	2,503 ± 216 (2,062–2,842) *n* = 15	2,285 ± 252 (1,729–2,547) *n* = 13	2,336 ± 248 (1,824–2,706) *n* = 21	2,260 ± 308 (1,957–2,829) *n* = 6	2,146 ± 187 (1,934–2,445) *n* = 12	2,539 ± 342 (1,783–3,054) *n* = 25

did not overlap and distributions met tests of the likelihood that they would not overlap with larger samples. Therefore, the two independent measures are considered diagnostic.

No intermediate song types between *fuscicauda* and adjacent forms were found. Recordings from Napo, Ecuador, where *aequatorialis* and *fuscicauda* were found just 30 km apart, recordings from Ucayali, Peru, where *notata* was found only 12 km from the río Ucayali near the type locality of *fuscicauda*, and recordings from Beni, Bolivia, where *approximans* and

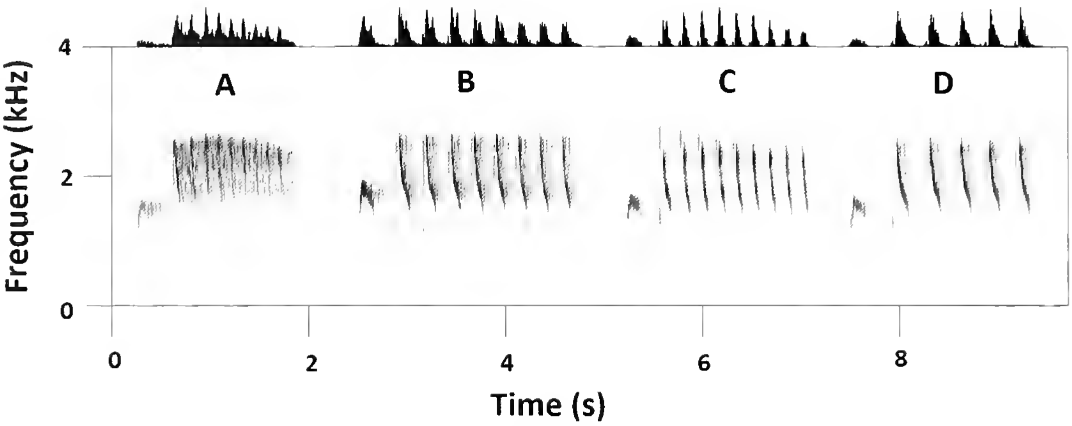

Figure 2. Oscillograms and sonograms of male song in recordings tentatively referred to *Cercomacra nigrescens ochrogyna* from east Amazonian Brazil. A: near mouth of rio Xingu; B: middle rio Xingu; C–D: Serra dos Carajás (rio Tocantins drainage). While the song in A resembles that of *approximans*, songs in B, C and D are slower paced and average more constant in pitch.

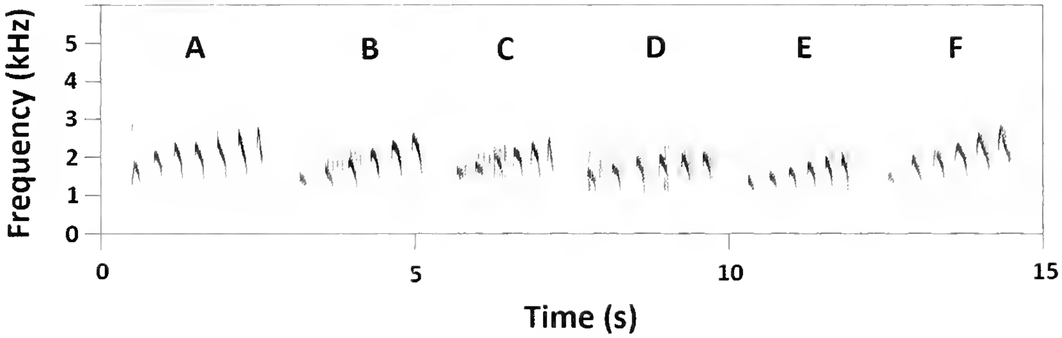

Figure 3. Sonogram of female songs of different taxa referred to Blackish Antbird *Cercomacra nigrescens*. A: *C. n. aequatorialis*; B: *C. n. notata*; C: *C. n. approximans*; D: *C. n. ochrogyna*; E: *C. n. nigrescens*; F: *C. n. fuscicauda*. Note the similarity.

