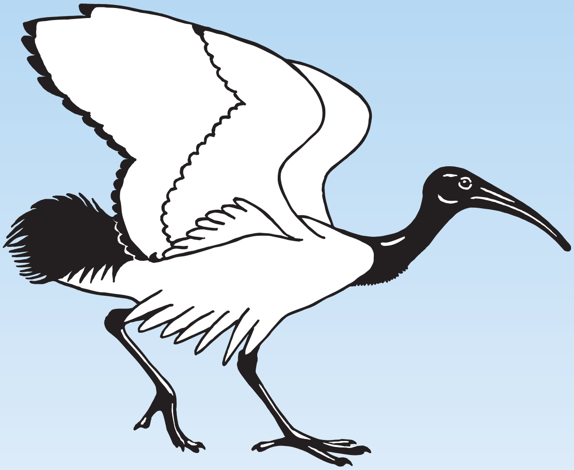
Bulletin of the British Ornithologists' Club



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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 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.

Please note that in 2017 evening meetings will take place on a Monday, rather than Tuesday as hitherto.

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

Monday 13 March 2017—6.30 pm—Julian Hume—*In search of the dwarf emu: extinct emus of Australian islands*.

Abstract: King Island and Kangaroo Island were once home to endemic species of dwarf emu that became extinct in the early 19th century. Emu egg shells have also been found on Flinders Island, which suggests that another emu species may have formerly occurred there. In 1906 J. A. Kershaw undertook a survey of King Island searching for fossil specimens and found emu bones in sand dunes in the south of the island. The available results included a photograph of the fossil locality, but gave no further information as to its whereabouts. Armed with this photograph, I recently travelled to King Island to try and discover where Kershaw had been 110 years before, and in this talk I will present the results of my palaeontological surveys of all three southern Australian islands to find emu subfossil bones. These surveys included a photographic record of many of the surviving birds and also demonstrate how the islands have been radically altered since their discovery in the first decade of the 19th century.

Biography: Julian Hume has travelled widely in search of avian palaeontological deposits, especially in the Mascarene Islands of Mauritius, Réunion and Rodrigues, as well as Hawaii, Madagascar and the islands off southern Australia. By profession, he is an artist specialising in extinct birds, but also has a Ph.D. in avian palaeontology and is a Scientific Associate of the Natural History Museum, Tring. He has written four books and published many papers on birds and their fossil history, with the second edition of his *Extinct birds* due out in 2017.

Monday 12 June 2017—6.30 pm—Alex Bond—*Gough Island: an unnatural history of mice and birds*.

Abstract: Nestled 2,800 km from any continent, the islands of Tristan da Cunha are among the most remote in the world, and possess some unique avian diversity. But this biodiversity is under threat, particularly on Gough Island, a UNESCO World Heritage Site, and arguably one of the 'crown jewels' of seabird islands. Though uninhabited, House Mice *Mus masculus* were introduced in the late 19th century, and now wreak havoc on the native biota. On Tristan da Cunha, the most remote inhabited island in the world, at least three species have become locally extinct in the last 200 years. I will provide a history of ornithological exploration of the islands and focus on our research demonstrating the negative effects of introduced mice on Gough's seabirds, as well as what we can do (and are doing) about it. We can still save the unique biodiversity of Gough, but must act fast or risk losing some of the most extraordinary 'British' birds.

Biography: Dr Alex Bond is a Senior Conservation Scientist at the RSPB Centre for Conservation Science. He leads the RSPB's programme of scientific research on Tristan da Cunha and Gough Island, and works elsewhere in the UK Overseas Territories (mostly the Pitcairn Islands) on island restoration, demography and marine conservation. He is also an Adjunct Researcher at the Institute for Marine and Antarctic Studies, Univ. of Tasmania, where he works on issues of marine pollution, primarily plastics. He has worked on island systems in eastern Canada, the Aleutians, South Atlantic, South Pacific, Hawaii and Tasman Sea, among others, and currently supervises six research staff and six research students around the globe. His website is http://alexanderbond.org.

The Chairman: Chris Storey, 22 Richmond Park Road, London SW14 8JT UK. Tel. +44 (0)208 8764728. E-mail: c.storey1@btinternet.com

Bulletin of the
BRITISH ORNITHOLOGISTS' CLUB

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CLUB ANNOUNCEMENTS

Chairman's Message

Welcome to the new online open-access journal. As you will have seen, we are publishing *Bull. Brit. Orn. Cl.* during 2017 on the BOC's website, moving in 2018 to the umbrella of BioOne. We hope that you will let us know your thoughts concerning the new format either at the meeting on 12 June or directly by e-mail.

We begin 2017 in our new charitable structure: we are now a Charitable Incorporated Organisation (CIO) with a board of trustees and a new constitution. The Charity Commission has endorsed our 'charitable objects' with confirmation that the work of the charity will be for the public benefit. Details of our new office address, bank account, the names of the trustees and their terms of office, together with the new constitution, have been posted on the website.

The fundamental decision to move the Bulletin to open-access and online was taken bearing in mind the realities of current trends in academic journal publication, the slow decline in the readership of the hard copy *Bull. Brit. Orn. Cl.* and our public benefit charitable responsibilities. Nevertheless, in moving to its new online-only format, the Bulletin's commitment to being fully Code compliant remains in place.

We have considered several possible online sites for *Bull. Brit. Orn. Cl.*, including our own. In the end, we have entered discussions with an American online publisher, BioOne. They have an impressive list of open-access ornithological journals, are enthusiastic about adding *Bull. Brit. Orn. Cl.* to their list and offer attractive services, including ensuring the journal will be fully searchable and accessible on all devices. Their website is: http://www.bioone.org.

However, we cannot take *Bull. Brit. Orn. Cl.* to the BioOne site until January 2018. This means that for the current year we are placing *Bull. Brit. Orn. Cl.* in .pdf format on our own website, where you are now reading the first issue of Vol. 137. In making this transition, we are beholden to Guy Kirwan, our *Hon. Editor*, and Eng-Li Green, our very capable designer and webmaster. I should add that our agreement with the Biodiversity Heritage Library stands and we will be integrating the BioOne arrangements with BHL in due course.

In another initiative, to reduce our costs we have removed our stock of books (the *Occasional Publications* plus the Uganda checklist) from Peterborough and they are now being stored by Richard Malin, our *Hon. Treasurer*. We propose to enable members / friends to purchase copies of individual titles for a nominal sum inclusive of postage, and details of these will shortly be issued and also placed on the website. In respect of the JPC checklists published jointly with the BOU, the current plan is that they will be sent to the Natural History Book Service for purchase in the normal way.

The meetings at the Barley Mow continue, but owing to changes in the Barley Mow's diary we have had to move our meetings to Mondays. I trust that this shift will fit in with your own arrangements. At the meeting on Monday 12 June, Alex Bond will talk on *Gough Island—an unnatural history of mice and men*. The meeting will include a review of the past year and the trustees will be available for questions. Details of the meetings on Monday 18 September and Monday 6 November are currently being arranged.

Finally, I hope very much that as many members as possible continue to support the Club as Friends of the BOC. The Club has seen many changes in its long history but none, I suspect, as challenging and far-reaching as those we are currently engaged in.

Chris Storey

The 984th meeting of the Club was held on Tuesday 15 November 2016 in the upstairs room at the Barley Mow, 104 Horseferry Road, Westminster, London SW1P 2EE. Thirteen members and three non-members were present. Members attending were: Miss H. Baker, Mr P. Belman, Mr S. Chapman, Mr M. Earp, Mr D. J. Fisher, Mr G. M. Kirwan (*Speaker*), Mr R. Langley, Mr R. W. Malin, Dr C. F. Mann, Mr D. J. Montier, Dr R. Prŷs-Jones, Mr S. A. H. Statham and Mr C. W. R. Storey (*Chairman*).

Non-members attending were: Mrs M. Gauntlett, Mr D. Russell and Ms J. White.

Guy Kirwan gave a talk entitled *When failure equals success: searching for the Critically Endangered Hooded Seedeater Sporophila melanops in central Brazil*. The mysterious Hooded Seedeater *Sporophila melanops* is known only from the type specimen, a male, collected in the 1820s by the Austrian naturalist and explorer Johann Natterer, on the rio Araguaia in central Brazil. A female specimen, postulated potentially to represent the same species, also collected in the state of Goiás, Brazil, by Gustav Baer in 1906, was identified decades later by Rodolphe Meyer de Schauensee. As was explained, Natterer's extraordinary travels in Brazil (17 years!) yielded a host of novelties and specimens of several species rediscovered only within the last *c*.2 decades. His contribution to Brazilian ornithology is understated versus his better-known contemporary, Spix, perhaps in part because his bird collections were only written up much later by Pelzeln in the late 1860s.

Guy explained how *Sporophila melanops* has become the great enigma of Brazilian ornithology, which prompted him and co-workers in Argentina and Brazil to search for it in the field (without success) and to study the two specimens in museums in Austria and the USA, as well as sequence their DNA. The results of their investigations have effectively removed any doubts regarding the status of the proposed species. Based on the morphological and genetic data, the female is either a Yellow-bellied *S. nigricollis* or Double-collared Seedeater *S. caerulescens*, whereas the male is one of the so-called 'capuchinos', a group of seedeaters with colourful male plumage that breed in the Southern Cone, but which are virtually undifferentiated molecularly. It is probably a Dark-throated Seedeater *S. ruficollis* showing melanism on the cap feathers, but it might be a melanistic-capped individual of a local population of seedeaters known to breed in the Esteros del Iberá, Corrientes, Argentina, to which the name *S. ruficollis* is potentially applicable; a hybrid provenance currently seems unlikely. The full results were published last year in *PloS ONE* 11(5): e0154231.

In addition to describing the major result of his work in this region of Brazil, which has effectively removed a species from the Red Data List, Guy also described some of the basic constituents of its avifauna. Together with colleagues in the USA and at the Museu Nacional, in Rio de Janeiro, their field work has yielded improved knowledge of the range and status of several globally threatened species and range extensions for many commoner birds. In addition, other work (recently published in the journal *Emu*) has elucidated an interesting hybridisation phenomenon in two species of riverine tanagers, Crimson-fronted Cardinal *Paroaria baeri* and Red-capped Cardinal *P. gularis*, with once again genetic data providing some of the key details.

What is the breeding range and breeding season of Pearly-breasted Cuckoo *Coccyzus euleri*? New records and breeding in French Guiana

by Olivier Claessens, Michel Giraud-Audine, Frédéric Royer & Lydie Sénécaux

Received 21 July 2016; revised 28 September 2016; published 13 March 2017

Summary.—Pearly-breasted Cuckoo *Coccyzus euleri* is a rare South American forest cuckoo and almost nothing is known concerning its breeding biology. It is considered to be a rare austral migrant in northern South America. In French Guiana, it was first documented in 2009 in Nouragues Nature Reserve. We detail seven new records in northern French Guiana in 2010–15, including a pair breeding. We provide information on the nest, nest site and behaviour. The breeding attempt failed during incubation, presumably due to predation. The new records were obtained in primary or old secondary forests contiguous to the primary forest block, between 9 August and 17 September. Most birds were spontaneously vocalising and strongly reacted to playback. These observations, and other known breeding records, raise questions as to the species' status in northern South America.

Pearly-breasted Cuckoo *Coccyzus euleri* is a poorly known and apparently rare South American cuckoo. Due to possible confusion with the commoner boreal migrant Yellow-billed Cuckoo *C. americanus*, the paucity of reliable records north of the Amazon and the secretive behaviour of this forest cuckoo, its breeding range and status in northern South America are unclear. It is perhaps best considered an austral migrant, which breeds mainly in southern and eastern Brazil, northern Argentina and Paraguay, but migrates to northern South America (Payne 2005, Claessens *et al*. 2011, Erritzøe *et al*. 2012, Payne *et al*. 2013). The species is uncommon and irregular in Venezuela, where its status is unclear (Hilty 2003, Payne 2005). It is scarce in Guyana (Braun *et al*. 2007), while in Surinam the species is known only from three historical specimens (Ottema *et al*. 2009). There are two records in North America: a vagrant collected on Sombrero Island (Anguilla), the northernmost of the Lesser Antilles (Banks 1988, AOU 1998), and a breeding pair at Lago Bayano, Panama, in 2014 (Campos Cedeño & Vallely 2015).

The breeding biology of Pearly-breasted Cuckoo is poorly known (Payne *et al*. 2013). Few nests have been found (see below) and most breeding reports were inferred from the body condition of specimens. Here we describe another breeding event, in French Guiana, and provide new data on the species' nest, nest site and nesting behaviour. We also discuss the nesting range of this cuckoo, via a review of all known breeding records.

Records in French Guiana (2009–15)

Up to 2015, eight records of Pearly-breasted Cuckoo, involving a total of 13 individuals, have been validated by the French Guiana Rarities Committee (Fig. 1). Pearly-breasted Cuckoo was recorded for the first time in French Guiana on 9 August 2009, when T. Deville photographed one in the forest canopy at Saut Pararé, Nouragues Nature Reserve, Régina

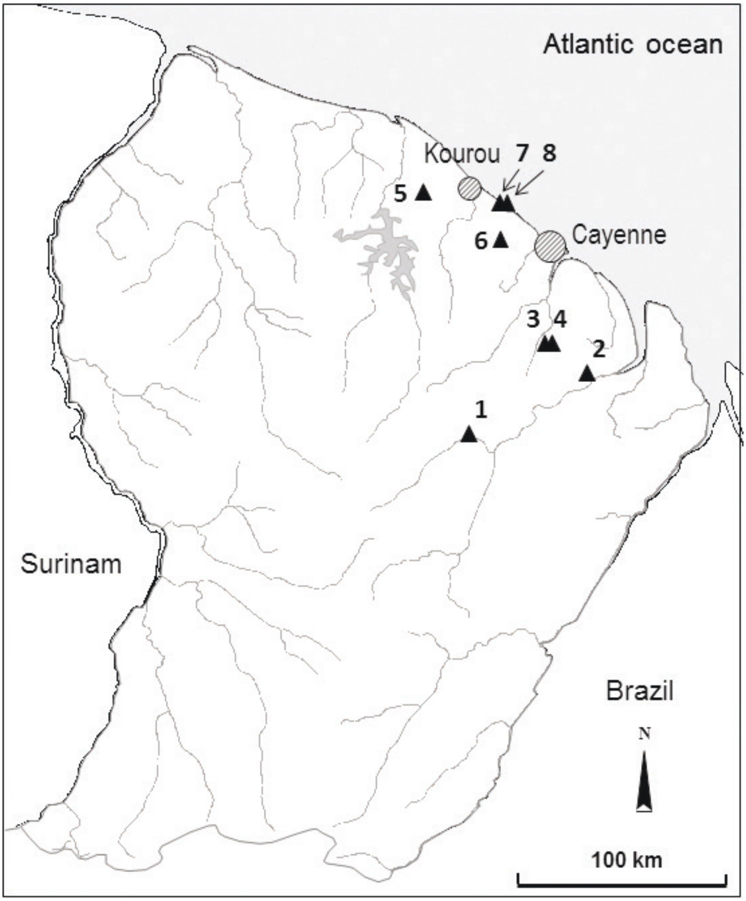

Figure 1. Records of Pearly-breasted Cuckoo *Coccyzus euleri* in French Guiana. 1. Saut Pararé, Nouragues Nature Reserve, Régina. 2. Montagnes Tortue, Régina. 3. Montagne Maripa, Roura. 4. Tibourou forest, Roura. 5. Creek Eau Claire, Kourou. 6. Creek Gilette, Quesnel (Risquetout), Macouria. 7–8. Road D13 to 'Guatemala', Macouria.

(04°02′N, 52°41′W) (Claessens *et al*. 2011). Undocumented records mentioned by Tostain *et al*. (1992) are now considered dubious (Comité d'Homologation de Guyane unpubl.).

In 2010, A. Renaudier observed at least seven individuals on 15–17 September at Montagnes Tortue, Régina (04°18′N, 52°13′W), on the track to Montagne Maripa, Roura (04°27′N, 52°21′W) and in Tibourou forest, Roura (04°27′N, 52°20′W), including at least five individuals within a few hundred metres at the last locality (Claessens *et al*. 2011, Claessens & Comité d'Homologation de Guyane 2015). Except one bird, all were spontaneously vocalising (giving the rattle call, or singing) in the canopy, and all responded to playback by answering, and some of them by flying overhead. The song was similar to a recording from Brazil (C. Albano, www.xeno-canto.org: XC6036). When seen, they appeared noticeably smaller and more slender than Dark-billed Cuckoo *C. melacoryphus* with which the observer was familiar, with a long tail and no rufous in the primaries. Sound-recordings made during the observations are archived at xeno-canto.org (XC72105–109).