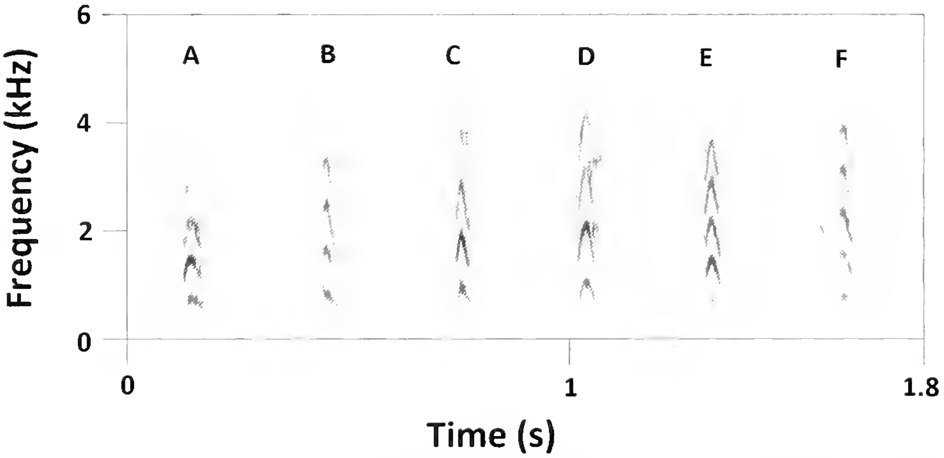

Figure 4. Sonogram of contact call of different taxa referred to Blackish Antbird *Cercomacra nigrescens*. A: *C. n. aequatorialis*; B: *C. n. notata*; C: *C. n. approximans*; D: *C. n. ochrogyna*; E: *C. n. nigrescens*; F: *C. n. fuscicauda*. Note the similarity.

fuscicauda occurred just 80 km from each other, were all clearly of one song type or the other. We detected no obvious habitat barrier between them in any of these areas.

Female song in all six forms was a series of 3–11 notes rising steadily from *c*.1,500 Hz to *c*.2,350 Hz and given at a fairly steady pace of *c*.3 notes per second. At the onset of duets

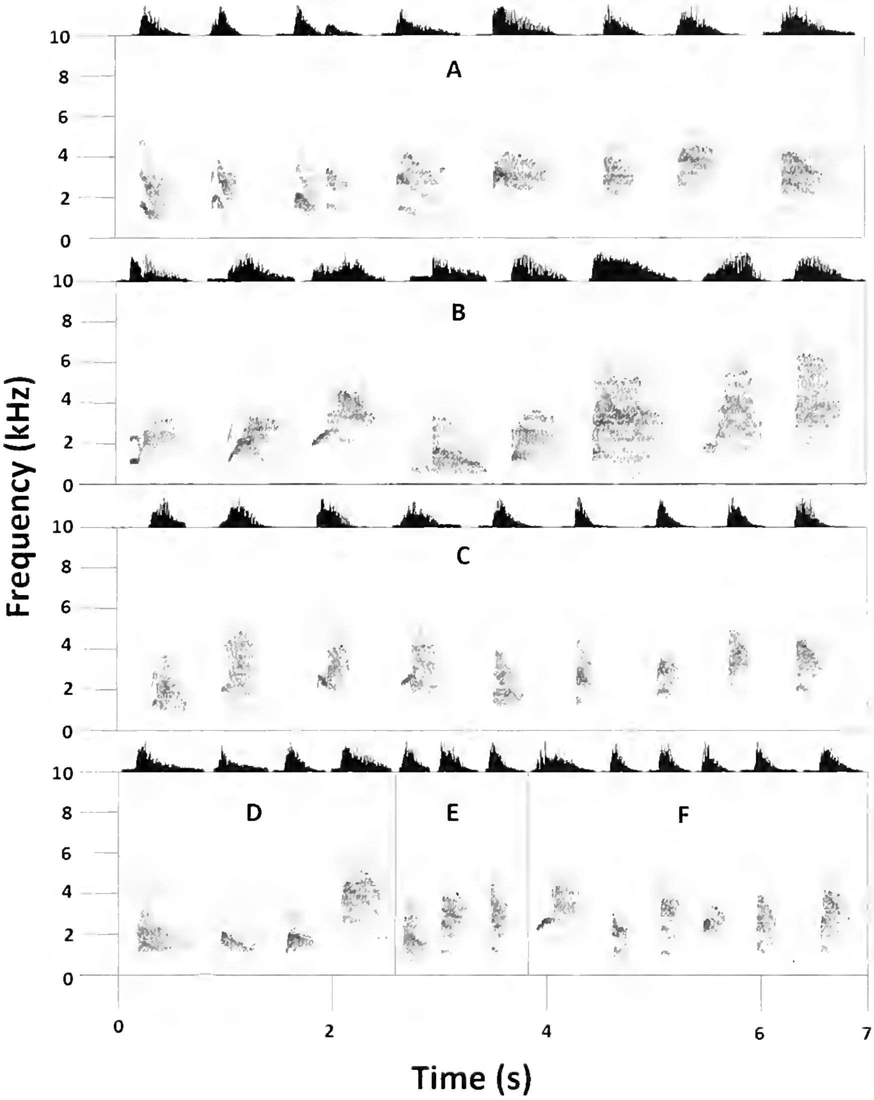

Figure 5. Oscillograms and sonograms of churred calls of Blackish Antbird *Cercomacra nigrescens*. A: *C. n. fuscicauda*; B: *C. n. aequatorialis*; C: *C. n. approximans*; D: *C. n. notata*; E: *C. n. ochrogyna*; F: *C. n. nigrescens*. Note that calls of *approximans*, *ochrogyna* and *nigrescens* average shorter than the others, but the general range of variation was so great that homology was difficult to verify.

it comprised fewer notes than later in the bout. As also found by Zimmer & Isler (2003) it was very similar in all six forms (Fig. 3). The last note was sometimes of slightly different quality, and at least in *aequatorialis*, *notata*, *approximans*, *ochrogyna* and *fuscicauda* the song was very rarely terminated with a few rapid notes, higher or lower, sometimes reminiscent of the male rattle. Female song (both beginning and end) averaged slightly higher pitched in *fuscicauda* than in other forms (Table 3).

Call notes recorded were of a variety of types. The most commonly recorded call was a single, slightly nasal note given by both sexes, apparently in contact. All six forms gave very similar versions of this call (Fig. 4).

Churred disturbance calls were slightly higher pitched in females than in males. They were given at various levels of excitement and differed widely in structure and quality, even within a single form (Fig. 5), rendering an assessment of homology difficult. However, most of the churred calls given by *approximans*, *ochrogyna* and *nigrescens* were shorter than those given by other forms (Fig. 5).

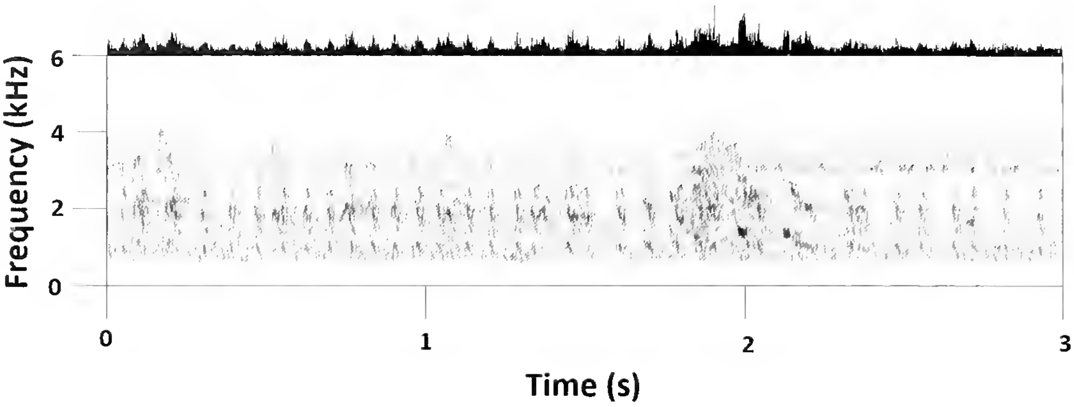

Figure 6. Oscillogram and sonogram of calls of a pair of *Cercomacra nigrescens fuscicauda* during a territorial dispute. This call of rapidly repeated notes weak in overtones compared to the contact call in Fig. 4 was sometimes sustained for 15 seconds or more, both members of the pair giving synchronised, higher pitched, louder bursts at intervals, in this example at start and after *c*.2 seconds.

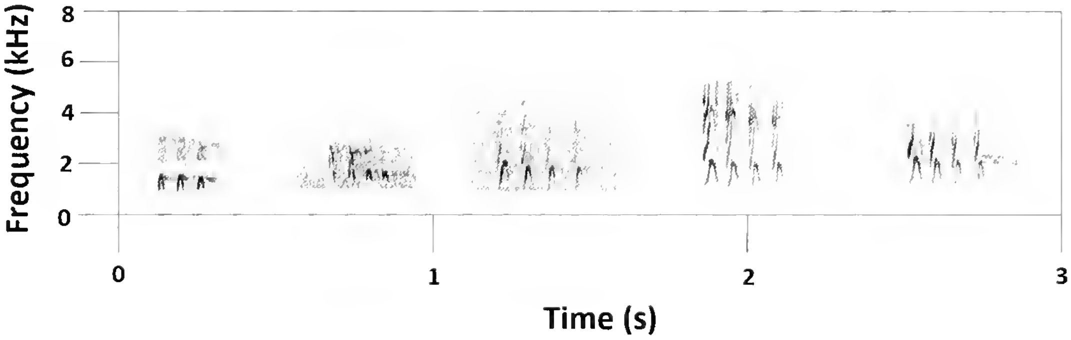

Figure 7. Sonogram of calls by five individuals of *Cercomacra nigrescens fuscicauda*. This rapid series of 3–4 notes was given by agitated birds and might be unique to *fuscicauda*.

Ten recordings of *fuscicauda* included other call types given during territorial disputes. Four of them were of a pair giving a longer series of low-pitched notes with weaker overtones than the contact calls, mainly at constant pitch, but interspersed at intervals by bursts of higher pitched louder notes (Fig. 6). Such bursts sometimes terminated longer series with a call of three or four notes in rapid succession, a call also given alone in high excitement or in alarm by surprised fleeing birds (Fig. 7).