In 2011, A. Renaudier observed an individual along the track to Eau Claire creek, Kourou (*c*.05°09′N, 52°54′W) on 31 August (Claessens *et al*. 2014). The bird was following a canopy flock including Purple-breasted Cotinga *Cotinga cotinga*, Pompadour Cotinga *Xipholena punicea*, Guianan Gnatcatcher *Polioptila guianensis* and Blue-backed Tanager *Cyanicterus cyanicterus*, among other species. It responded to playback of the species' song using the rattle call.

There were no records of *C. euleri* in 2012; however, A. Renaudier was by then no longer in French Guiana. On 10 and 16 August 2013, an adult was photographed (Fig. 2) and sound recorded by OC, FR & G. Jacotot, near Gilette creek, at Quesnel (Risquetout forest), Macouria (04°56'N, 52°32'W). The bird first sang spontaneously and subsequently emitted rattle calls, as if disturbed by the observers. Following playback, it perched overhead. On 16 August, it responded to playback with rattle calls but did not sing. On 14 August 2013, a few days after the first observation in Risquetout, a pair was found by MGA, FR & LS on road D13 to 'Guatemala', Macouria, 10 km south-west of Kourou (05°05'N, 52°33'W). The pair was followed in a breeding attempt (see below) until 1 September, when they disappeared and the nest was abandoned. On 28 August 2013, a few minutes after the presence of the pair near their nest was confirmed, a third individual was photographed by MGA, some 650 m away on the same road (05°05'N, 52°32'W). Details of the white undertail markings confirmed that it was a different individual. There were no records in 2014–15 despite specific searches by OC.

Except the 'Guatemala' site, the localities mentioned above are all within or at the border of the primary forest block, in north-east French Guiana. Tibourou, Risquetout and Eau Claire are old, low-canopy, lowland secondary forests, contiguous with the primary forest block. Distance to the forest edge was shortest at Risquetout, only 2 km. Other sites are several dozen km from edges, discounting roads, tracks or rivers. The forest at Saut Pararé in Nouragues Nature Reserve is high-canopy (>40 m) pristine lowland forest. The nesting site near 'Guatemala' appears atypical for the species, a 300 m-wide, low-canopy (*c*.10 m) woodlot on a sandy bar, surrounded by coastal mangrove on one side and by swampy savannas, pastures and cultivated areas on the other. The nest was <100 m from a cleared area and <250 m from a natural edge with savanna.

Breeding event

On 14 August 2013, along road D13 to 'Guatemala', FR, LS & MGA heard the song of a Pearly-breasted Cuckoo at 07.38 h, *c*.100 m away. A second individual answered nearby with rattle calls. The second bird was discovered by LS, 5–6 m above ground in a tree, and was watched for *c*.15 minutes, during which time FR sound-recorded the vocalisations of both individuals (recording archived by the French Guiana rarities committee). At 08.20 h, the male (identified by its behaviour) perched near the female, holding either a caterpillar or small twig in its bill (Fig. 3). The female adopted a submissive posture, its body flattened and wings slightly drooped, whereupon the pair copulated. It is unclear if the male offered the item to the female or not, but it departed shortly afterwards; the female remained another 13 minutes on the same perch, before leaving at 08.33 h.

On 17 August, just one individual was heard by MGA. During the next two weeks, both individuals were regularly observed and heard by many birdwatchers. Two different vocalisations were frequently heard until incubation started. The song was a series of loud and somewhat rough, frog-like notes (e.g. A. Renaudier, XC72107), given by both sexes. A rattle call (e.g. M. Giraud-Audine, XC147847; A. Renaudier, XC72105) was interpreted as contact or aggression, rather than alarm, as it was often emitted in response to playback.

Nestbuilding was observed on 24–25 August. On 24 August, one bird (later identified as the male) was observed flying back and forth over the road, carrying items in its bill, permitting FR & LS to discover the nest in a tree by the road, *c*.10 m from where they had copulated ten days before. The nest was sited *c*.10 m above ground in a small tree, 2 m below its crown, on the distal part of a horizontal branch. As the tree was invaded by a liana, the nest was well concealed by dense foliage and tangled branches, and it was only partially visible from the road. The dense understorey with many spiny palms prevented

Figure 2. Pearly-breasted Cuckoo *Coccyzus euleri*, Risquetout forest, Macouria, French Guiana, 10 August 2013 (F. Royer)

Figure 3. Male Pearly-breasted Cuckoo *Coccyzus euleri* holding something in its bill and perching beside the female, just prior to copulation, 'Guatemala', Macouria, French Guiana, 14 August 2013 (F. Royer)

Figure 4. Male Pearly-breasted Cuckoo *Coccyzus euleri* feeding on a hairy caterpillar, 'Guatemala', Macouria, French Guiana, 1 September 2013 (M. Giraud-Audine)

closer access to the tree. Mean canopy height in the vicinity of the nest was <15 m. The cuckoo collected material in another tree partly invaded by a liana less than 20 m away, on the other side of the road. Having collected a twig, the male crossed the road, perched *c.*2–3 m from the nest and then proceeded by hopping from perch to perch, heavily concealed by vegetation, always following the same route through the canopy. Items were passed to the female, who remained in the nest arranging it, whereas the male departed immediately. Most material was collected in nearby trees. Twice that day, the male changed tactics and returned following a longer absence with a bill full of thin fibres, which the female placed at the base of the nest. Once a dead leaf was brought. During our observations, nest construction was exclusively performed by the female, who received material from the male's bill. Nine visits by the male were observed that day between 07.40 h and 08.50 h. On 25 August between 07.30 h and 12.00 h, the male visited the nest five times with material collected in a tree on the other side of the road. Material was passed to the female in the nest, who arranged it without changing position. Nest materials that day were identified as pieces of a dead liana, 'grass-like' filaments (perhaps bark strips), moss and a dead leaf.

As the nest was left unattended for long periods on 25 August, we believe that eggs had not yet been laid. On 28 August and the next days, however, the female was obviously incubating. Thus, egg laying occurred between 26 and 28 August. On 28 August, between 09.45 h and 10.45 h, the female left the nest for just ten minutes and returned inconspicuously; she was still present in the evening. On many occasions on 28 August and 1 September, we noticed the strange position of the incubating female, as judged from our

TABLE 1
Breeding records of Pearly-breasted Cuckoo *Coccyzus euleri*. Localities are listed from north to south. Where not given in the original publication, coordinates are from Paynter (1982, 1995) or Paynter & Traylor (1991). COP: Colección Ornitológica Phelps, Caracas; FMNH: Field Museum of Natural History, Chicago; MZUSP: Museum of Zoology, University of São Paulo; WA = wikiaves.com.br.

No.	Country	Locality	Latitude	Longitude	Date	Evidence	References
1	Venezuela	San José de los Caracas, Distrito Federal	10°37′N	66°34′W	25 May 1942	Specimen: male with large testes	COP 18010
2	Colombia	Cartagena, Bolívar	10°24′N	75°32′W	22 January 1915	Specimen (Carnegie Museum, Pittsburgh): incompletely grown juvenile	Carriker (1955), Payne (2005)
3	Panama	Lago Bayano	09°11′N	78°45′W	July 2014	Photo: breeding pair	Campos Cedeño & Vallely (2015)
4	Venezuela	Caicara, Bolívar	07°37′N	66°10′W	10 June 1905	Specimen: female with enlarged ovary	Cherrie (1916)
5	French Guiana	Road D13 to 'Guatemala', Macouria	05°05′N	52°33′W	Late August 2013	Photo and video: breeding pair	This paper
6	Venezuela	Río Sipapo, Caño Cuao (*sic*), Amazonas	04°58′N	67°43′W	April 1943	Specimens: two males with large testes	COP 22363, 22364
7	Brazil	Fazenda Encrenca, Amajari, Roraima	03°50′N	61°24′W	23 April 2007	Specimen: male in breeding condition	MZUSP 79091 (L. F. Silveira *in litt.* 2016)
8	Brazil	Igarapé Serrinha, Colonia de Apiau, Roraima	02°38′N	61°12′W	6 October 1987	Specimen: female with exploded follicles	FMNH 343751 (not 323751; Payne 2005)
9	Brazil	Pousada Rio Trombetas, Oxiriminá, Pará	01°46′N	55°52′W	4 June 2016	Photo: adult carrying food to a nest	N. Lage, WA2159645
10	Brazil	Linhares, Espírito Santo	19°23′S	40°04′W	January 2013	Photo: nestling	M. Candeias, WA864092
11	Brazil	Fazenda Barreiro Rico, São Paulo	22°41′S	48°06′W	November	Specimen (MZUSP): female with egg in oviduct	Magalhães (1999)
12	Paraguay	Reserva Natural del Bosque Mbaracayú, Canindeyú	24°08′S	55°31′W	28 October 1996	Sight record: a pair copulating	Capper *et al.* (2001)
13	Argentina	Arroyo Urugua-i, km 30, Misiones	*c.*25°54′S	*c.*54°36′W	October to December	Specimens: six birds in breeding condition	Partridge (1961)
14	Argentina	Manchalá, Tucumán	*c.*27°05′S	*c.*65°24′W	11 December 1922	Egg	Smyth (1928)
15	Argentina	Arroyo Correa, Río Paraná Delta, Buenos Aires	*c.*33°43′S	*c.*59°15′W	18 December 1932	Specimen and nest	Pereyra (1933)

observation point: breast inside the nest, head scarcely visible, and rump and tail raised upright well above the nest rim, as if incubating using the breast. The female maintained this position on the nest, only once rotating by a quarter of a turn during our observations.

On 1 September, the male was seen feeding within 50 m of the nest while the female was incubating (Fig. 4). The male was observed once with a Dark-billed Cuckoo, another austral migrant, without any interaction. Just one call was heard that day, in contrast with frequent calls and songs heard during the preceding days.

On 3 and 7 September, however, the nest was found abandoned and no cuckoos were heard or seen. The regular presence in the area of a large troop of Common Squirrel Monkeys *Saimiri sciureus*, an occasional nest predator (Rylands & Mittermeier 2013), suggests to us that the nest could have been predated. The nest site was impossible to access, meaning that we were unable to climb the tree to examine it.

Other breeding records

All 15 known breeding records are summarised in Table 1 and mapped in Fig. 5. Most reports were inferred from the body condition of specimens. However, a male collected at Chajuraña, Bolívar, in August 1942 (mentioned by Payne 2005) was in fact an immature male without signs of breeding (Colección Ornitológica Phelps, COP 19552; M. Lentino

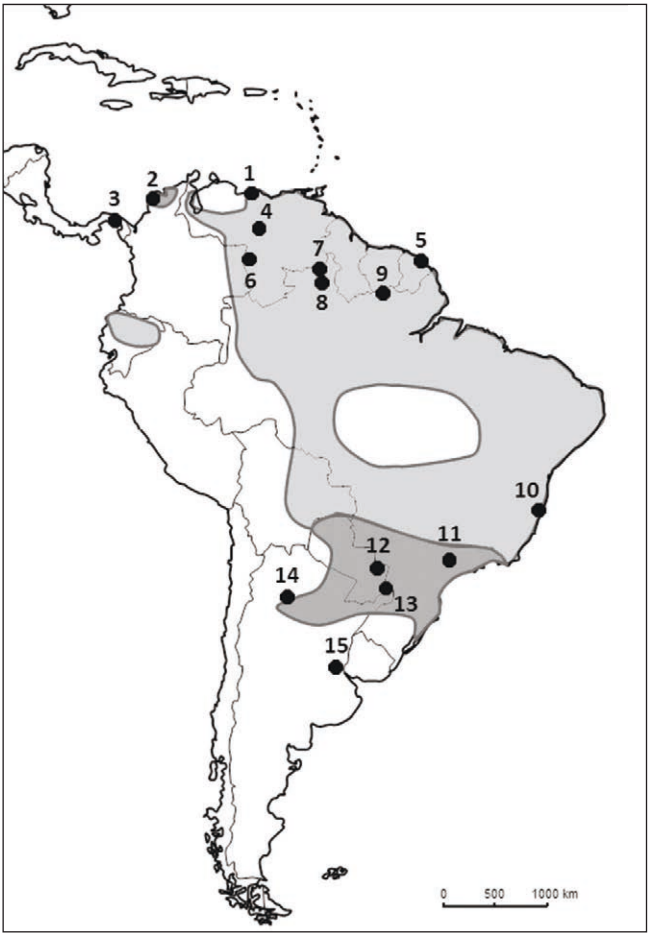

Figure 5. Distribution and breeding records of Pearly-breasted Cuckoo *Coccyzus euleri*. Dark grey = breeding area; pale grey = non-breeding area (after Erritzøe *et al*. 2012). Dots = breeding records. See Table 1.

in litt. 2016). A male and a female collected in June 2001 at Isla Tigrera on the río Caroni, Bolívar, were singing but showed no gonadal development (COP 80345–346; M. Lentino *in litt*. 2016).

Five nests besides that in French Guiana have been found: an egg was collected in Tucumán, Argentina, on 11 December 1922 (Smyth 1928); a nest collected in Buenos Aires province, Argentina, on 18 December 1932 was attributed to *C. americanus* (Pereyra 1933), of which *C. euleri* was considered a subspecies at the time (Willis & Oniki 1990); an almost fledged chick, claimed to be this species, on a nest apparently constructed of twigs, was photographed in Espírito Santo, south-east Brazil, on 18 January 2013 (M. Candeias; www.wikiaves.com.br WA864092); a breeding pair that fledged two young was photographed in Panama in July 2014 and is the first country and Middle American record (Campos Cedeño & Vallely 2015); and an adult carrying food to a nearby nest was photographed in Pará, northern Brazil, on 4 June 2016 (N. Lage; WA2159645); the nest was well concealed in dense foliage, 7 m up in a tree, and the nestlings were not seen (N. Lage *in litt*. 2016). Pereyra (1933) and Campos Cedeño & Vallely (2015) provided brief descriptions of the species' nest.

In addition, a pair of *C. euleri* was photographed copulating near Manaus, Amazonas (03°05'S, 60°00'W) on 13 July 2014 (R. Czaban *in litt*. 2014; WA1384436). The male fed the female a caterpillar while copulating. They copulated twice, each time after being attracted by playback, and it is assumed that copulation was induced by this. The male answered once by singing briefly prior to copulation. They were not heard or seen again in the following weeks, thus actual breeding was not proven and these birds were perhaps transients (M. Cohn-Haft *in litt*. 2014).

Discussion

Our observations provide new data on the breeding biology of Pearly-breasted Cuckoo. Although superficial, our description of the nest and nest site is in accordance with that photographed in south-east Brazil (M. Candeias; WA864092) and the descriptions by Campos Cedeño & Vallely (2015) and N. Lage (*in litt*. 2016). They are similar to other *Coccyzus* (Payne 2005, Erritzøe *et al*. 2012). Unfortunately the nest's inaccessibility and abandonment meant that we could not assess clutch size or incubation period.

Vocal activity was intense during courtship and nestbuilding, but then declined sharply. Our record of the male presenting a small twig or a caterpillar to his mate while copulating is consistent with those of Capper *et al*. (2001) and R. Czaban (WA1384436; *in litt*. 2014). Courtship feeding is the rule in *Coccyzus* (Payne 2005, Erritzøe *et al*. 2012). Ritualised courtship behaviour presumably strengthens the pair bond, demonstrates the male's ability to feed nestlings and / or facilitates copulation acceptance by the female (Lack 1940, Logue 2007).

Czaban's observation provides new insight into the pair bond. That the male copulated in reaction to playback suggests that he might have sought to insure ownership of his mate in face of a supposed rival (R. Czaban *in litt*. 2014, M. Cohn-Haft *in litt*. 2014). As they were not definitely breeding, this could indicate that the birds were paired while on migration or overwintering, a behaviour not previously described for cuckoos (Erritzøe *et al*. 2012).

These observations raise crucial questions concerning the distribution and biology of *C. euleri*. First, what is the true breeding range of the species? It is generally accepted that the species is an austral breeder, nesting in southern Brazil, Paraguay and north-east Argentina, with a large non-breeding range extending north to Venezuela and the Guianas (Erritzøe *et al*. 2012). However, the northern limit of its breeding range is uncertain (Payne 2005). An alternative is to consider a large breeding range covering much of eastern South America (Payne *et al*. 2013), as suggested by the nesting event in French Guiana.

Mapping all of the known breeding records (Fig. 5) reveals two disjunct breeding areas: one in southern South America (southern Brazil, Paraguay and Argentina), and the other in northern South America (eastern Panama, northern Colombia, Venezuela, northernmost Brazil and the Guianas). More than half of the breeding localities in Table 1 lie north of the equator. However, if they represent sites within the species' 'usual' breeding range, then it is surprising that it was previously overlooked in French Guiana and other countries in northern South America with dynamic ornithological communities, e.g. Venezuela. In French Guiana, the first documented records were made as recently as 2009 (Claessens *et al*. 2011) and in Venezuela it is considered to be a vagrant (Hilty 2003). All confirmed records in French Guiana are between 9 August and 17 September, which matches the status of the species being an austral migrant. This leads us to hypothesise that *C. euleri* breeds occasionally outside its normal range, as also suggested by the Roraima record. The multiple records in French Guiana in 2013, vs. the species' rarity in other years, might indicate an exceptional influx, which could promote opportunistic breeding.

The discovery of a nesting pair at 'Guatemala' was made possible only due to multiple factors: it was in an area regularly visited by birdwatchers, who were alert to the species' vocalisations, having watched an individual nearby recently; the birds were discovered before eggs were laid, when they were singing frequently; and the nest was near a road. These circumstances are potentially unlikely to occur again in French Guiana. A few days later, the birds would have been silent and probably have gone overlooked. Had they been further from the road, or the nest out of sight in the forest canopy, the breeding event would never have being noted. It is tempting to speculate that this event was not the first, or last, in the country. In French Guiana, several records were made in September 2010 and late August 2011, including at least five birds in the same area, all by the late A. Renaudier (Claessens & Comité d'Homologation de Guyane 2015). Based on our observations and those of Campos Cedeño & Vallely (2015), we believe that rattle calls, which are the best means of locating the species in the non-breeding areas, are contact or aggressive calls, and indicate the presence of at least two birds.

What is the true breeding season? August and September are usually considered the end of the non-breeding period and the start of return migration by austral migrants. Thus, breeding at this time is highly unexpected. Although nest contents could not be ascertained, the female's behaviour demonstrates that eggs were laid. All but one of the breeding records in the north of the species' range, see Table 1, were in April–October, i.e. the presumed non-breeding period for an austral migrant. Surprisingly, an incompletely grown juvenile collected in January in Colombia (Payne 2005) was found during the austral breeding season, despite being in the Northern Hemisphere.

On the one hand, the paucity and seasonal pattern of records in French Guiana and in neighbouring countries suggest an austral migrant that occasionally breeds outside the 'normal' breeding range. But, on the other hand, the distribution of nesting records suggests two distinct breeding areas, with a prolonged season equating to the Northern Hemisphere pattern in the north of its range. More data are necessary to confirm the species' status in northern South America.

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References:
American Ornithologists' Union (AOU). 1998. *Check-list of North American birds*. Seventh edn. American Ornithologists' Union, Washington DC.
Banks, R. C. 1988. An old record of the Pearly-breasted Cuckoo in North America and a nomenclatural critique. *Bull. Brit. Orn. Cl.* 108: 87–90.
Braun, M. J., Finch, D. W., Robbins, M. B. & Schmidt, B. K. 2007. *A field checklist of the birds of Guyana*. Second edn. Smithsonian Institution, Washington DC.
Campos Cedeño, E. & Vallely, A. C. 2015. First modern North American record and first indication of breeding by Pearly-breasted Cuckoo (*Coccyzus euleri*) in Panama. *North Amer. Birds* 68: 174–176.
Capper, D. R., Clay, R. P., Madroño N., A., Mazar Barnett, J., Burfield, I. J., Esquivel, E. Z., Kennedy, C. P., Perrens, M. & Pople, R. G. 2001. First records, noteworthy observations and new distributional data for birds in Paraguay. *Bull. Brit. Orn. Cl.* 121: 23–37.
Carriker, M. A. 1955. Notes on the occurrence and distribution of certain species of Colombian birds. *Nov. Colombianas* 2: 48–64.
Cherrie, G. K. 1916. A contribution to the ornithology of the Orinoco region. *Mus. Brooklyn Inst. Arts Sci., Sci. Bull*. 2: 133–374.
Claessens, O., Brammer, F. P., Deville T. & Renaudier, A. 2011. First documented records of Pearly-breasted Cuckoo *Coccyzus euleri* for French Guiana, and an overlooked specimen from Ecuador. *Bull. Brit. Orn. Cl*. 131: 128–133.
Claessens, O., Rufray, V., Tostain, O. & Comité d'Homologation de Guyane. 2014. Les oiseaux rares en Guyane en 2010 et 2011. Rapport du Comité d'Homologation de Guyane. (www.chn-france.org/upload_content/rapport%20chg%202010-2011.pdf).
Claessens, O. & Comité d'Homologation de Guyane 2015. Rare birds in French Guiana in 2008–10. *Cotinga* 37: 66–78.
Erritzøe, J., Mann, C. F., Brammer, F. P. & Fuller, R. A. 2012. *Cuckoos of the world*. Christopher Helm, London.
Hilty, S. L. 2003. *Birds of Venezuela*. Christopher Helm, London.
Lack, D. 1940. Courtship feeding in birds. *Auk* 57: 169–178.
Logue, D. M. 2007. A Greater Ani (*Crotophaga major*) gives a nuptial gift while copulating. *Orn. Neotrop*. 18: 311–312.
Magalhães, J. C. R. 1999. *As aves na Fazenda Barreiro Rico*. Ed. Plêiade, São Paulo.
Marks, J. S., Cannings, R. J. & Mikkola, H. 1999. Family Strigidae (typical owls). Pp. 76–242 *in* del Hoyo, J., Elliott, A. & Sargatal, J. (eds.) *Handbook of the birds of the world*, vol. 5. Lynx Edicions, Barcelona.
Ottema, O. H., Ribot, J. H. & Spaans, A. L. 2009. *Annotated checklist of the birds of Suriname*. WWF Guianas, Paramaribo.
Partridge, W. H. 1961. Aves de Misiones nuevas para la Argentina. *Neotrópica* 7: 25–28.
Payne, R. B. 2005. *The cuckoos*. Oxford Univ. Press.
Payne, R., Bonan, A. & de Juana, E. 2013. Pearly-breasted Cuckoo (*Coccyzus euleri*). *In* del Hoyo, J., Elliott, A., Sargatal, J., Christie, D. A. & de Juana, E. (eds.) *Handbook of the birds of the world Alive*. Lynx Edicions, Barcelona (http://www.hbw.com/node/54892).
Paynter, R. A. 1982. *Ornithological gazetteer of Venezuela*. Mus. Comp. Zool., Cambridge, MA.
Paynter, R. A. 1995. *Ornithological gazetteer of Argentina*. Second edn. Mus. Comp. Zool., Cambridge, MA.
Paynter, R. A. & Traylor, M. A. 1991. *Ornithological gazetteer of Brazil*. 2 vols. Mus. Comp. Zool., Cambridge, MA.
Pereyra, J. A. 1933. Miscelanea ornitológica. *Hornero* 5: 215–219.
Phelps, W. H. & Phelps, W. H. Jr. 1958. Lista de las aves de Venezuela con su distribución, Tomo II, Parte 1. No Passeriformes. *Bol. Soc. Venez. Cienc. Nat*. 19: 1–317.
Rylands, A. B. & Mittermeier, R. A. 2013. Family Cebidae (squirrel monkeys and capuchins). Pp. 348–413 *in* Mittermeier, R. A., Rylands, A. B. & Wilson, D. E. (eds.) *Handbook of the mammals of the world*, vol. 3. Lynx Edicions, Barcelona.
Smyth, C. H. 1928. Descripción de una colección de huevos de aves argentinas. *Hornero* 4: 125–152.
Tostain, O., Dujardin, J.-L., Érard, C. & Thiollay, J.-M. 1992. *Oiseaux de Guyane*. Société d'Études Ornithologiques, Brunoy.
Willis, E. O. & Oniki, Y. 1990. Case 2727. *Coccyzus euleri* Cabanis, 1873 (Aves, Cuculiformes): proposed conservation of the specific name. *Bull. Zool. Nomencl*. 47: 195–197.

Addresses: Olivier Claessens, Clos de Bénédicte C14, 2510 route de Montabo, FR-97300 Cayenne, France, e-mail oclaessens@wanadoo.fr. Michel Giraud-Audine, 5389 rue Carapa, FR-97355 Macouria, France. Frédéric Royer & Lydie Sénécaux, 12 rue de Saintonge, FR-17350 Grandjean, France.

The dark side of birds: melanism—facts and fiction

by Hein van Grouw

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Summary.—Melanism is generally defined as an increase of dark pigment in the plumage, resulting in a blackish appearance. Furthermore, melanism is often associated with mutations of one gene that encodes the melanocortin 1 receptor (MC1R), a protein involved in regulating melanin pigmentation. However, there is often no increase of pigment and melanism does not necessarily involve dark pigment alone. Also, many different mutations in many different genes promote melanism, which may explain why it is the commonest colour morph in birds. In the past, melanistic birds were sometimes mistakenly named as new species. Ironically, it now appears that melanistic birds do indeed differ from their normal-coloured conspecifics in more than just colour.

> 'Every morphism thus has implications in the field of genetics, ecology, selection theory, field natural history, and taxonomy.' (J. Huxley, 1955)

Melanism, from the Greek *melanos* (= dark-coloured), is generally defined as an increased amount of dark pigmentation (melanin). However, in this paper it will be demonstrated that an aberrant dark plumage is not necessarily the result of increased amounts of pigment, and that melanism can result in a paler plumage than normal.

Colour aberrations, especially melanism, have always confused ornithologists. In the past, when nothing was known concerning plumage pigmentation and mutations, aberrant-coloured birds were often viewed as being new taxa, and were even described scientifically. Perhaps the oldest and best-known example of a melanistic aberration named as a new species is Mountain Partridge *Perdix montana* (Brisson 1760). Brisson knew this 'species' only from the mountains of Lotharingen, France, hence *montana* (of the mountains). It proved, however, that '*montana*' occurred throughout Europe. Frisch (1763) described the same melanistic variety from Germany as 'Blackish-brown Partridge' (Schwarz-braune Rebhuhn, see Fig. 1) *P. fuscus*, and Latham (1823), based on two specimens in Bullock's museum (1795–1819) that were shot in Cheshire, north-west England, called them Cheshire Partridge. Subsequently, it became apparent that all of these 'species' were in fact

Figure 1. Hand-coloured copper engraving of '*Perdix fuscus*' from *Vorstellung der Vögel Deutschlands* (1763) by Johann Leonhard Frisch; the same mutation as Brisson's *Perdix montana*, i.e. a melanistic Grey Partridge *P. perdix* (Hein van Grouw, © Natural History Museum, London)

TABLE 1
Some examples of melanistic individuals named as new species.

'New' species	**Actual species**
Mountain Partridge, *Perdix montana* Brisson, 1760	Grey Partridge *Perdix perdix* (Linnaeus, 1758)
Sabine's Snipe *Scolopax sabinii* Vigors, 1825	Common Snipe *Gallinago gallinago* (Linnaeus, 1758)
Dicaeum aterrimum Lesson, 1830	Bananaquit *Coereba flaveola* (Linnaeus, 1758)
Pyrocephalus obscurus Gould, 1839	Vermilion Flycatcher *Pyrocephalus rubinus* (Boddaert, 1783)
Chestnut-coloured Partridge *Ortyx castaneus* Gould, 1842	Northern Bobwhite *Colinus virginianus* (Linnaeus, 1758)
Black Fantail *Rhipidura melanura* G. R. Gray, 1843	New Zealand Fantail *Rhipidura fuliginosa* (Sparrman, 1787)
Black Woodhen *Gallirallus fuscus* Du Bus, 1847	Weka *Gallirallus australis* (Sparrman, 1786)
English Rock Dove *Columba affinis* Blyth, 1847	Rock Dove *Columba livia* J. F. Gmelin, 1789
Rufous-bellied Coucal *Centropus epomidis* Bonaparte, 1850	Senegal Coucal *Centropus senegalensis* (Linnaeus, 1766)
Black-shouldered Peafowl *Pavo nigripennis* P. L. Sclater, 1860	Indian Peafowl *Pavo cristatus* Linnaeus, 1758
Perdix atro-rufa Soland, 1861	Red-legged Partridge *Alectoris rufa* (Linnaeus 1758)
Verreaux's Quail *Synoicus lodoisiae* J. Verreaux & des Murs, 1862	Common Quail *Coturnix coturnix* (Linnaeus, 1758)
Black Penguin *Eudyptes atratus* Hutton, 1875	Fiordland Penguin *Eudyptes pachyrhynchus* G. R. Gray, 1845
Tetrastes griseiventris Menzbier, 1880	Hazel Grouse *Tetrastes bonasia* (Linnaeus, 1758)
Monarcha ugiensis Ramsay, 1882	Chestnut-bellied Monarch *Monarch castaneiventris* J. Verreaux, 1858
Cory's Bittern *Ardetta neoxena* Cory, 1886	Least Bittern *Ixobrychus exilis* (J. F. Gmelin, 1789)
Sharpe's Rail *Stictolimnas sharpei* Büttikofer, 1893	Buff-banded Rail *Gallirallus philippensis (Linnaeus, 1766)*
Von Huegel's Snipe *Gallinago huegeli* Tristram, 1893	New Zealand Snipe *Coenocorypha aucklandica* (G. R. Gray 1845)
Willkonsky's Owl *Syrnium willkonskii* Menzbier, 1896	Tawny Owl *Strix aluco* Linnaeus, 1758

the same melanistic form of Grey Partridge *P. perdix*. Mistaking an aberrant-coloured bird for a new species (for more examples see Table 1) usually occurred if the aberration was quite common in the relevant species / population.

Once an aberration like melanism represents a certain percentage of the entire population, then the aberration is often considered a natural colour morph within that species. Overall, melanism is reported to be the commonest form of polymorphism in birds (Mundy 2006). To define, however, whether melanism can be viewed as a recognised morph or as an only occasional aberration is not clear cut. Further, besides their colour, melanistic birds often also differ in behaviour resulting in, for example, different habitat preferences.

Under appropriate conditions, melanistic morphs may therefore separate themselves from their typical-coloured conspecifics and consequently evolve into new taxa. That this is true shall be demonstrated here and the examples also confirm a 60-year-old evolution theory that states that there is a link between polymorphism and the faster evolution of new species. The examples presented, however, all involve melanism according to the traditional definition: increased amount of dark pigment. Whether other forms of melanism also promote speciation will also be discussed.

Melanins and plumage coloration

The main pigments in birds that afford plumage its colour are melanins and carotenoids. As only melanins are responsible for melanism, carotenoids will not be discussed further here. Melanin occurs in two discernible forms: eumelanin and phaeomelanin (Lubnow 1963). Depending on their concentration and distribution within the feather, eumelanin is responsible for black, grey and / or dark brown feathers, whereas phaeomelanin is responsible for warm reddish brown to pale buff colours. Both melanins together can produce a wide range of greyish-brown colours. Melanin is produced by cells called melanocytes located mainly in the skin and feather follicles (from which the feathers grow). Melanocytes within the feather follicles produce melanin, which is added to the feather cells as the feather grows. However, melanin distribution does not always occur at a constant rate. In most species, the feathers have certain patterns and / or colour differences caused by the type, amount and distribution of melanin. During feather growth, sudden changes from the production of eumelanin to phaeomelanin can occur, giving rise to different patterns.

In mammals, several genes regulate the production and deposition of the two distinct types of melanin (Lamoreux 2010), of which the two most important are the extension (MC1R) and agouti (ASIP) genes. The agouti gene regulates the distribution of eumelanin and phaeomelanin on each hair and over the surface of the body, while the extension gene is responsible for controlling the type of melanin being produced: eumelanin or phaeomelanin. Melanin cells do not produce both types of pigment simultaneously, but they can rapidly switch from one to the other. This complex control of melanin patterning is often referred to as the melanin-type switching mechanism. Primary control over this switch is exerted by both the agouti gene, which encodes the agouti signalling protein (ASIP), and the extension gene that encodes for the melanocortin 1 receptor (MC1R), with which ASIP interacts. Normally, these genes together determine which of, where and when the two types of melanin will be manufactured by the pigment cell during hair development (Lamoreux 2010).