Discussion

Habitat and geographic distribution.—As mentioned earlier, nearly all species in the [*C. tyrannina*] group are allo- or parapatric, and differ in habitat where their ranges overlap. Where *C. nigrescens* co-occurs with *C. tyrannina* it is mostly confined to *várzea*, *C. tyrannina* to *terra firme*, and where it co-occurs with *C. laeta* the latter is mostly confined to white-sand forest (Snethlage 1913, Zimmer 1931, Zimmer & Isler 2003). The range of *C. serva*, however, is entirely encompassed by that of *C. nigrescens*. In view of their seemingly similar habitat requirements, it is difficult to explain how they manage to co-exist in some areas. To the east, *C. serva* is replaced by *C. n. approximans* with little or no overlap, and through most of the lowland part of the range of *C. serva*, *C. n. fuscicauda* is confined to a narrow niche of seasonally flooded forest, thickets and *Gynerium* cane on river islands and banks (Ridgely & Greenfield 2001, Zimmer & Isler 2003, Schulenberg *et al*. 2007; also descriptions given for recording sites on MLNS and XC recordings, and pers. obs.). In the south-east Peruvian lowlands and at lower elevations in the Andean foothills, however, a partitioning of niches appears to be incomplete. The Andean forms of *C. nigrescens* occur at higher elevations (to 2,100 m) than *C. serva*, but where the ranges of the two species overlap, at elevations of 700–1,100 (locally to 1,500) m, no habitat difference is apparent (Ridgely & Greenfield 2001, Schulenberg *et al.* 2007; pers. obs.). Both species can be heard on some tape-recordings, but it is possible that individual territories do not overlap. The incomplete niche partitioning in some areas and the rather local occurrence of *C. n. fuscicauda*, at least in Peru (Schulenberg *et al.* 2007) might suggest that *C. serva* expanded its range fairly recently.

Based on vocal evidence and published specimens the six described forms of *C. nigrescens* are distributed as follows.

C. n. nigrescens: Guianas. Birds from Sao João de Baliza and along the rio Branco and immediately adjacent rio Negro, Roraima, Brazil (Naka *et al.* 2007) are vocally similar and are tentatively referred here. A recording from the mouth of the rio Japurá nearly 600 km west of Manaus (M. Cohn-Haft, unpubl.) probably also belongs here. 0–90 m.

C. n. approximans and *ochrogyna*: from rio Madeira, western Amazonas, Brazil, and Beni and Santa Cruz, north-east Bolivia east through Rondônia and Mato Grosso to Pará, Brazil, generally south of the Amazon, but locally on both banks. The range of *ochrogyna* is uncertain. The type locality is on the rio Araguaia (an affluent of the rio Tocantins) in extreme north-east Mato Grosso, and no recordings are available from there or the immediate vicinity. We tentatively refer all birds from the Xingu and Tocantins drainages to this form, but note that song recorded near the mouth of the rio Xingu resembles that of *approximans*, while songs from near the middle rio Xingu (Pinkaiti on the rio Riozinho) and the Tocantins drainage (Serra dos Carajás) are slower paced and possibly more constant in pitch (Fig. 2). 10–660 m.

C. n. aequatorialis and *notata*: from northern Napo, eastern Ecuador (*aequatorialis*) south to north-west Cusco, south-east Peru (*notata*), intergrading in San Martín, Peru. 700–2,100 m.

C. n. fuscicauda: from Napo and Sucumbíos, Ecuador, and south-east Amazonas, Colombia (Leticia) south through eastern Peru and adjacent Acre and south Amazonas (upper rio Purus drainage: unpubl. recordings by M. Cohn-Haft), Brazil, to northern Beni and Cochabamba, Bolivia. 100–600 m, locally to 850 m (XC57243). In Beni recorded only 80 km from *approximans*, in Napo, just 30 km from *aequatorialis* and in Ucayali only 12 km from *notata*.

With no obvious habitat barrier between *fuscicauda* and neighbouring forms of *C. nigrescens* where they are in closest proximity, they must be presumed to come into contact with each other. The lack of intermediate song types near the contact zones is evidence that they either maintain their integrity despite limited hybridisation, or that they do not interbreed at all.

Evolution.—Without data on the genetic distances between the various forms of *C. nigrescens*, scenarios linking speciation events to the upheaval of the Andes and Amazonian dynamics caused by climatic fluctuations would be speculative. However, the similarities between female songs and contact calls do suggest that all six taxa form a monophyletic unit. Additionally, the incomplete niche partitioning with *C. serva* suggests that *fuscicauda* may have speciated as a result of a recent expansion of that species.

Elevating *fuscicauda* to species rank leaves a disjunct and possibly paraphyletic *C. nigrescens* with populations in the Guianas and Brazil north of the Amazon, in east Amazonian Brazil, and in the Andes. The Amazonian Brazil population is separated from the Andean by 850 km and from the Guianan by 350 km. These three populations may have reached genetic incompatibility and thus require consideration as species, but we did not find vocal evidence to support this during the present study, except for possibly in *ochrogyna* (see above).

Conclusion

We suggest that *fuscicauda* be raised to the rank of biological species based on the criteria of Isler *et al.* (1998). Two vocal characters were found to differ diagnostically and the lack of recordings of intermediate song types provides evidence that *fuscicauda* does not interbreed with adjacent, clearly parapatric forms. We follow previous suggestions of Riparian Antbird (Krabbe & Nilsson 2003) as a vernacular name. Throughout much of its range *fuscicauda* is confined to seasonally flooded forest or stands of *Gynerium* cane and adjacent thickets on sandbars and river banks, and it appears to be always associated with riparian habitats, whereas the other forms of *C. nigrescens* also occur in other habitats, the Andean forms exclusively so.

Acknowledgements

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The taxonomy and nomenclature of Grey-headed Bristlebill *Bleda canicapillus* (Hartlaub)

by John Penhallurick & Lincoln Fishpool

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Summary.—All authorities over the past century have cited Grey-headed Bristlebill *Bleda canicapillus* as having been named by Hartlaub in 1854, but in fact the name dates from 1850. The type locality has been given as Sierra Leone, while the population in Senegambia has been separated as race *morelorum*. However, Hartlaub's name is based on a type from Gambia, while analysis of a series of specimens from Nigeria to Gambia suggests individual variation in the species is extensive and does not support Érard's (1991) claim of a subspecific difference. We believe that the species should be considered monotypic.

Grey-headed Bristlebill *Bleda canicapillus* (Hartlaub) was considered monotypic until Érard (1991) proposed that populations in Senegambia were, when compared with material from Guinea, Côte d'Ivoire and Ghana, sufficiently distinct to merit subspecific recognition. Although he initially named Senegambian birds *moreli*, Érard (1992) emended this to *morelorum*, in accordance with Art. 31.1.2 of the *International code of zoological nomenclature* (ICZN 1999: 37), as the name explicitly honoured a husband and wife team.

Moreover, Érard's proposal appears to have assumed that the locality of Hartlaub's type was Sierra Leone, albeit not explicitly. The citation for Hartlaub's type is given by Rand (1960: 274) as: *Trichophorus canicapillus* Hartlaub, 1854, *J. Orn*. 2: 25 – Sierra Leone, Gambia. The correct citation for *Bleda canicapillus* is to Hartlaub's publication in 1850, and the reference to Sierra Leone stems from Hartlaub's (1850) citation of 'Brimstone-bellied Thrush, Lath. *Gen. Hist*. V: 103'. Latham (1822: 103) reads: 'Thrush 112.—BRIMSTONE-BELLIED THRUSH. Length seven inches. Bill stout, dusky, at the base a few hairs; top and sides of the head ash-colour; rest of the plumage above olive-green; beneath from the chin pale yellow; tail rounded, the three outer feathers with the ends pale yellow, but chiefly on the inner webs; the wings reach to the middle of the tail; the first quill is half the length of the others, the second reaches three-fourths, but the fourth is the longest; legs brown. Inhabits Sierra Leone.'

The reference here to Latham's 'Brimstone-bellied Thrush' is sufficient to provide a description for Hartlaub's bird (F. D. Steinheimer *in litt*. 2007), based on Art. 12.2.1 of the *Code* (ICZN 1999: 16). Thus, it is incorrect to treat—as Sclater (1930) did—Hartlaub's 1850 citation as a *nomen nudum*. Rand regarded Latham's picture and the specimen in the Überseemuseum Bremen as syntypes. Previously, however, Sclater (1930: 378), though also citing the 1854 paper, had given the type locality as 'Sierra Leone (ex Beitr. Orn. Westafr. p.25 [=24],1852, nom. nud.)'. In fact, the correct date of the first part of Hartlaub's *Beitrag zur Ornithologie Westafrica's*, published in *Abhandlungen aus dem Gebiete der Naturwissenschaften* vol. 2(2): 1–56, is 1850 (www.archive.org/stream/12beitragzurorni00hart#page/n5/mode/2up). On p. 24 of this work is: '*Trichophorus canicapillus*, nob[is] n[ova] sp[ecies].- Brimstone bellied Thrush, Lath. Gen. Hist. V 103. - Sierra Leone. Mus. Brem.' The correct citation is therefore: *Trichophorus canicapillus* Hartlaub, 1850, Beitrag zur Ornithologie Westafrica's [Erster Beitrag]. *Abhandlungen aus dem Gebiete der Naturwissenschaften* 2(2): 24.

TABLE 1
Bill measurements of *Bleda canicapillus* specimens at BMNH, Tring: length from tip to skull, width at distal edge of nares. Data for Senegal taken from Érard (1991).

	Males		**Females**	
	Bill length	**Bill width**	**Bill length**	**Bill width**
Senegal				
Range	19.5		19.5–20.5	
n	1		2	
Gambia*	20.9	5.0		
n	1			
Guinea Bissau				
Mean	22.55	5.25	19.15	4.65
Range	21.4–23.7	4.8–5.7	19.0–19.3	4.5–4.8
n	2		2	
Sierra Leone				
Mean	21.74	4.94	19.47	4.7
Range	20.6–22.4	4.3–5.6	19.0–20.3	4.5–4.8
n	7		3	
Liberia				
Mean	21.88	4.80	20.50	5.13
Range	20.1–23.1	4.4–5.3	18.8–21.6	4.9–5.6
n	5		9	
Ghana				
Mean	22.1	5.27	19.60	4.5
Range	21.6–22.9	5.2–5.3		
n	3		1	
Nigeria				
Mean	22.93	5.34	21.09	5.03
Range	21.0–24.7	5.0–5.5	19.8–22.5	4.6–5.4
n	8		8	
Total (BMNH)	26		23	

* The sole Gambian specimen at BMNH is unsexed, but inferred from measurements to be male. Other unsexed specimens (Sierra Leone = 3, Ghana = 7) excluded.