Research shows that, in birds, a comparable extension gene is responsible for the production of melanin (Kerje *et al*. 2003, Mundy 2005, Vidal 2010a,b). How the melanin-type switching mechanism in birds works is still poorly known. However, it is reasonable to assume that a comparable agouti gene is present in birds as well, as many species possess feathers with distinct patterns of both melanin types. Several studies have indicated an avian equivalent of the agouti gene in Japanese Quail *Coturnix japonicus* (Hiragaki *et al*. 2008, Nadeau *et al*. 2008). So evidence suggests that there is a gene in birds responsible for melanin-type switching, which regulates the distribution of eumelanin and phaeomelanin on each feather. For convenience, it will be also termed the agouti gene in this paper.

In many bird species, however, (adult) plumage colour is determined by eumelanin alone. In spite of the lack of phaeomelanin, one can assume that in species with only eumelanin, an agouti locus is still involved in regulating the distribution of eumelanin within each feather. When inactivated by the presence of ASIP, the MC1R will not signal and the melanocytes will produce no melanin at all. The black-and-white patterns in the flight feathers of, for example, Common Magpie *Pica pica*, Great Spotted Woodpecker *Dendrocopos major* and Common Hoopoe *Upupa epops* are probably the result of an agouti gene.

As mentioned, eumelanin does not always occur as black, but can also show as different shades of brown or grey. The pigment synthesis process is responsible for whether the eumelanin will be black or brown; incompletely oxidised eumelanin results in more brownish pigment granules, and grey is due to the way the black melanin pigment granules are arranged in the feather. These processes are controlled by other genes totally independent of the extension gene and / or the agouti gene. Most forms of melanism are heritable and inheritance patterns follow simple Mendelian principles.

Melanism and MC1R

Based on publications over the last 15 years, melanism in wild birds is often associated only with MC1R encoded by the extension gene, which determines the type of pigment produced inside the pigment cell by encoding (activating) the melanocortin 1 receptor. When activated, MC1R will send signals to the pigment cell to enable it to produce eumelanin. Without activation the pigment cells will produce phaeomelanin only.

Mutations of the extension gene can create a melanocortin 1 receptor that is constantly active, even of not stimulated, or conversely can lower the receptor's activity. Mutations for continually active MC1R are mostly inherited dominantly and result in a dark, black plumage, as mainly eumelanin is produced. Examples of these occur in the domestic chicken (Crawford 1990) and Bananaquit *Coereba flaveola* (Theron *et al*. 2001), and probably also in New Zealand Fantail *Rhipidura fuliginosa* (Caughley 1969) and Vermilion Flycatcher *Pyrocephalus rubinus* (van Grouw & Nolazco 2012) in which dark morphs are also dominant in inheritance. Mutations of the extension gene causing dysfunctional MC1R often result in a paler plumage based mainly on phaeomelanin, and these are mostly recessive. The mutation known as recessive red (symbol e) in the domestic pigeon / Feral Pigeon *Columba livia* is an example of this (van Grouw & de Jong 2009; Fig. 2D). A similar mutation occurs in Common Woodpigeon *Columba palumbus* (Fig. 3) and '*montana*', the reddish-brown morph of Grey Partridge (Fig. 4), is also a probable example of a mainly phaeomelanin-based plumage due to inactive MC1R.

As variation in MC1R encoded by the extension gene has been demonstrated to be associated with dark and pale plumages, Haas *et al*. (2009) tested whether this also applied to the colour differences between Carrion Crow *Corvus corone corone*, Hooded Crow *C. c. cornix* and their hybrids. However, they found neither any evidence of variation in MC1R related to the degree of melanism nor any significant genetic variation in the extension gene between the black and the grey crows. These results suggest melanism is attributable to other, additional causes. In addition to mutations of the extension gene, mutations of the agouti gene alone can also cause melanism. As described above, the agouti gene can influence 'communication' between the extension gene and the pigment cell by producing the agouti signalling protein, as ASIP inactivates MC1R independently and the melanocyte will then produce only phaeomelanin. Without ASIP interference, only eumelanin is produced. In this way ASIP normally regulates patterns of eumelanin and phaeomelanin pigment deposition in individual feathers by activating or inactivating the MC1R. Thus, mutations of the agouti gene, whereby no ASIP is produced, thereby causing MC1R to signal constantly, results in dark eumelanic (blackish) plumage that is mostly recessive in inheritance. The recessive dark morph of Montagu's Harrier *Circus pygargus* (Pandolfi 2000) is probably a mutation of the agouti gene. Mutations responsible for a constant production of ASIP, therefore producing only phaeomelanin, are mostly dominant, with an example

Figure 2. Feral Pigeons *Columba livia*: (A) wild phenotype, Leiden, the Netherlands, 19 August 2007; the grey wing-coverts and black wingbars are the result of different distribution of the same quantity of black melanin granules (Hein van Grouw); (B) T-pattern chequer, Leiden, the Netherlands, 19 August 2007; as a result of a dominant mutation of the pattern gene, the pigmentation over almost the entire wings is distributed as usually found only in the black wingbars, resulting in a blackish appearance, but the rump, tail and underparts are unaffected (Hein van Grouw); (C) Black, Leiden, the Netherlands, 19 August 2007; due to a dominant mutation known as 'spread', all pigment granules are equally spread, resulting in black plumage throughout (Hein van Grouw); (D) Recessive red, Pismo, California, USA; due to a recessive mutation of the extension gene that inactivates MC1R, phaeomelanin alone is produced (Robert Shriner)

of this found in Common Quail *Coturnix coturnix* (Fig. 5) and Japanese Quail (Hiragaki *et al*. 2008). The eumelanistic morphs in different isolated populations of Chestnut-bellied Monarch *Monarcha castaneiventris* on the Solomon Islands are the result of two different mutations. The eumelanic plumage of birds on the small island of Santa Ana is the result of a variation of the MC1R, while equally black birds on two other small islands, Ugi and Three Sisters, possess a mutation of the agouti gene (Uy *et al*. 2016).

To summarise, melanism can be due to mutations of the extension gene resulting in variation in MC1R, or mutations of the agouti gene resulting in variation in ASIP. Genetic studies in domesticated bird species, however, have identified many different genes which can cause different forms of melanism. Unsurprisingly, the commonest are extension and agouti, but there are many more, some reasonably common, and many can probably cause melanism in wild species too.

3

Figure 3. Common Woodpigeon *Columba palumbus* specimens (NHMUK 1930.8.14.1, NHMUK 2000.11.1, NHMUK 1923.3.8.1); the phaeomelanised plumage is probably the product of a similar mutation as 'recessive red' in Feral Pigeon *C. livia* (*cf*. Fig. 2D) (Harry Taylor, © Natural History Museum, London)

Figure 4. '*Perdix montana*', the phaeomelanistic variety of Grey Partridge *P. perdix*, NHMUK 1939.12.9.3717, Nasavad, Slovakia, 10 November 1932 (at left) and NHMUK 1939.12.9.3716, Norfolk, England, October 1911; the gene for this recessive mutation is present throughout the range of the species and is therefore a frequently recurring variety on the borderline of being recognised as a morph (Harry Taylor, © Natural History Museum, London)

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Figure 5. 'Yellow' is a dominant mutation of the agouti gene in Common Quail *Coturnix coturnix* (NHMUK 1996.41.441, England) resulting in a coloration based on mainly phaeomelanin (Harry Taylor, © Natural History Museum, London)

Figure 6.. Hooded Crow *Corvus corone cornix* (left, NHMUK 1965.M.19466), Carrion Crow *C. c. corone* (right, NHMUK 2013.5.13) and their hybrid offspring, with in centre a first-generation hybrid (NHMUK 1965.M.19463), left of it a backcross Hooded Crow (NHMUK 1879.3.7.1) and right a backcross Carrion Crow (NHMUK 1925.2.12.1); both the Hooded Crow and all of the hybrids display many patterned feathers with black centres and grey fringes (Harry Taylor, © Natural History Museum, London)

Different forms of melanism

Several mutations in the domestic pigeon / Feral Pigeon, for example, are known to yield a blackish appearance without the quantity of melanin in the plumage being increased. In these cases, the melanistic forms are all due to a change in the arrangement of pigment granules, rather than more granules being present (van Grouw & de Jong 2009). The wild phenotype of *Columba livia* is slate blue-grey with a black tail-band and two black wingbars (Fig. 2A). The grey and black are the result of different distributions of the same amount of black melanin granules. In the grey parts the black granules are clumped and, due to the reflection of the light, what we see appears blue-grey. In the black parts the granules are spread equally and the colour appears black.

The two black wingbars are controlled by the pattern gene, symbolised as C, which regulates the way the pigment granules are arranged in specific feathers. Mutations of the pattern gene have resulted in both a bar-less phenotype and several phenotypes with black-spotted wings (chequered), while the remainder of the plumage pigmentation is scarcely affected. Only in the most extreme form, in which the wings are almost all black (T-pattern chequer, C^T), is the rest of the plumage obviously darker as well (Fig. 2B). The tail and rump, however, remain normal-coloured. Chequered pigeons are common, and among the semi-wild pigeons historically kept in large dovecotes for their eggs, squabs and dung in England (the ancestors of current Feral Pigeons) the trait was so common that Blyth (1847) considered them related to, but different from, Rock Dove. He named them *Columba affinis* (Latin *affinis* = related, allied). Another common melanistic mutation in the pigeon, unrelated to the pattern gene, also spreads the pigment granules equally and is therefore named 'spread' (symbol S). Spread, however, distributes all granules in the manner usually found only in the black wingbars and tail-band, resulting in entirely black plumage, including the rump and tail (Fig. 2C).

6A

6B

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Figure 7. Melanistic Water Rail *Rallus aquaticus* (NHMUK 1939.12.9.3699, Ireland, 13 November 1902), with increased eumelanin, resulting in almost solid black plumage (Harry Taylor, © Natural History Museum, London)

Figure 8A. Melanistic Common Snipe *Gallinago gallinago* (NHMUK 1939.12.9.3643, Ireland), the same form as was previously described as Sabine's Snipe *Scolopax sabinii* Vigors, 1825; (B) Melanistic Common Quail *Coturnix coturnix* (NHMUK 1996.41.442, England, 1895), the same form as was previously described as Verreaux's Quail *Synoicus lodoisiae* Verreaux & des Murs, 1862 (Harry Taylor, © Natural History Museum, London)

It is reasonable to assume that dark morphs in species with predominantly slate-grey plumage are more likely to be the result of 'spread mutations' rather than increased melanin. A possible example is Northern Fulmar *Fulmarus glacialis* (Flood & van Grouw 2015). The difference in colour between Carrion Crow and Hooded Crow, however, is caused by the way the pigment is arranged (pers. obs.). As in both Hooded Crow and the hybrids, many individual, grey feathers are 'patterned' with black (Fig. 6), one can assume that melanism in crows is controlled by a pattern gene comparable with those in the pigeon.

Based on the above, melanism does not necessarily reflect an increase of pigment but may be the result of a changed distribution in the same quantity of melanin. Consequently, a better definition of melanism would be: a condition characterised by abnormal deposits of melanin in skin and feathers, as 'abnormal deposit' covers both a changed distribution and an increased amount. In general the appearance of a melanistic bird is dark, mostly blackish, but not always so. There are three ways melanism can affect birds' plumage: (1) all of the plumage is darker and appears blackish (eumelanin, Fig. 7), dark brown (both

Figure 9. Common Chaffinch *Fringilla coelebs*, Utö Island, Finland, 13 April 2013, with increased phaeomelanin resulting in predominantly reddish-brown plumage (Jorma Tenovuo)

melanins, Fig. 8) or reddish brown (phaeomelanin, Fig. 9); (2) normally dark markings are bolder and noticeably 'overrun' their typical boundaries (the rest of the plumage is often somewhat darker as well, Figs. 10–12); and (3) normal pattern and pigment distribution is changed, but the plumage is not necessarily darker (and can even be paler). See Appendix.

Melanism: accepted morph or aberration?

Melanistic forms are certainly not an uncommon phenomenon in birds. In certain species it is so common that the dark form represents a fairly large percentage of the entire population and is therefore considered to be a colour morph. In these cases the term 'dark morph' is often used instead of aberration. Northern Fulmar, Montagu's Harrier, Chestnut-bellied Monarch, Variable Oystercatcher *Haematopus unicolor*, Lesser Snow Goose *Anser caerulescens*, Common Pheasant *Phasianus colchicus*, New Zealand Weka *Gallirallus australis*, Pomarine Skua *Stercorarius pomarinus*, Arctic Skua *S. parasiticus*, Bananaquit *Coereba flaveola* and Blackcap *Sylvia atricapilla* (Fig. 12) are just a few examples in which a dark morph is accepted as a standard colour aberration within the species.

More than 300 bird species are known to exhibit polymorphisms (Galeotti *et al*. 2003) of which melanism is the commonest (Mundy 2006). Based on the many melanistic morphs in birds, dark forms are no more compromised than normal-coloured individuals (otherwise they would not have become established morphs). Genes (alleles) causing melanistic plumage are probably present in almost all species, as occasional dark individuals can be recorded in any population occasionally. In species in which no dark morph is recognised, single melanistic individuals often survive, and indeed breed. Therefore, in principle, what started as a colour aberration in a species can eventually become an established morph.

In general, a population is considered to be polymorphic when individuals of the same age and sex display one of several heritable colour variants for which the expression is not sensitive, or only at a low level, to the environment or body condition (Buckley 1987). It is difficult to decide, however, when a colour variant in a species can be considered a recognised morph or if it is only an occasional aberration. Ford (1945) seemed to be aware of that problem and defined polymorphism as 'the coexistence in one interbreeding

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10B

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Figure 10. Melanistic White Wagtail *Motacilla a. alba*, Ardivachar, South Uist, Outer Hebrides, Scotland, September 2015; the normal black head markings have overrun their boundaries, whilst the rest of the plumage is darker as well (John Kemp)

Figure 11. Melanistic Great Tit *Parus major*, Rotterdam, the Netherlands, November 2008; the normal black head and breast markings have overrun their boundaries, whilst the rest of the plumage is darker as well (Harvey van Diek)

population of two or more sharply distinct and genetically determined forms, the least abundant of which is present in numbers too great to be due solely to recurrent mutation'. However, this is still vague: how many individuals are equivalent to 'numbers too great'?

Although one can assume that at least a certain percentage of the population needs to be of a different colour before a species can be identified as polymorphic, whether that must be 10%, 20% or even 50% of the population is unclear and debatable. For example, the melanistic form of Grey Partridge discussed earlier (Fig. 4) is occasionally recorded anywhere within the entire natural range of the species. Although this form comprises less than 10%, and probably < 1% of the Grey Partridge population, nevertheless in some works it is considered a recognised colour morph.

Melanism or new species?

In melanism the pigment granules are not changed in shape or size, thus express their full colour. Therefore the plumage of a melanistic bird is often not obviously aberrant, i.e. the plumage appears 'natural' but can be completely different to any known species. That melanistic birds were, especially in the past, mistaken for 'new species' is therefore understandable. Sometimes 'new species' were named on the basis of a single specimen with differently coloration, like Sharpe's Rail *Stictolimnas sharpei* (Hume & van Grouw 2014) and Chestnut-coloured Partridge *Ortyx castaneus* (Fig. 13). The latter was described by Gould (1842) because its different markings had persuaded him that it represented a distinct taxon. Eight years later, Gould (1850) was still convinced of its distinctiveness, as under *O. castaneus* he wrote 'The only example of this species that has come under my notice, I obtained in a living state at the sale of the collection of the late Zoological Gardens at Manchester. I must admit that I have always had a suspicion that the individual in question had assumed some unnatural style of colouring, and that it was merely a variety of *Ortyx Virginianus* or *O. Cubanensis*; but the rich chestnut colouring of the body, the black colouring of the forehead and throat, and the conspicuous markings of the sides and abdomen, are characters so different from what are observable in those species, that I have no other alternative than to describe and figure it as distinct.'