There is also the reference in Hartlaub (1850) to 'Mus. Brem.'. This clearly points to a specimen, and we have confirmed that specimen no. 8213 in the Überseemuseum, Bremen is Hartlaub's type. It has two labels: an orange one: '*Trichophorus canicapillus* Hartlaub, 1852 / Fundort: Gambia, Westafrica', and an older, brown label: 'Criniger 8213 / *Trichophorus canicapillus* Hartl. Beitr. W. Afr. 1850 / p.24. W. Afr. Sp. 254. / Finsch Monog. J. f. Orn. 1867 / p.31. / Typus der Art! / Westafrica / Gambia.' This specimen is undoubtedly the type. Rand (1960: 274) was incorrect in positing two syntypes, one of them being Latham's (1822) 'Brimstone-bellied Thrush'.

As mentioned above, Érard (1991) assumed that Sierra Leone was the sole type locality attached to Hartlaub's name. Instead, the type locality of Hartlaub's type specimen is Gambia, which makes Érard's (1992) *morelorum* a junior synonym of Hartlaub's name.

There remains the issue of whether two subspecies can be recognised. Érard (1991) maintained that birds from Senegambia differ from the nominate over the rest of the species' range (Guinea-Bissau to Nigeria) in having; (i) paler yellow underparts, (ii) paler terminal spots on the outer rectrices, (iii) a paler grey head, (iv) browner or greyer, less green upperparts, and (v) a shorter and wider bill. Based on an examination, independently by both authors, of the 59 specimens of *Bleda canicapillus* in the Natural History Museum (BMNH), Tring, which, significantly, include material from Sierra Leone and Guinea Bissau, we conclude that the species is monotypic. Taking the differences claimed by Érard (1991) in order.

(i) Underparts coloration.—While there is little overall difference in specimens from Nigeria to Liberia, there is a significant amount of variation in the breast, belly and flanks of the 13 specimens from Sierra Leone. For example, the underparts of BMNH 1930.12.3.322 (male, from Buedu near Kailahun) are, like those from further east, bright yellow with darker olive-green patches confined to the breast-sides and flanks. In the underparts of BMNH 1930.12.3.321 (female, Kamasigi), the amount of olive-green on the breast-sides and flanks is more extensive and the correspondingly more restricted area of yellow on the central breast and belly is duller. This trend is continued in BMNH 1904.6.5.232 (unsexed, Bo), where only the central breast and belly is dirty yellow. Lastly, the palest underparts of all 59 specimens at Tring occurred in a specimen from Sierra Leone (BMNH 1966.16.1632 Benguema, male). Furthermore, the label on this specimen records 'testes enlarged', so any possibility that this is merely a young bird is discounted.

Tring has four specimens from Guinea Bissau (BMNH 1910.5.6.625–628, Gunnal, Portuguese Guinea) and one from Gambia (unsexed, Vellum Cat. XV.440a, no precise locality). The underparts of the former, all from the same locality and collected within one month of each other, vary in the saturation of the yellow and in the amount of olive-green suffusion on the flanks and lower breast in particular. The underparts coloration and pattern of the Gambian specimen are comparable with those of the Benguema, Sierra Leone specimen, if somewhat darker. Overall, therefore, specimens from the western range of *canicapillus* exhibit much variation in this character, and there is no clear, geographically restricted difference in underparts coloration consistent with that described by Érard (1991).

(ii) Terminal spots on outer rectrices.—Variation in the colour of the terminal spots on the outer tail feathers broadly mirrors that described for the underparts. Thus, in specimens from Liberia eastwards, the spots are yellow, while in those from Sierra Leone west, they are yellow or obviously more pale. They are palest in BMNH 1930.12.3.322 (Buedu near Kailahun, Sierra Leone) and Vellum Cat. XV.440a from Gambia. However, the variation in the intensity of colour in the material from Sierra Leone and Guinea Bissau is again at odds with what Érard (1991) suggested.

(iii) Head colour.—We found relatively little variation among all 59 specimens at Tring—although the Gambian specimen mentioned above was among the darkest—and conclude that this character is invalid.

(iv) Upperparts coloration.—Variation in the material in Tring is modest and only partially consistent with Érard's findings. Thus, while birds from the west (Gambia and Guinea Bissau) are dull green or dull brownish green, and those from Liberia east trending greener, there is again variation in the Sierra Leone material, with BMNH 1930.12.3.322 (Buedu near Kailahun) greenest, BMNH 1966.16.1632 (Benguema) brownest, and the rest intermediate. However, there is also variation in specimens from Nigeria, where at least four have dull greenish-brown backs (BMNH 1966.16.1634, female, Ede; 1966.16.1638, female, Mamu Forest Reserve; BMNH 1947.24.17–18, female and male, Owerri). Once more, therefore, the validity of this character is questionable.

(v) Bill size.—Érard (1991) also stated that bill size is 'shorter, appearing conspicuously wider' in *morelorum*. Our measurements of bill length (Table 1) of a much larger sample indicate that it is at least equally likely that birds in Senegambia are at the end of a cline of decreasing size from east to west, and do not support Érard's suggestion that bill width in Senegambia is greater than in birds from elsewhere.

Finally, we also compared the Gambian specimen (Vellum Cat. XV.440a) with Érard's type of *morelorum*, using photographs of the latter (CG 1984, no. 528) kindly supplied by A. Préviato of the Museum National d'Histoire Naturelle, Paris. This generally resembles the coloration of the BMNH specimen ventrally, but the central upper breast is noticeably paler. We also compared these two specimens from Senegambia with photographs of Hartlaub's type. This specimen, also from Gambia, is rather yellower than the other two, although still dingy. In view of the above, we conclude that there is no subspecific variation in *Bleda canicapillus* and the species should be treated as monotypic.

Acknowledgements

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The sunbird genera *Anthodiaeta* and *Hedydipna* revisited

by Clive F. Mann & Robert A. Cheke

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Cabanis (1851) erected the sunbird genera *Anthodiaeta* and *Hedydipna* for *Cinnyris collaris* Vieillot, 1819, and *Nectarinia metallica* M. H. C. Lichtenstein, 1823, respectively, and specified *C. platura* Vieillot, 1819, as the type species of *Hedydipna* whilst spelling it *platyura*. Several authors including Shelley (1877) and Roberts (1922, 1931, 1932, 1940) retained *collaris* within *Anthodiaeta*, but Sclater (1930) placed *collaris* within *Anthreptes* and maintained *platura* and *metallica* in *Hedydipna*. Delacour (1944) synonymised both *Anthodiaeta* and *Hedydipna* with *Anthreptes*. Wolters (1977) subsumed *Anthodiaeta* within *Hedydipna* in which he placed *platura*, *metallica* and *collaris*, but placed *A. pallidigaster* W. L. Sclater & Moreau, 1933, in *Lamprothreptes* Roberts, 1922, albeit with a question mark. Irwin (1999) followed Wolters but added *pallidigaster* to *Hedydipna*. Fry *et al.* (2000) and Cheke & Mann (2001) followed Irwin (1999) in using *Hedydipna* for *collaris*, *platura*, *metallica* and *pallidigaster*.

Mann & Cheke (2006), followed by Cheke & Mann (2008), proposed that *Anthodiaeta* should replace *Hedydipna* in the outdated belief that position priority applied to genera, since Cabanis had erected *Anthodiaeta* on the page preceding his erection of *Hedydipna*. However, arguments concerning position priority now usually only apply to the designation of type species (Recommendation 69A, ICZN 1999: 73). Furthermore, Mann & Cheke failed to recognise that Wolters (1977, 1979) may have acted as a first reviser. Art. 24.2.1. of the *International code of zoological nomenclature* states: 'When the precedence between names or nomenclatural acts cannot be objectively determined, the precedence is fixed by the action of the first author citing in a published work those names or acts *and selecting them* [our italics]; this author is termed the 'First Reviser.' Although Wolters (1977: 86) did not explicitly select *Hedydipna* over *Anthodiaeta*, he did so implicitly, and the relevant section of Wolters (1979: 275) can be interpreted as an explicit selection, leaving little doubt that he was first reviser.

Given the above, *contra* Mann & Cheke (2006), *Hedydipna* should be used and not *Anthodiaeta* for *collaris*, *platura*, *metallica* and *pallidigaster* if they are considered congeneric. However, *platura* and *metallica* differ from *collaris* and *pallidigaster* in having (a) a non-breeding eclipse plumage in males; (b) no pectoral tufts; (c) no metallic plumage in females; (d) elongated rectrices in males, although the taxonomic value of this character is ignored in *Cinnyris* for example; (e) weaker bill serrations; (f) nests that are placed in bushes and not suspended and (g) DNA differences, as Bowie (2003), who lacked samples of *pallidigaster* or *metallica*, found that *platura* was well separated from *collaris* based on nuclear and mitochondrial data from 102 species of sunbirds. Therefore we propose that Cabanis' original generic designations should be retained with *Hedydipna platura*, *H. metallica*, *Anthodiaeta collaris* and *A. pallidigaster* as valid species.

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Specimen of Indian Pitta *Pitta brachyura* from the Islamic Republic of Iran

by Paul van Els & Matthew L. Brady

Received 17 October 2013

On 19 November 1968, mammalogist Douglas M. Lay collected a juvenile female Indian Pitta *Pitta brachyura* that was deposited at the Museum of Natural Science, Louisiana State University (LSUMZ 85937; Fig. 1). The bird was 'shot in thick *Populus euphratica* and *Tamarix* sp. "jungle"' along the Karkheh River, 17 km south-west of the city of Shush, Khuzestan province, in south-western Iran. The locality, 17 km south-west of Shush, is not precisely situated along the Karkheh River, and presumably reflects an inaccuracy on the behalf of the collector, who we unsuccessfully attempted to contact, meaning we are unable to present more data concerning the specimen's collection. There are no records in Iran or anywhere else in the Middle East (Scott & Adhami 2006, Porter & Aspinall 2010).