On most occasions, the confusion was based on melanistic forms that occurred, or still occur, quite commonly in the relevant species / populations. That more individuals were found was, for many ornithologists, evidence that these aberrant birds were indeed distinct species. For example, Menzbier (1896) wrote in his description of Willkousky's Owl 'At first I thought that this specimen was but a merely individual melanism [*sic*] of *Syrnium aluco* [Tawny Owl]; but in the spring of this year I received from Mr. Willkousky a skin of another specimen coloured in the same manner as the first, which had been obtained in a

Figure 12. Melanistic morph of Eurasian Blackcap *Sylvia atricapilla heineken*, Madeira, 27 April 2008; the normal black head markings have overrun their boundaries, whilst the rest of the plumage is darker as well (Hadoram Shirihai)

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Figure 13. Gould's Chestnut-coloured Partridge *Ortyx castanea*, which was a melanistic Northern Bobwhite *Colinus virginianus*; the normal black head markings have overrun their boundaries, whilst the rest of the plumage is darker as well, the latter mainly due to increased phaeomelanin hence 'Chestnut-coloured' (Hein van Grouw, © Natural History Museum, London)

vineyard in the district of Shushov. After a careful examination of this specimen, I am now convinced that this Owl is a very good new species, differing from *Syrnium aluco* both in its general colour and character of markings…'. Although rare, melanistic Tawny Owls (Fig. 14A) are still occasionally recorded throughout Europe (and unconnected to the grey and rufous colour morphs of this species). In other *Strix* species, dark forms are also known and are less uncommon. In Ural Owl *S. uralensis* (Fig. 14B), for example, the melanistic form is often treated in the literature as a recognised morph.

Another example of a dark morph that was confused for a new species is the Weka *Gallirallus australis*. In 1847, a dark-coloured rail from New Zealand was described and named *Gallirallus fuscus* by Du Bus. In 1869, Buller described the Black Woodhen *Ocydromus nigricans*, which occurred only on the south-west coast of South Island. Having compared the type specimens of *fuscus* and *nigricans*, Buller (1873) concluded they were the same species, 'which is quite distinct…, but different from South Island Woodhen *O. australis* [= Weka]'. Buller also remarked that Black Woodhen 'inhabits the sea-shore and feeds among the kelp and seaweeds', unlike *australis* which inhabits mainly forest, woodland, scrub and grassland. Differences in behaviour / habitat together with differences in colour also occur in other species. There are, for example, differences in foraging behaviour between the white and dark morphs of Pacific Reef Heron *Egretta sacra* (Rohwer 1990). The differences occur both in the habitat used for feeding as well as the techniques used. Different perch site selection is recorded in Red-tailed Hawks *Buteo jamaicensis* (Preston 1980). Pale-coloured hawks occupy open perch sites, while dark hawks more frequently select perch sites

Figure 14A. Melanistic Tawny Owl *Strix aluco*, Switzerland, April 2015 (Bertrand Ducret); (B) melanistic morph of Ural Owl *Strix uralensis*, southern Poland, May 2008 (Chris van Rijswijk)

characterised by dense stem cover, and it is suggested that the morphs are associated with perch sites that best conceal them from prey. These examples are certainly not exceptions as will be demonstrated further below.

Melanism-dependent selection: yes or no?

Assuming that the plumage coloration of each species has evolved under natural selection over a long period to produce a colour / pattern best suited for survival, why do colour morphs also survive? In general, polymorphism is expected to have important effects on fitness. Some research has investigated the fitness effects of melanistic morphs, and positive effects have been found, for example, in Feral Pigeon. It appears that the plumage colour of juvenile Feral Pigeons is associated with features that influence its survival to adulthood in an urban environment. Strongly melanistic fledglings are more likely to attain adulthood, compared to the wild phenotype (Haag-Wackernagel *et al*. 2006). There is also some evidence in Feral Pigeons that melanistic males have a longer breeding season and are more fertile than the wild phenotype (Murton *et al*. 1973). Coloration per se may not directly influence survival, but there appears to be a link between plumage coloration, especially melanism, and behavioural and physiological characteristics associated with survival. In general, more strongly melanistic individuals are more resistant to stress, more aggressive and differ in metabolism (Roulin & Ducrest 2011, Poelstra 2013, Corbel *et al*. 2016). In Feral Pigeon this may explain why more melanistic phenotypes occur in the centre of large cities, while in small towns and natural or rural habitats the wild phenotype is more common.

Figure 15. Feral Pigeons *Columba livia* with phaeomelanised plumage (ash-red) but different wing patterns: (A) Barred (the white primaries and head feathers are the product of leucism), (B) Chequer and (C) T-pattern chequer, Leiden, the Netherlands, 19 August 2007 (Hein van Grouw)

Thus, in some cases, colour morphs of a species may behave differently due to their respective physiological properties. Eventually, colour morphs may evolve into distinct taxa. An example of this is perhaps Carrion Crow vs. Hooded Crow. Besides differences in plumage (melanistic versus non-melanistic), they also differ in vocalisations and habitat selection, the latter especially during the breeding season (Rolando & Laiolo 1994). Nevertheless, in the areas of overlap they do interbreed and, although melanism in crows is probably based on more than one gene, the alleles for black appear dominant (pers. obs., based on colour of first-generation offspring and that of backcrosses to the parental species; Fig 6). Although Carrion Crow and Hooded Crow hybridise, pair composition is not random (Saino & Villa 1992, Rolando 1993, Risch & Andersen 1998). Also, hybrids prefer to breed with 'grey' crows rather than 'black' crows (Rolando & Laiolo 1994), which may suggest that the Hooded phenotype is the original colour. The preference for 'grey' may also explain the non-random pair formation in areas of overlap, if Hooded Crows only select a melanistic partner in the absence of their own phenotype. In general, reproductive success, defined as the number of chicks reared to about fledging, is greater in Carrion Crows than Hooded Crows (Saino & Villa 1992). This may reflect the fact that Carrion Crow is more aggressive (Saino & Scatizzi 1991) and more stress-resistant (Poelstra 2013).

Carrion Crow and Hooded Crow inhabit separate but adjoining ranges in Europe, with some narrow areas of overlap. The popular hypothesis to explain the differences between them are that they diverged from a common ancestor and, during an extended period of geographical separation, these populations underwent genetic differentiation before meeting again. Genetic studies, however, reveal no significant molecular differentiation

(Haring *et al*. 2007, Haas *et al*. 2009), suggesting that the forms have either not been separated, or at least not for long. Another possible scenario, however, is that at some point a colour aberration occurred, probably the melanistic form, and that, due to different behaviour and physiology related to melanism, this form finally evolved into a distinct taxon. A similar phenomenon appears to have produced the dark-coloured Basalt Wheatear *Oenanthe lugens warriae*, a subspecies of Mourning Wheatear *O. lugens*. Until recently, the dark-coloured birds were considered to be a dark morph of nominate *O. lugens*. The breeding range of Basalt Wheatear is, however, restricted to the basalt deserts of eastern Jordan and southern Syria, with no or little evidence of hybridisation with Mourning Wheatear (Shirihai *et al*. 2011, Khoury *et al*. 2013). Although genetically insignificantly differentiated from nominate Mourning Wheatear, Basalt Wheatear differs sufficiently in plumage colour, breeding habitat selection and biometrics to recognise it taxonomically (Shirihai *et al*. 2011). Thus it appears that dark morphs, due to their different behaviour, can evolve into new taxa.

That the above scenarios are more than a hypothesis was demonstrated by Hugall & Stuart-Fox (2012), who showed that bird species with multiple plumage colour forms within the same population speciate faster than those with only a single colour morph. Earlier, Gray & McKinnon (2007) had already suggested that coloration differences among individuals may directly promote speciation events. All of this research was, however, not new as the tendency of colour polymorphs to evolve more quickly had been predicted more than 60 years earlier by the evolutionary biologist, Sir Julian Huxley (1955). Whether he was misunderstood by his contemporaries, or was simply not taken seriously, the proof appears to be available. And if we do not believe in the above examples among crows and wheatears, differences in behaviour / habitat choice by melanistic morphs occur in other species in which the dark morph is still considered to be the same taxon.

In Senegal Coucal *Centropus senegalensis*, for example, two colour morphs occur in the populations of Ghana and Nigeria. The typical form, with creamy-white underparts and black more or less confined to the crown, occurs throughout the species' range without any strong habitat preference but is less associated with wet areas (Erritzøe *et al*. 2012). The dark form, however, with an all-black head and breast, and reddish-brown belly, which was recognised taxonomically in the past (see Table 1), occurs mainly in coastal Ghana and Nigeria, as well as Ivory Coast and Liberia. The two morphs interbreed freely, but the dark morph appears to prefer especially wet areas, with higher rainfall and is therefore more dependent on certain habitats than the typical form.

Another example is Vermilion Flycatcher, wherein the population around Lima, Peru, is polymorphic, with dark and red morphs occupying the same areas and interbreeding randomly. However, just as in Feral Pigeons, the dark phenotype is commoner in the more urbanised areas of the city, while towards the outskirts the number of red morphs increases (van Grouw & Nolazco 2012). This suggests that certain fitness effects related to the melanistic morph are beneficial in highly urban environments, e.g. stress resistance. Mate selection does not (yet) appear to be based on colour, but this can be explained by the fact that, although melanism may indirectly favour the fitness of dark individuals in an urban environment, evolution in the species is still in its relative infancy.

A similar process appears to have occurred in Bananaquit; black morphs occur in several populations within the species' range. On several of the islands off northern Venezuela the populations only comprise black morphs, which are recognised as subspecies (*melanornis*, *lowii* and *laurae*), underlining the statement that melanism promotes speciation. On the islands of Grenada and St. Vincent the populations are (still) polymorphic, but the two morphs occupy different habitats. Melanistic birds occur in moist forest at all altitudes, whereas (normal) yellow-and-black birds persist only in dry lowland habitats.

Although already separated by habitat preference, in the few, narrow areas of overlap pair composition is random (Wunderle 1981), but some post-mating isolation (= unsuccessful fertilisation and development) is suspected (MacColl & Stevenson 2003), suggesting that speciation has commenced.

Nevertheless, it must be stated that in other species, e.g. Lesser Snow Goose *Anser c. caerulescens*, intensive studies have failed to find definitive evidence of natural selection for morphs (Cooke *et al*. 1995). This does not mean, however, that such selection does not exist.

Discussion

Morphism, a term introduced by Huxley (1955) to denote genetic polymorphism as opposed to other kinds of polymorphism such as seasonal, cyclical, geographical, etc., appears to be an important factor in promoting speciation. Note, however, that polymorphism does not of necessity lead to speciation, as this depends also on many other factors. Morphism in a species probably is initiated as an occasional colour aberration. If a selective balance operates between the aberrant and normal colour morphs, based on selective advantage vs. disadvantage, the aberration may become an established morph. Pigment aberrations often combine with different behaviour and physiology, and these differences may prove advantageous in certain habitats, ultimately leading to speciation.

As mentioned earlier, recent studies have revealed that in birds, strongly melanistic individuals are more resistant to stress, more aggressive and differ in their metabolism. Legendre (1941) had already noted that the melanistic morph of *Phasianus colchicus* is more vigorous and robust than normal-coloured individuals. The mutation occurred for the first time within feral populations in England in the late 1800s, and has persisted ever since. Also, in other countries where the species was introduced, it flourished. In this, and all other given examples of strongly melanistic morphs with positive effects for fitness, the melanin involved is eumelanin alone. But what of phaeomelanin; do strongly phaeomelanised individuals possess the same link between plumage colour and behavioural and physiological characteristics associated with survival, as eumelanised individuals? Although '*montana*', the reddish 'morph' of Grey Partridge, persistently re-appears due to the recessive nature of the mutation, there is no evidence that this phaeomelanised variety increases numerically anywhere in the species' natural range.

A form of melanism that is dominant in inheritance and also results in predominantly phaeomelanised plumage (different from Gould's *castaneus*) occurs in Northern Bobwhite *Colinus virginianus*. This red mutation is weaker and less fertile than normal individuals and, although it achieved a probable frequency of *c*.15% for a few years within a small area, it has failed to persist in the wild even when purposely bred and released (Cole *et al*. 1949).

Another example is the Feral Pigeon. A dominant mutation, known as dominant red or ash-red (symbol B^A, van Grouw & de Jong 2009), lacks almost all eumelanin in the plumage, resulting in pale, ash-grey body, flight and tail feathers, with additional phaeomelanin in the neck feathers and wing pattern. Ash-red is a very common mutation in many breeds of domestic pigeons, but relatively rare in feral populations (pers. obs.). In Vienna, for example, <5% of the city's feral population is ash-red (Haag-Wackernagel *et al*. 2006), which appears unexpected given that the mutation is dominant in inheritance over the black / grey wild phenotype. In fact, it is dominant and sex-linked, thus all male offspring (= 50% of all offspring) of an ash-red female crossed with a wild phenotype male are ash-red. Depending on whether an ash-red male is homozygote (pure) or heterozygote (impure) for the mutation, when mated with a wild phenotype female either all offspring or 50% will be ash-red—both males and females in the latter. Thus any ash-red pigeon, irrespective of its sex and mate, will produce at least 50% ash-red offspring. Based on this, one would expect a much higher percentage of ash-red individuals in Feral Pigeon populations, meaning that there is presumably high mortality among juvenile ash-red pigeons. Ash-red is independent of the wing pattern, thus ash-red pigeons come in barred, chequered and T-pattern chequered wing patterns (Fig. 15; see Different forms of melanism). According to research in Vienna, ash-red barred juveniles have a high probability of reaching adulthood, while ash-red juveniles with chequer or T-pattern chequer have a rather low survival rate (Haag-Wackernagel *et al*. 2006). This is remarkable as eumelanised juveniles with chequer or T-pattern chequer wings possess a higher success rate, compared to their barred counterparts. These findings suggest that, at least among Feral Pigeons in cities, negative effects on fitness are linked to strongly phaeomelanised plumage. Whether the same applies to Feral Pigeons in rural areas, or for other species in their natural habitat is unknown. However, what is known is that there is much more to the phenomenon of melanism than an increase of dark eumelanin resulting in dark plumage alone.

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References:

Blyth, E. 1847. Drafts for a Fauna indica. *Ann. Mag. Nat. Hist*. 19: 101–108.

Brisson, M. J. 1760. *Ornithologia*, vol. 1. Paris.

Buckley, P. A. 1987. Mendelian genes. Pp. 1–44 *in* Cooke, F. & Buckley, P. A. (eds.) *Avian genetics*. Academic Press, Orlando.

Buller, W. L. 1869. Notes on Herr Finsch's review of Mr. Walter Buller's *Essay on New Zealand Ornithology* by the author. *Trans. & Proc. NZ Inst*. 1: 105–112.

Buller, W. L. 1873. *A history of the birds of New Zealand*. London.

Caughley, G. 1969. Genetics of melanism in the Fantail *Rhipidura fuliginosa*. *Notornis* 16: 237–240.

Cole, L. J., Stoddard, H. L. & Komarek, E. V. 1949. Red Bobwhite, a report and corrections. *Auk* 66: 28–35.

Cooke, F., Rockwell, R. F. & Lank, D. B. 1995. *The Snow Geese of La Perouse Bay, natural selection in the wild*. Oxford Univ. Press.

Corbel, H., Legros, A., Haussy, C., Jacquin, L., Gasparini, J., Karimi, B. & Frantz, A. 2016. Stress response varies with plumage colour and local habitat in feral pigeons. *J. Orn*. 157: 825–837.

Crawford, R. D. 1990. *Developments in animal and veterinary sciences, 22: poultry breeding and genetics*. Elsevier, Amsterdam.

Erritzøe, J., Mann, C. F., Brammer, F. P. & Fuller, R. A. 2012. *Cuckoos of the world*. Christopher Helm, London.

Flood, R. L. & van Grouw, H. 2015. Unfamiliar plumage types of Fulmars in the North Atlantic. *Brit. Birds* 108: 331–348.

Ford, E. B. 1945. Polymorphism. *Biol. Reviews* 20: 73–88.

Frisch, J. L. 1763. *Vorstellung der Vögel Deutschlands*. Berlin.

Galeotti, P., Rubolini, D., Dunn, P. O. & Fasola, M. 2003. Colour polymorphism in birds: causes and functions. *J. Evol. Biol*. 16: 635–646.

Gould, J. 1842. [On various new species of *Ortyx*]. *Proc. Zool. Soc. Lond*. 10: 181–184.

Gould, J. 1850. *Monograph of partridges of America*. London.

Gray. S. M. & McKinnon, J. S. 2007. Linking color polymorphism maintenance and speciation. *Trends Ecol. & Evol*. 22: 71–79.

van Grouw, H. 2013. What colour is that bird? The causes and recognition of common colour aberrations in birds. *Brit. Birds* 106: 17–29.

van Grouw, H. & Jong, J. de. 2009. [*Genetics in the pigeon, modern Mendelism and more for the pigeon fancier*]. NBS, Surhuisterveen. (In Dutch.)

van Grouw, H. & Nolazco, S. 2012. The nature of melanism and some other colour aberrations in the Vermilion Flycatcher (*Pyrocephalus rubinus obscurus*). *Bol. Inf. UNOP* 7: 26–37.

Haag-Wackernagel, D., Heeb, P. & Leiß, A. 2006. Phenotype-dependent selection of juvenile urban Feral Pigeons *Columba livia*. *Bird Study* 53: 163–170.

Haas, F., Pointer, M. A., Saino, N., Brodin, A., Mundy, N. I. & Hansson, B. 2009. An analysis of population genetic differentiation and genotype-phenotype association across the hybrid zone of carrion and hooded crows using microsatellites and MC1R. *Mol. Ecol*. 18: 294–305.

Haring E., Däubl, B., Pinsker, W., Kryukov, A. & Gamauf, A. 2012. Genetic divergences and intraspecific variation in corvids of the genus *Corvus* (Aves: Passeriformes: Corvidae) – a first survey based on museum specimens. *J. Zool. Syst. & Evol. Res*. 50: 230–246.

Hiragaki, T., Inoue-Murayama, M., Miwa, M., Fujiwara, A., Mizutani, M., Minvielle, F. & Ito, S. 2008. Recessive black is allelic to the yellow plumage locus in Japanese Quail and associated with a frameshift deletion in the ASIP gene. *Genetics* 178: 771–775.

Hugall, A. F. & Stuart-Fox, D. 2012. Accelerated speciation in colour-polymorphic birds. *Nature* 485: 631–634.

Hume, J. P. & van Grouw, H. 2014. Colour aberrations in extinct and endangered birds. *Bull. Brit. Orn. Cl*. 134: 168–193.

Huxley, J. 1955. Morphism in birds. *Acta XI Congr. Intern. Orn*., Experientia Suppl. III: 309–328.

Kerje, S., Lind, J., Schütz, K., Jensen, P. & Andersson, L. 2003. Melanocortin 1-receptor (MC1R) mutations are associated with plumage colour in chickens. *Anim. Genet*. 34: 241–248.

Khoury, F., Haddad, M., Al-Jbour, S. & Rahahleh, F. 2013. A mixed pair of pale and black morph Mourning Wheatears *Oenanthe lugens lugens* in the southern highlands of Jordan. *Sandgrouse* 35: 134–137.

Lamoreux, M. L., Delmas, V., Larue, L. & Bennett, D. 2010. *The colors of mice, a model genetic network*. Wiley-Blackwell, Chichester.

Latham, J. 1823. *A general history of birds*, vol. 8. Winchester.

Legendre, M. 1941. Les variation de plumage et de forme chez les oiseaux IV. Les mutations (1). *L'Oiseau & R.F.O*. 11: 1–16.

Lubnow, E. 1963, Melanine bei Vögeln und Säugetieren. *J. Orn*. 104: 69–81.

MacColl, A. D. C. & Stevenson, I. R. 2003. Stasis in the morph ratio cline in the Bananaquit on Grenada, West Indies. *Condor* 105: 821–825.

Menzbier, M. A. 1896. [*Syrnium willkonskii* sp. n.]. *Bull. Brit. Orn. Cl*. 6: 6.

Meyer, A. B. 1887. *Unser Auer-, Rackel- und Birkwild und seine Abarten*. Vienna.

Mundy, N. I. 2005. A window on the genetics of evolution: *MC1R* and plumage colouration in birds. *Proc. Roy. Soc. B.* 272: 1633–1640.

Mundy, N. I. 2006. Genetic basis of color variation in wild birds. Pp. 469–506 *in* Hill, G. E. & McGraw, K. J. (eds.) *Bird coloration*, vol. 1. Harvard Univ. Press, Cambridge, MA.

Murton, R. K., Westwood, N. J. & Thearle, R. J. 1973. Polymorphism and the evolution of continuous breeding season in the pigeon *Columba livia*. *J. Reproductive Fertility* Suppl. 19: 561–575.

Nadeau, N. J, Minvielle, F., Ito, S., Inoue-Murayama, M., Gourichon, D., Follett, S. A., Burke, T. & Mundy, N. I. 2008. Characterization of Japanese Quail *yellow* as a genomic deletion upstream of the avian homolog of the mammalian ASIP (*agouti*) gene. *Genetics* 178: 777–786.

Pandolfi, M. 2000. First dark morph brood of Montagu's Harriers (*Circus pygargus*) in 14 years in Italy. *J. Raptor Res*. 34: 340–341.

Poelstra, J. 2013. The genetics of speciation and colouration in Carrion and Hooded Crows. Digital comprehensive summaries of Uppsala dissertations from the Faculty of Science and Technology 1088. Uppsala Univ.

Preston, C. R. 1980. Differential perch site selection by color morphs of the Red-tailed Hawk (*Buteo jamaicensis*). *Auk* 97: 782–789.

Risch, M. & Andersen, L. 1998. Selektive Partnerwahl der Aaskrähe (*Corvus corone*) in der Hybridisierungszone von Rabenkrähe (*C.c. corone*) und Nebelkrähe (*C. c. cornix*). *J. Orn*. 139: 173–177.

Rohwer, S. 1990. Foraging differences between white and dark morphs of the Pacific Reef Heron *Egretta sacra*. *Ibis* 132: 21–26.

Rolando, A. 1993. A study on the hybridization between carrion and hooded crow in northwestern Italy. *Ornis Scand*. 24: 80–83.

Rolando, A. & Laiolo, P. 1994. Habitat selection of hooded and carrion crows in the alpine hybrid zone. *Ardea* 82: 193–199.

Roulin, A. & Ducrest, A.-L. 2011. Association between melanism, physiology and behaviour: a role for the melanocortin system. *Eur. J. Pharmacology* 660: 226–233.

Saino, S. & Scatizzi, L. 1991. Selective aggressiveness and dominance among Carrion Crows, Hooded Crows and hybrids. *Boll. Zoll*. 58: 255–260.

Saino, N. & Villa, S. 1992. Pair composition and reproductive success across a hybrid zone of carrion crows and hooded crows. *Auk* 109: 543–555.

Schaaning, H. T. 1921. Bjerkreim-orren *Lyrurus tetrix bierkreimensis* subsp. nova. *Stavanger Mus. Arshhefte* 31(2): 1–27.

Sclater, P. L. 1860. On the Black-shouldered Peacock of Latham. *Proc. Zool. Soc. Lond*. 28: 221–222.

Searle, A. G. 1968. *Comparative genetics of coat colour in mammals*. Logos Press, London.

Shirihai, H., Kirwan, G. M. & Helbig, A. J. 2011. A new taxon in the Mourning Wheatear *Oenanthe lugens* complex. *Bull. Brit. Orn. Cl.* 131: 270–291.

Theron, E., Hawkins, K., Bermingham, E., Ricklefs, R. E. & Mundy, N. I. 2001. The molecular basis of an avian plumage polymorphism in the wild: a *melanocortin-1-receptor* point mutation is perfectly associated with the melanic plumage morph of the Bananaquit, *Coereba flaveola*. *Current Biol*. 11: 550–557.

Uy, J. A. C., Cooper, E. A., Cutie, S., Concannon, M. R., Poelstra, J. W., Moyle, R. G. & Filardi, C. E. 2016. Mutations in different pigmentation genes are associated with parallel melanism in island flycatchers. *Proc. Roy. Soc. B* 283: 20160731.

Vidal, O., Araguas, R. M., Fernandez, E., Heras, S., Sanz, N. & Pla, C. 2010a. Melanism in guinea fowl (*Numida meleagris*) is associated with a deletion of phenylalanine-256 in the MC1R gene. *Anim. Genet*. 41: 656–658.

Vidal, O., Vinas, J. & Pla, C. 2010b. Variability of the melanocortin 1 receptor (MC1R) gene explains the segregation of the bronze locus in turkey (*Meleagris gallopavo*). *Poultry Sci*. 89: 1599-1602.

Wunderle, J. M. 1981. An analysis of a morph ratio cline in the Bananaquit (*Coereba flaveola*) on Grenada, West Indies. *Evolution* 35: 333–344.

Address: Bird Group, Dept. of Life Sciences, Natural History Museum, Akeman Street, Tring, Herts. HP23 6AP, UK, e-mail: h.van-grouw@nhm.ac.uk

Appendix

If darkish-coloured birds were not sufficiently confusing, forms of melanism causing a completely different, but very natural-looking pattern have baffled ornithologists even more. These forms often cause an extreme variation of the original plumage. The colour of the melanin itself (the shape or size of the pigment granules) is unaffected, but the way it is distributed over the feathers is, resulting in wholly different markings and patterns (Figs. 16–17), and even an overall paler appearance (Fig. 18). In sexually dimorphic species, the appearance of females alone may be significantly paler, whereas males are often less affected and may be slightly darker, resulting in an even more extreme difference between the sexes. A well-known example is Black-shouldered Peafowl, named *Pavo nigripennis* by Sclater (1860) which is a colour mutation of Indian Peafowl *P. cristatus*. Males hardly differ from normal-coloured birds, except in having solid black 'shoulders', hence their name, rather than the normal barring (Fig. 19). Females, however, are considerably paler with different markings and appear strikingly different from normal-coloured individuals (Fig. 20). This extreme

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Figure 16. Specimen of Red-legged Partridge *Alectoris rufa* with a form of melanism that has changed the usual pattern and markings (left, NHMUK 1923.1.29.1) and a normal-coloured individual (right, NHMUK 1907.12.20.7); due to a mutation, the black head and throat markings are altered and the solid-coloured back, shoulders and wing feathers (based mainly on eumelanin) now exhibit distinctive patterns based on both melanin types, and some parts resemble the flanks plumage (Harry Taylor, © Natural History Museum, London)

Figure 17. Chukar *Alectoris chukar* (NHMUK 1939.12.9.3715), same mutation as in Fig. 16. (Harry Taylor, © Natural History Museum, London)

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Figure 18. Hazel Grouse *Tetrastes bonasia* (NHMUK 1987.24.122) with a form of melanism that has altered the typical pattern and markings, resulting in a paler appearance (Harry Taylor, © Natural History Museum, London)

sexual dimorphism convinced Sclater (1860) to name Black-shouldered Peafowl as a species and not a hybrid or domestic variety: 'I cannot consider it a domesticated variety, because of the differences in both sexes appear to be constant, and to descend to the progeny…'. Similar mutations occur in Mallard *Anas platyrhynchos* (Fig. 21) and Asian Blue Quail *Synoicus chinensis* (Fig. 22).

Pattern-changing mutations have not only been mistaken for new species. In Black Grouse *Lyrurus tetrix*, for example, Meyer (1887) believed they were hybrids instead. Hybrids between Black Grouse and ptarmigan *Lagopus* sp. were well known in Meyer's time and he considered the hybrids to differ in the degree of feathering on their feet, depending on which species was the male parent: if the latter was a ptarmigan, then the offspring had ptarmigan feet (Fig. 23), whereas if the male was a Black Grouse then it had feet like this species (Fig. 24). Whether ptarmigan-footed hybrids' male parents are indeed always ptarmigans is unknown, but Black Grouse-footed birds he depicted were Black Grouse and not hybrids. The totally different feather markings and patterns due to mutations, which gave the birds a more whitish appearance, fooled Meyer. Apparently, he never observed a male affected by the same mutation, or at least he neither

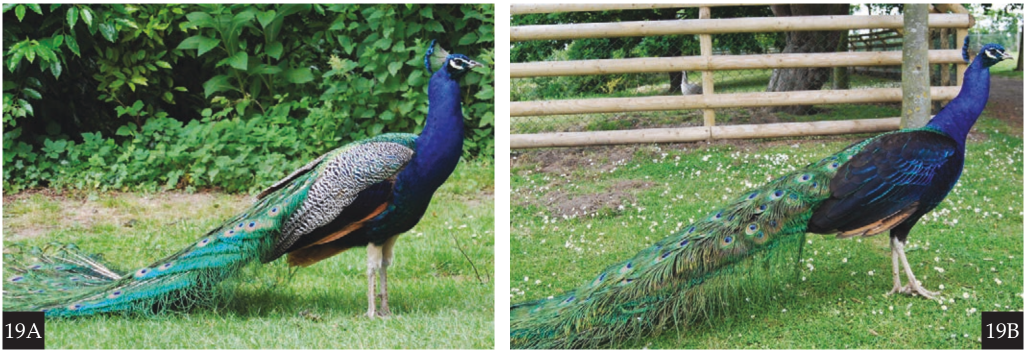

Figure 19. Normal-coloured and black-shouldered male Indian Peafowls *Pavo cristatus*; apart from parts of the wing and shoulders, this mutation does not affect the rest of male plumage (Hein van Grouw)

Figure 20. Normal-coloured and black-shouldered female Indian Peafowls *Pavo cristatus*; the 'black-shoulder' mutation has a major effect on female plumage (Hein van Grouw)

Figure 21. A form of melanism in Mallard *Anas platyrhynchos* that affects female plumage much more than male plumage (Hein van Grouw)

mentioned nor illustrated one, as otherwise he probably would have realised his mistake (Figs. 25–26). These mutations were not uncommon in Scandinavia and Russia, and in the early 1900s in the Bjerkreim area, Norway, were sufficiently numerous that Schaaning (1921) described them as a new subspecies, *Lyrurus tetrix bjerkreimensis* (Fig. 27), because '…the plumage of the male is similar to the spring plumage of male Willow Ptarmigan *Lagopus lagopus*.'

Figure 22. Forms of melanism (C and D) in Asian Blue Quail *Synoicus chinensis* that affect female plumage much more than male plumage (Pieter van den Hooven)

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Figure 23. Pl. 14 in A. B. Meyer (1887) *Unser Auer-, Rackel- und Birkwild und seine Abarten* showing Black Grouse *Lyrurus tetrix* × ptarmigan *Lagopus* sp. hybrids (Hein van Grouw, © Natural History Museum, London)

Figure 24 (facing page). Pl. 15 in A. B. Meyer (1887) *Unser Auer-, Rackel- und Birkwild und seine Abarten* showing what Meyer believed to be Black Grouse *Lyrurus tetrix* × ptarmigan *Lagopus* sp. hybrids; however, these birds are aberrant-coloured female Black Grouse (*cf.* Figs. 25–26) (Hein van Grouw, © Natural History Museum, London)

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Figure 25. Form of melanism in Black Grouse *Lyrurus tetrix* (NHMUK 1996.41.320, male, and NHMUK 1987.24.143, female) that alters the pattern and markings, resulting in a paler appearance than normal; compare the female with left-hand bird in Fig. 24. (Harry Taylor, © Natural History Museum, London)

Figure 26. Another form of melanism in Black Grouse *Lyrurus tetrix* specimens at Zoological Research Museum Alexander Koenig, Bonn, which alters the pattern and markings, resulting in a paler appearance than normal; compare female with right-hand bird in Fig. 24. (Hein van Grouw)

„BJERKREIM-ORREN“

Lyrurus tetrix. Varietet: 3 ♂♂ og ♀ i Stavanger Museum

Figure 27. Depiction in Schaaning (1921) of another form of melanism in Black Grouse *Lyrurus tetrix* that changes the pattern and markings, resulting in a paler appearance than normal (Hein van Grouw, © Natural History Museum, London)

Nesting evidence, density and vocalisations in a resident population of Savannah Sparrow *Passerculus sandwichensis wetmorei* in Guatemala

by Knut Eisermann, Claudia Avendaño & Esteban Matías

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Summary.—We report the discovery of a resident population of Savannah Sparrows *Passerculus sandwichensis wetmorei* in grassland on a high plateau of the Sierra Los Cuchumatanes in western Guatemala. We observed a nest containing a nestling, and 11 fledglings of other breeding pairs in July 2016, which represent the first confirmation of the species nesting south-east of the Isthmus of Tehuantepec, *c.*700 km from the nearest known breeding locality in central Mexico. We provide the first description of juvenile plumage for this subspecies. Furthermore, we describe the song of *P. sandwichensis wetmorei* for the first time, which is similar in structure and signal characteristics to that of northern populations. Based on transects, we estimate a population density of 0.7–4.3 adults / ha in the study area, in the Parque Regional Municipal Todos Santos Cuchumatán, which is similar to published data from the USA and Canada. This is the first documentation of *P. sandwichensis wetmorei* since the type specimens were collected more than 100 years ago.