P. brachyura breeds in tropical submontane forest and scrub from north-central (Sikkim) and perhaps north-east India (Assam, breeding unconfirmed) and central Nepal, through north-east Pakistan and south-west to the Indian states of Gujarat and Maharashtra (Grimmett *et al.* 1999, Birdlife International 2013). The species is a long-distance migrant and winters from central India south to Sri Lanka, mostly in the southern part of that range. Except records in south-east Pakistan and the Indian Thar desert (Kamal 1978, Singh 2004), long-distance vagrancy is unknown. A closely related (Irestedt *et al.* 2006) migratory species, Blue-winged Pitta *P. moluccensis* of South-East Asia, has strayed to Christmas Island and Australia, which are 500–3,000 km from the non-breeding range (Serventy 1968, Benson

Figure 1. Dorsal (above) and ventral (below) views of Indian Pitta *Pitta brachyura* specimen (LSUMZ 85937) from Khuzestan province, Islamic Republic of Iran, 19 November 1968, collected by Douglas M. Lay (Paul van Els)

1970). The nearest breeding grounds of Indian Pitta are in the Margalla Hills of north-east Pakistan, *c.*2,300 km east-northeast of Khuzestan. However, this population is very small (18–20 pairs, Roberts 1992), making it probable that the specimen originated from further away. The westernmost population departs the breeding grounds in October, later than eastern birds (Roberts 1992). The mid-November date of the Iran record is slightly later than the mean arrival date on the wintering grounds in Sri Lanka (Brown 1931), but may be the result of a vagrant lingering, as has been noted in other species (Post 2008, Breaks 2009), or an attempt to overwinter. Furthermore, the specimen lacks the red on the underparts indicative of an adult, which lends further support to a vagrant origin, because juveniles frequently comprise a large proportion of vagrants (Baker 1977, Alerstam 1990, Taylor *et al.* 1994, Thorup *et al.* 2011).

The specimen measurements are as follows: maxilla 19.3 mm, mandible 22.8 mm, tarsus 33.9 mm, wing 103.5 mm. No mass was recorded. These measurements fall within the size range typical of the species (Erritzoe & Erritzoe 1998). The specimen has worn primaries and rectrices, mostly shortened barbs on the outer vanes, but also broken rachides, which could indicate a captive origin. Pittas are occasionally kept in captivity (Steinbacher 1940), both as pets and for food (Lambert & Woodcock 1996). Furthermore, CITES was only implemented in 1975 (Favre 1989), seven years after the date of collection, and we are unaware of other controls on the cagebird trade in the region prior to this. Caged birds from the Indian subcontinent, e.g. Common Myna *Acridotheres tristis*, Red Avadavat *Amandava amandava*, and Rose-ringed *Psittacula krameri* and Alexandrine Parakeets *P. eupatria*, were relatively common in the 1970s in Iran (D. A. Scott pers. comm.). However, records of captive Indian Pittas, at least until 1986, are few, with no more than 70 known individuals traded (Thomsen *et al.* 1986). An alternative cause of the damage may be due to shot, which problem is common in specimens.

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A second Sabine's Gull *Xema sabini* in Brazil

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The north-east Brazilian coast in the states of Maranhão and Pará hosts internationally significant numbers of waterbirds and has recently proven to be an excellent 'hunting ground' for Palearctic vagrants (Almeida *et al.* 2013, Lees *et al.* in press). In August 2013 AFT, MT, AT & DC participated in a bird tour of Maranhão, led by T. Rodrigues. They subsequently archived their images on WikiAves (hereafter WA; www.wikiaves.com). On 6 September 2013 ACL noticed that WA1074998 taken at Praia Raposa, in the municipality of Raposa (02°24'S, 44°05'W) on 24 August 2013 and captioned as a Laughing Gull *Leucophaeus atricilla* was a first-summer Sabine's Gull *Xema sabini,* an identification confirmed via contact with AFT who along with AT, MT & DC posted additional photographs. Identification was straightforward given the bird's small size, evident alongside a Common Tern *Sterna hirundo* (WA1075741), extensive white 'moons' in the primaries and a 'half-hood' effect produced by the white head contrasting with the grey nape (Fig. 1). The bird was aged as a first-summer based on the all-dark bill, lacking the yellow tip of an adult.

Figure 1. Sabine's Gull *Xema sabini,* Praia Raposa, municipality of Raposa, Maranhão, Brazil, 24 August 2013 (A. F. Távora)

Sabine's Gull has a circumpolar breeding distribution, and winters along the Pacific coast of South America, off Peru and Chile in the Humboldt Current, and along the west coast of Namibia and South Africa in the Benguela Current (Mayaud 1965, Olsen & Larsson 2004, Stenhouse *et al.* 2012). It is rare in the eastern Atlantic south of the Gulf Stream (Moser & Lee 2012) with just three previous records from eastern South America: two in French Guiana and one in Brazil. Both those from French Guiana involved birds at sea: a winter-plumaged adult photographed by O. Tostain, 15–20 km off Grand Connétable island (04°50'N, 51°56'W, 18 km from the Approuague estuary), on 1 November 1999, and an immature photographed by E. Hansen off Îles du Salut, 14 km north of Kourou, on 31 December 2004 (Comité d'Homologation de Guyane *per* O. Claessens). The sole previous Brazilian record was an adult photographed at Praia do Cassino, 4 km south of Casino, Rio Grande do Sul, on 16 November 2009 (Parrini & Carvalho 2009). Stenhouse *et al.* (2012) used geolocators to track the migrations of adults breeding in Greenland, finding that southbound birds appeared not to venture far from the coast but northbound birds took a shorter, more direct, route towards Ascension Island. Most first-summer birds do not return to breed (Olsen & Larsson 2004) and probably remain in their wintering areas where they may be prone to transatlantic vagrancy caused by the intense storms prevalent in the Southern Ocean during the austral winter.

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