The Savannah Sparrow *Passerculus sandwichensis* complex is widespread in grasslands and other open habitats throughout North America, Mexico and northern Central America (Wheelwright & Rising 2008). Northern populations are migratory, spending the boreal winter in the southern USA, Mexico and Central America (Rising & Beadle 1996, Wheelwright & Rising 2008). Plumage coloration and morphology are variable, and currently three populations are often recognised as separate species from Savannah Sparrow: Belding's Sparrow *P. guttatus*, Large-billed Sparrow *P. rostratus* and San Benito Sparrow *P. sanctorum*, all in southern California and north-west Mexico (Rising 2010, 2011). In Guatemala, Savannah Sparrow is a rare winter visitor, as well as a local resident (Eisermann & Avendaño 2007). Resident Savannah Sparrows in the Guatemalan highlands have been described as *P. s. wetmorei*, which have darker upperparts than birds from the nearest resident population in the Mexican highlands (van Rossem 1938, Hubbard 1974). Material pertaining to *P. s. wetmorei* is very rare in ornithological collections and the eight syntypes in the Natural History Museum, Tring (NHMUK, including the holotype NHMUK 1899.2.1.2893; Warren & Harrison 1971) are probably the only specimens (A. C. Vallely pers. comm.). The validity of the subspecies is controversial. Dickinson & Christidis (2014) recognised it based on the most recent taxonomic review of Savannah Sparrows to have directly compared *P. s. wetmorei* (Hubbard 1974). However, Rising (2010, 2011) considered *P. s. wetmorei* synonymous with *P. s. sandwichensis*, based solely on observations in northern populations where most morphological variation is clinal. The resident status of Savannah Sparrow in Guatemala has also been questioned due to the lack of definitive nesting records (Land 1970, Howell & Webb 1995, Rising & Beadle 1996, Rising 2001, Wheelwright & Rising 2008, Rising 2011), and *P. s. wetmorei* has been considered probably extinct (Wheelwright & Rising 2008, Dickinson & Christidis 2014). Identification of subspecies of Savannah Sparrow in the field is difficult (Rising & Beadle 1996, Rising 2010). Repeated observations of the species in the Sierra Los Cuchumatanes, dpto. Huehuetenango, in western Guatemala, during the boreal autumn to spring period, from September to May (Eisermann & Avendaño 2007; pers. obs.), could not be assigned to resident or migratory populations. We therefore revisited the area during summer 2016 to determine the status of Savannah Sparrow in the area. Here we report nesting evidence and density of a breeding population in the Sierra Los Cuchumatanes, and document the previously undescribed song of males in this population.

Study area and methods

We studied a population of Savannah Sparrows in the central part (locally known as 'Planes del Diablo', 15°31′14″N, 91°33′56″W) of the Parque Regional Municipal "K'ojlab'l Tze' Te' Tnom Todos Santos Cuchumatán" (hereafter: PRM Todos Santos Cuchumatán), Sierra Los Cuchumatanes, dpto. Huehuetenango, in western Guatemala. The area is *c*.24 km north-west of the type locality of *P. s. wetmorei* at Hacienda Chancol (van Rossem 1938). Sierra Los Cuchumatanes is the highest non-volcanic mountain range in Central America, reaching 3,800 m. The upper part of this sierra consists of upper-Paleozoic to Mesozoic sediments (Anderson *et al*. 1973). PRM Todos Santos Cuchumatán is part of a plateau at 3,700 m. Landscape in the study area was shaped by glaciers during the late Quaternary (Lachniet & Roy 2011) and is characterised by undulating terrain with moraines and small temporal lakes. Vegetation is *páramo* grassland dominated by *Muhlenbergia quadridentata* (Fig. 1), interspersed by exposed rocks, herbs and some juniper shrubs *Juniperus standleyi*. The region has been used for sheep grazing for centuries (Steinberg & Taylor 2008) but, following the establishment of PRM Todos Santos Cuchumatán in 2009, grazing has been restricted to certain areas. The *páramo* is bordered by open pine forests dominated by *Pinus hartwegii*. A temperate climate prevails with a mean annual min. temperature of 5°C and a mean annual max. of 20°C. Mean annual precipitation is 1,500 mm, and mean monthly precipitation is 10–25 mm during the dry season (December–March) vs. 70–300 mm during the wet season (April–November) (MAGA 2002).

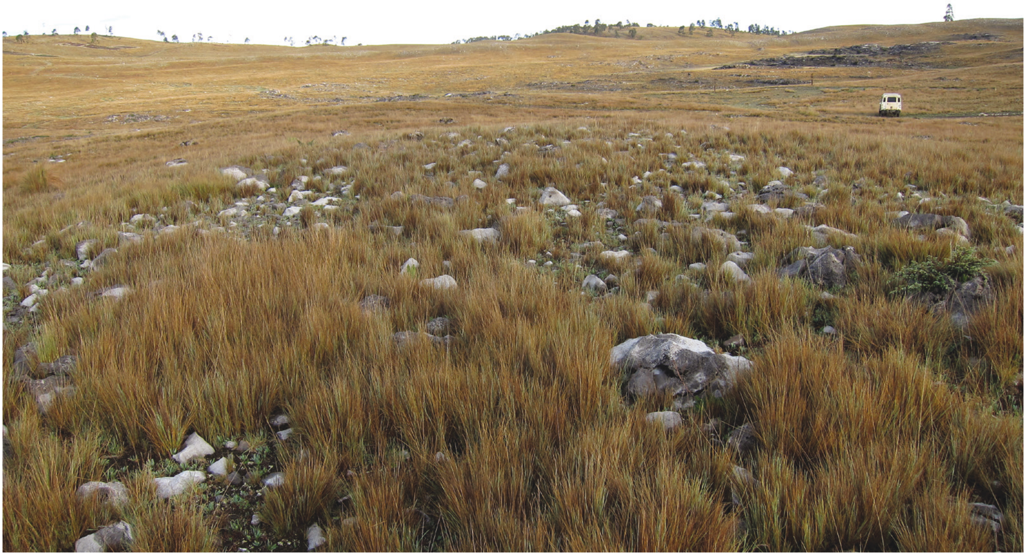

Figure 1. Habitat of a breeding population of Savannah Sparrow *Passerculus sandwichensis wetmorei* at 3,700 m in PRM Todos Santos Cuchumatán, dpto. Huehuetenango, Guatemala, 5 June 2016; the undulating landscape, shaped by glaciers during the late Quaternary, is currently covered with grassland dominated by *Muhlenbergia quadridentata* (Poaceae) (Knut Eisermann)

We observed Savannah Sparrows in the study area on 30 April, 3–5 June, 2–3 July and 27–28 August 2016. To rapidly assess population size, we conducted a census of Savannah Sparrows by walking five 310–530-m transects on 3 July. We recorded all individuals within a perpendicular distance of 30 m from each transect (strip width: 60 m), together with information on age (adult, fledgling). We assumed that most adults were attending fledglings or young in nests, and therefore should be foraging and easily detected. Detection probability of Savannah Sparrows decreases sharply beyond 50 m (Diefenbach *et al*. 2003). To estimate population density of adults, we assumed that most birds would flush at a distance of within 30 m from the observers, and discarded the number of adults recorded >30 m from the transect line, as well as any fledglings. To calculate population density, counts were transformed into *n* / ha, using each transect as a sample unit. Upper and lower limits of number of adults were calculated based on a 95% confidence interval of the mean. Means are given with standard deviation (SD).

To determine the size of the grassland area at 'Planes del Diablo', we mapped the habitat based on a satellite image with 0.5 m ground resolution from January 2014. We used software ESRI ArcView 3.2 for mapping and spatial analyses.

KE recorded vocalisations of Savannah Sparrows in the breeding population at PRM Todos Santos Cuchumatán using a Fostex FR-2LE digital recorder (enhanced by Oade Brothers Audio with an ultra-low noise, high-speed FET preamp) and Sennheiser M67 directional microphone with a sample rate of 96 kHz. Sonograms were produced using Raven Pro 1.5 (Bioacoustics Research Program 2012). We marked onset and offset of signals in the sonograms using the curser in Raven Pro 1.5, and measured duration and peak frequency (frequency with max. power [dB]). Some cuts from the recordings are available online at http://xeno-canto.org using the XC catalogue number given in the text.

Results

Nesting evidence.—During a brief visit to 'Planes del Diablo' on 30 April 2016, we observed at least 30 adult Savannah Sparrows along a driving route of *c*.4 km, including display flights of males. Song activity was low but some males gave single songs.

On 3–5 June 2016, males were frequently singing. From a point overlooking an area of *c*.1.5 ha, we saw four singing males. Two copulations were recorded during the period, but no other breeding behaviour was witnessed, presumably because the nesting season had only just started. Fig. 2 presents different adult Savannah Sparrows of the breeding population.

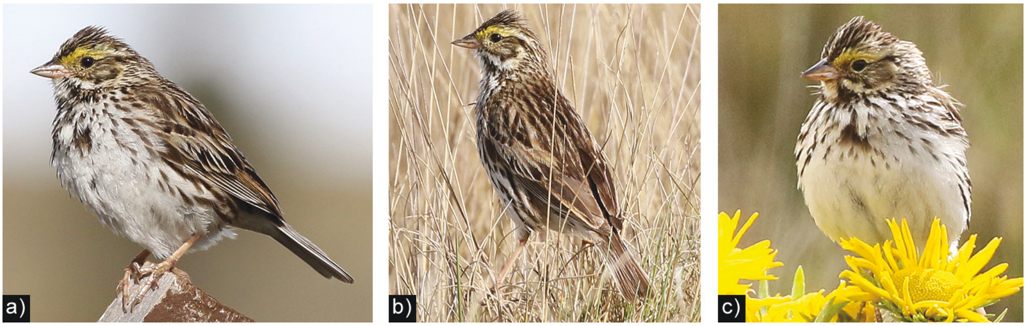

Figure 2. Different adult Savannah Sparrows *Passerculus sandwichensis wetmorei* of a breeding population in PRM Todos Santos Cuchumatán, dpto. Huehuetenango, Guatemala: (a) lateral; (b) dorsal, 5 June 2016; and (c) frontal view showing the neatly marked median crown-stripe, 2 July 2016 (Knut Eisermann)

Figure 3. Nesting evidence of Savannah Sparrow *Passerculus sandwichensis wetmorei* in PRM Todos Santos Cuchumatán, dpto. Huehuetenango, Guatemala: (a) nest with a single nestling, 2 July 2016 (a second nestling was found dead 20 cm from the nest); (b) recently fledged juvenile, barely able to fly, 3 July 2016, (c–d) two fledglings well able to fly, tail *c.*40% grown, 3 July 2016; (e) dependent juvenile with tail *c.*80% grown, 3 July 2016; and (f) immature, 27 August 2016 (Knut Eisermann)

On 2–3 July 2016, we found a nest of Savannah Sparrow with a nestling and a dead young 20 cm away (presumably removed from the nest by the adults). The nest was a cup of grass, placed in a depression on the ground, hidden in 15–20 cm-tall grass (*Muhlenbergia* *quadridentata*; Fig. 3). The outer diameter of the nest was 9 cm, inner diameter 7 cm, and the cup was 5 cm deep.

Additionally, we recorded a total of 11 fledglings of Savannah Sparrow throughout the area. These ranged in age from recently fledged and barely able to fly, to several days post-fledging with tails *c*.80% grown (Fig. 3). Their plumage differed from adults by lacking a yellow supercilium, by having a buff breast with dark streaks (whitish with dark streaks in adults) and by beige-tipped greater wing coverts forming a narrow wingbar. The bill of juveniles was darker (mainly greyish with a small pinkish area) than in adults (mainly pinkish with a greyish culmen). Most of the fledglings uttered intense begging calls.

On 27 August 2016, most of the Savannah Sparrows observed at close range were adult-like (*n* = 32), with yellow supercilia. One was identified as a young bird (Fig. 3f) based on the lack of yellow on the supercilium, slightly buff breast with dark streaks, and beige tips to the greater wing-coverts. Song activity was low on this day, and no behaviour indicating nesting (adults carrying nesting material or food, copulations, intense alarm calls of adults, begging calls of juveniles) was observed during four hours of observation along a line covering *c*.5 km.

Population density and habitat extension.—We recorded a total of 40 adult and eight juvenile Savannah Sparrows during transects on 3 July 2016. The mean number of adults / ha was 2.1 ± 1.7 (*n* = 5 transects, 95% confidence interval: 0.7–4.3 adults / ha), discarding birds further than 30 m from the transects, and all recorded juveniles. Grassland habitat at 'Planes del Diablo' in the central PRM Todos Santos Cuchumatán covers *c*.300 ha. Based on the size of available habitat and the estimated density, the population of Savannah Sparrows at the 'Planes del Diablo' is estimated to be 210–1,280 adults.

We recorded singing males at other sites also in Sierra Los Cuchumatanes during June–July 2016: near Chichim (15°33′13″N, 91°34′46″W), east of Laguna Ordóñez (15°30′14″N, 91°32′17″W) and near Paquix (15°26′01″N, 91°27′34″W) (Fig. 4).

Vocalisations.—KE recorded the song of four males (XC333471–473). All songs had a similar structure, comprising 2–4 introductory *chip* notes, followed by a middle section with several *ch*-notes, short trills and descending short whistles, a dominant buzz, and a terminal section consisting of a short descending whistle and a short trill running into a whistle. The introduction, dominant buzz and terminal section had the same structure in all songs recorded. The middle section varied (Fig. 5). Song duration was 2.1–3.1 seconds (mean 2.5 ± 0.3, *n* = 37 songs of four males). Of 37 songs, 19 had three introductory *chip* notes, 16 had two introductory notes and two songs had four introductory notes. Table 1 summarises the mean duration and peak frequency of the notes in all songs.

Discussion

Our observations of nesting Savannah Sparrows in the Sierra Los Cuchumatanes in the western Guatemalan highlands represent the first confirmation of a breeding population south-east of the Isthmus of Tehuantepec. Residency has been previously suggested based on specimens collected in June 1897 (van Rossem 1938), but it has been doubted due to the lack of additional documentation (Howell & Webb 1995, Wheelwright & Rising 2008, Rising 2011). Jones (2002) erroneously reported a nest from dpto. Totonicapán, Guatemala, although the observer did not in fact observe any nesting behaviour (J. Berry pers. comm.).

The nesting season of Savannah Sparrow in Guatemala appears to be synchronised with the wet season. Based on our observations in 2016 (display flights of males on 30 April, frequent singing and copulations on 3–5 June, nest and fledglings on 2–3 July), the breeding season extended from late April to July (peak activity June–July), and probably into August. The first four months of 2016 were unusually dry in the Sierra Los Cuchumatanes. Peak

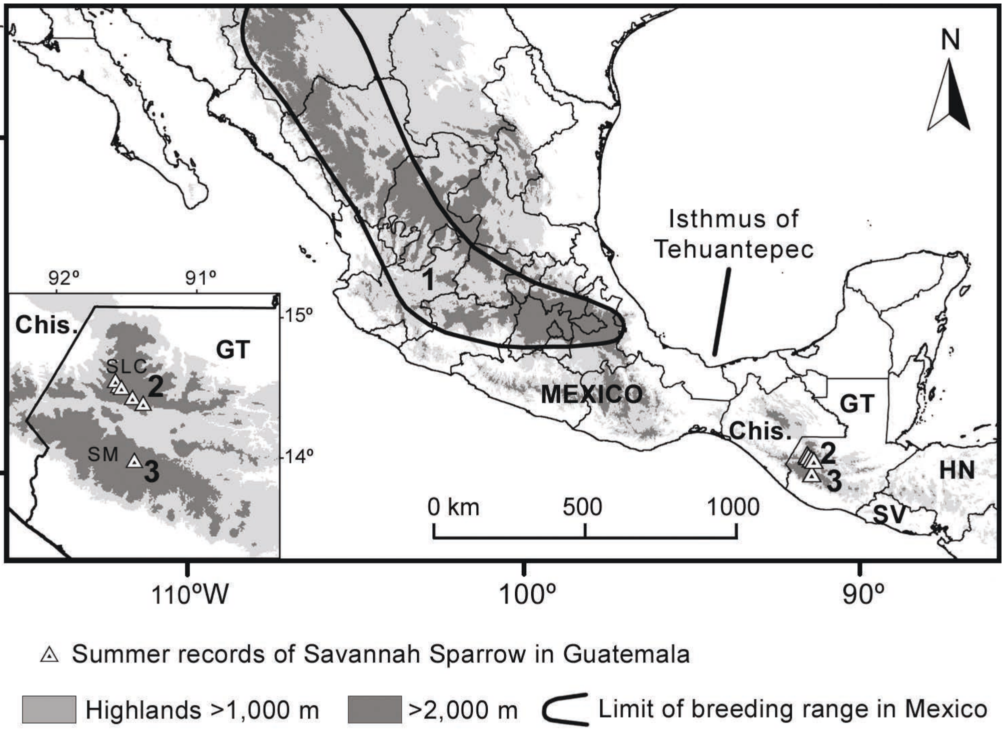

Figure 4. (1) Approximate breeding range of Savannah Sparrow *Passerculus sandwichensis* in Mexico (*sensu* Howell & Webb 1995); (2) summer records in the Sierra Los Cuchumatanes, Guatemala, including recent nesting and other summer records (June–July 2016), and historic summer records (June 1897, van Rossem 1938); and (3) summer record from Sierra Madre range in June 2002 (J. Berry *in* Eisermann & Avendaño 2007). Chis. = Chiapas, Mexico, GT = Guatemala, HN = Honduras, SV = El Salvador. Inset map shows location of summer records of Savannah Sparrow in the Sierra Los Cuchumatanes (SLC) and Sierra Madre (SM) ranges in Guatemala.

breeding may begin earlier (April–May) in years with a normal wet season, which usually starts in April (MAGA 2002). It remains unknown if adults raise two broods per season, as in some northern populations (Wheelwright & Rising 2008). Future research in other *páramo* grasslands in the Guatemalan highlands, especially in dptos. San Marcos, Quetzaltenango, Totonicapán and Quiché, should enable an assessment of the total population of breeding Savannah Sparrows in the Guatemalan highlands. Breeding Savannah Sparrows should also be looked for in the highlands of Chiapas, Mexico.

Our recent observations in the Sierra Los Cuchumatanes during June–July 2016 are the only documented summer records of Savannah Sparrow in Guatemala since the specimen records at Hacienda Chancol in June 1897 (van Rossem 1938), *c.*24 km south-east from the recent nesting record, and undocumented observations from the Sierra Madre Mountains near San Francisco El Alto, dpto. Totonicapán, in 2002 (J. Berry *in* Eisermann & Avendaño 2007) (Fig. 4). We attribute the scarcity of records in Guatemala during summer to an observational lacuna, not to the sparrow's extreme rarity. The population density of 0.7–4.3 adults / ha at our study site in the Sierra Los Cuchumatanes is similar to study sites in the mainland USA and Canada, where breeding bird densities of 0.7–2.3 pairs / ha have been reported (see Wheelwright & Rising 2008). We consider Savannah Sparrow to be locally common in the Sierra Los Cuchumatanes. We recognise that our numbers are rough estimates, because the small number of transects and records did not permit us to calculate

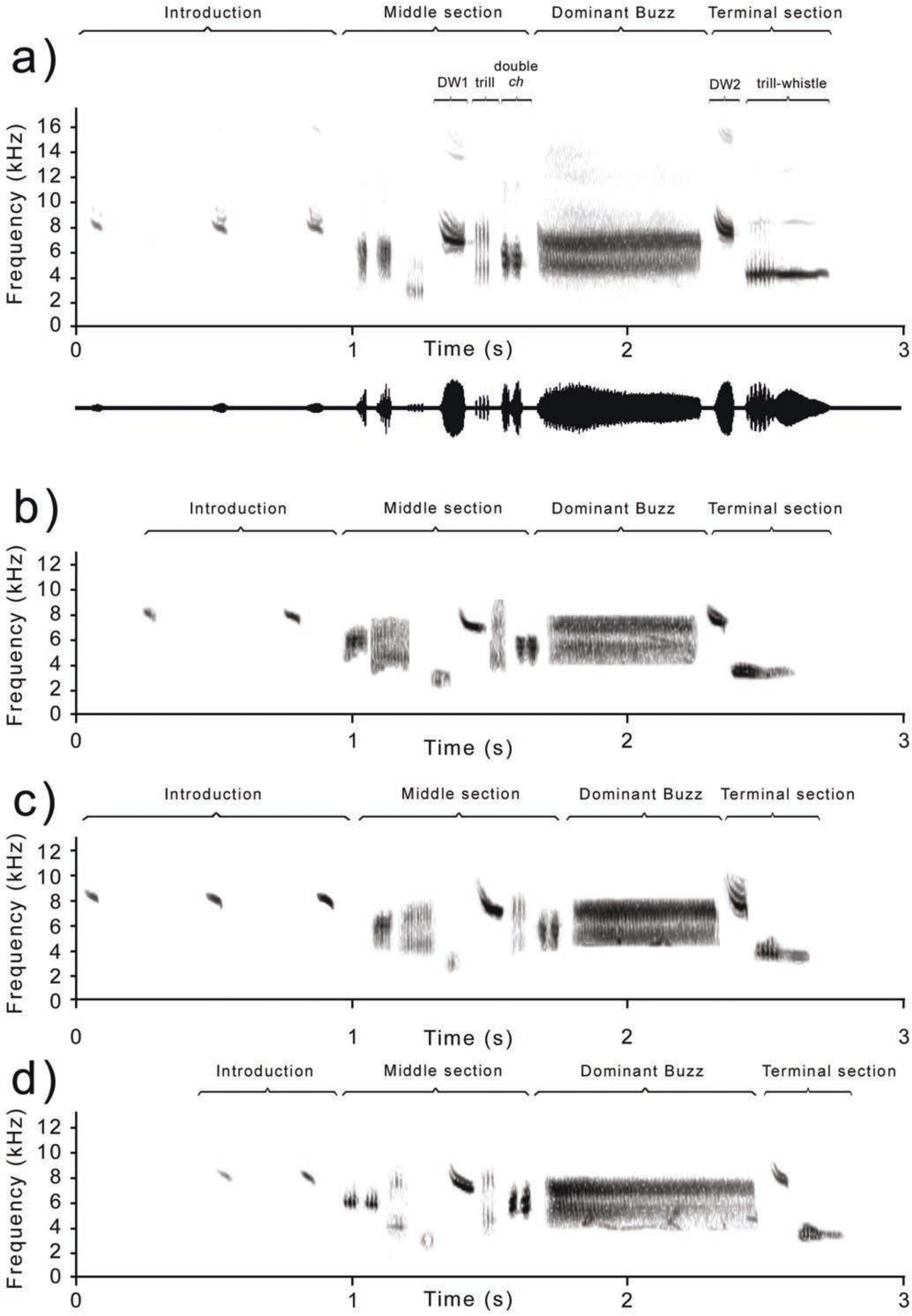

Figure 5. Sonograms of songs of four male Savannah Sparrows *Passerculus sandwichensis wetmorei* in PRM Todos Santos Cuchumatán, dpto. Huehuetenango, Guatemala: (a) 5 June 2016 (Knut Eisermann, XC333471), including waveform, (b) 5 June 2016 (Knut Eisermann, XC333471), (c) 3 June 2016 (Knut Eisermann, XC333472), (d) 3 June 2016 (Knut Eisermann, XC333473). DW = descendent whistle. See Table 1 for signal measurements of marked notes.

TABLE 1
Mean (± SD) and range of signal characteristics of songs of breeding Savannah Sparrows *Passerculus sandwichensis wetmorei* in PRM Todos Santos Cuchumatán, dpto. Huehuetenango, Guatemala, in June 2016, *n* = 37 songs of four males.

Song section (see Fig. 5)	**Duration (seconds)**	**Peak frequency (kHz)**
Entire song (*n* = 37)	2.5 ± 0.3 (2.1–3.1)	
Introduction:		
Chip note (*n* = 97)	0.06 ± 0.01 (0.04–0.12)	7.906 ± 202 (6.938–8.250)
Middle section:		
Descending whistle (DW1) (*n* = 37)	0.10 ± 0.01 (0.08–0.11)	6.927 ± 132 (6.750–7.125)
Trill (n = 37)	0.05 ± 0.01 (0.03–0.06)	6.471 ± 1.268 (4.125–7.500)
Double *ch* note (*n* = 37)	0.08 ± 0.004 (0.07–0.10)	5.063 ± 378 (3.188–5.625)
Dominant section:		
Buzz (*n* = 37)	0.60 ± 0.06 (0.5–0.8)	6.456 ± 646 (4.688–6.938)
Terminal section:		
Descending whistle (DW2) (*n* = 37)	0.08 ± 0.005 (0.07–0.09)	7.566 ± 222 (7.313–8.063)
Trill-whistle (n = 37)	0.29 ± 0.07 (0.16 – 0.39)	4.074 ± 355 (3.375–4.313)

detection probabilities and therefore prepare more reliable estimates using distance sampling methodology (Buckland *et al*. 2001).

Only male Savannah Sparrows are known to sing (Wheelwright & Rising 2008). Songs in northern populations are 2–3 seconds long and very variable. The song in all populations documented to date comprises a long buzz, preceded by several introductory notes and varied chips, trills, short buzz notes or whistles, and terminated by a trill (Sung & Handford 2006, Wheelwright & Rising 2008, Williams *et al*. 2013). The song of *P. s. wetmorei* was previously undescribed; the songs we recorded in the breeding population at PRM Todos Santos Cuchumatán had a similar structure to those of northern populations (Fig. 5).

Most of the more than 20 named subspecies of Savannah Sparrow are not recognised by Rising (2007, 2011) and Rising *et al*. (2009), because most geographic variation is clinal and many subspecies descriptions are not based on quantitative data. Breeders in the Guatemalan highlands are, however, morphologically distinctive compared to the nearest breeding population in the central Mexican highlands (van Rossem 1938, Hubbard 1974), *c*.700 km north-west of the isthmus (Fig. 4). Van Rossem (1938) described the eight specimens of *P. s. wetmorei* collected by W. B. Richardson in June 1897 as dorsally 'darker and browner' than residents in the central Mexican highlands (*P. s. brunnescens*), with upperparts similar to the darkest specimens of Savannah Sparrow (*P. s. alaudinus*) from around San Francisco, California, but with underparts 'much less heavily streaked'. Our confirmation of a breeding population in the Guatemalan highlands, together with its isolation from the nearest breeding population in the Mexican highlands, separated by the lowlands of Tehuantepec, may justify a taxonomic re-evaluation of *P. s. wetmorei*. We hope that this study will motivate more research into the life history, demography and taxonomy of this little-known race of Savannah Sparrow.

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References:

Anderson, T. H., Burkart, B., Clemons, R. E., Bohnenberger, O. H. & Blount, D. N. 1973. Geology of the western Altos Cuchumatanes, northwestern Guatemala. *Bull. Geol. Soc. Amer*. 84: 805–826.

Bioacoustics Research Program. 2012. *Raven Pro: interactive sound analysis software (v. 1.5)*. Cornell Lab of Ornithology, Ithaca, NY.

Buckland, S. T., Anderson, D. R., Burnham, K. P., Laake, J. L., Borchers, D. L. & Thomas, L. 2001. *Introduction to distance sampling: estimating abundance of biological populations*. Oxford Univ. Press, New York.

Dickinson, E. C. & Christidis, L. (eds.) 2014. *The Howard and Moore complete checklist of the birds of the world*, vol. 2. Fourth edn. Aves Press, Eastbourne.

Diefenbach, D. R., Brauning, D. W. & Mattice, J. A. 2003. Variability in grassland bird counts related to observer differences and species detection rates. *Auk* 120: 1168–1179.

Eisermann, K. & Avendaño, C. 2007. *Lista comentada de las aves de Guatemala / Annotated checklist of the birds of Guatemala.* Lynx Edicions, Barcelona.

Howell, S. N. G. & Webb, S. 1995. *A guide to the birds of Mexico and northern Central America*. Oxford Univ. Press, New York.

Hubbard, J. P. 1974. Geographic variation in the Savannah Sparrows of the inland southwest, Mexico and Guatemala. *Occ. Pap. Delaware Mus. Nat. Hist*. 12: 1–21.

Jones, H. L. 2002. The nesting season, June through July 2003: Central America. *N. Amer. Birds* 56: 494–495.

Lachniet, M. S. & Roy, A. J. 2011. Guatemala and Costa Rica. Pp. 843–848 *in* Ehlers, J., Gibbard, P. L. & Hughes, P. D. (eds.) *Quaternary glaciations—extent and chronology*. *Developments in Quaternary sciences*, vol. 15. Elsevier, Amsterdam.

Land, H. C. 1970. *Birds of Guatemala*. Livingston, Wynnewood, PA.

MAGA (Ministerio de Agricultura, Ganadería y Alimentación) (2002) *Atlas de Guatemala.* CD-ROM. MAGA, Guatemala City.

Rising, J. D. 2001. Geographic variation in size and shape of Savannah Sparrows (*Passerculus sandwichensis*). *Stud. Avian Biol*. 23: 1–65.

Rising, J. D. 2007. Named subspecies and their significance in contemporary ornithology. *Orn. Monogr*. 63: 45–54.

Rising, J. D. 2010. The many Savannah Sparrows. *Birding* 42: 44–55.

Rising, J. D. 2011. Genus *Passerculus* Bonaparte, 1838. Pp. 550–551 *in* del Hoyo, J., Elliott, A. & Christie, D. A. (eds.) *Handbook of the birds of the world*, vol. 16. Lynx Edicions, Barcelona.

Rising, J. D. & Beadle, D. D. 1996. *A guide to the identification and natural history of the sparrows of the United States and Canada*. Academic Press, San Diego, CA.

Rising, J. D., Jackson, D. A. & Fokidis, H. B. 2009. Geographic variation in plumage pattern and coloration of Savannah Sparrows. *Wilson J. Orn*. 121: 253–264.

van Rossem, A. J. 1938. Descriptions of twenty-one new races of Fringillidae and Icteridae from Mexico and Guatemala. *Bull. Brit. Orn. Cl*. 58: 124–138.

Steinberg, M. & Taylor, M. 2008. Guatemala's Altos de Chiantla: changes on the high frontier. *Mountain Res. & Development* 28: 255–262.

Sung, H. C. & Handford, P. 2006. Songs of the Savannah Sparrow: structure and geographic variation. *Can. J. Zool*. 84: 1637–1646.

Warren, R. L. M. & Harrison, C. J. O. 1971. *Type-specimens of birds in the British Museum (Natural History)*, vol. 2. Trustees of the Brit. Mus. (Nat. Hist.), London.

Wheelwright, N. T. & Rising, J. D. 2008. Savannah Sparrow (*Passerculus sandwichensis*) *In* Poole, A. (ed.) *The birds of North America Online*. Cornell Lab of Ornithology, Ithaca, NY. http://bna.birds.cornell.edu.bnaproxy.birds.cornell.edu/bna/species/045 (accessed 5 July 2016).

Williams, H., Levin, I. I., Norris, D. R., Newman, A. E. M. & Wheelwright, N. T. 2013. Three decades of cultural evolution in Savannah Sparrow songs. *Anim. Behav*. 85: 213–223.

Addresses: Knut Eisermann and Claudia Avendaño, PROEVAL RAXMU Bird Monitoring Program, Cobán, dpto. Alta Verapaz, Guatemala, e-mails: knut.eisermann@proeval-raxmu.org, claudia@proeval-raxmu.org. Esteban Matías, Coordinator of Commissions of Natural Resources in the Parque Regional Municipal "K'ojlab'l Tze' Te' Tnom Todos Santos Cuchumatán", Consejo Nacional de Áreas Protegidas (CONAP), Todos Santos Cuchumatán, dpto. Huehuetenango, Guatemala, e-mail: esteban.matias@hotmail.com

New bird distributional data from Cerro Tacarcuna, with implications for conservation in the Darién highlands of Colombia

by Luis Miguel Renjifo, Augusto Repizo, Juan Miguel Ruiz-Ovalle, Sergio Ocampo & Jorge Enrique Avendaño

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Summary.—We conducted an ornithological survey of the Colombian slope of Cerro Tacarcuna, the highland region adjacent to the 'Darién Gap' on the Colombia / Panama border, and one of the most poorly known and threatened regions in the world. We present novel data on distribution, habitat, breeding biology and vocalisations for 27 species, including the first confirmed records in Colombia of Ochraceous Wren *Troglodytes ochraceus* and Beautiful Treerunner *Margarornis bellulus*, and the first records in the Darién highlands of Black-headed Antthrush *Formicarius nigricapillus*, Scaly-throated Foliage-gleaner *Anabacerthia variegaticeps*, Yellow-throated Chlorospingus *Chloropingus flavigularis hypophaeus* and, based on previously overlooked specimens, report the first confirmed records for Colombia of Sooty-faced Finch *Arremon crassirostris*. In addition, we collected the first Colombian specimens of Violet-capped Hummingbird *Goldmania violiceps*, Bare-shanked Screech Owl *Megascops clarkii*, Tacarcuna Tapaculo *Scytalopus panamensis* and Varied Solitaire *Myadestes coloratus*. For several subspecies endemic to the region, we collected the first or second specimens for Colombia. Finally, we discuss the elevational ranges of Darién endemic species and subspecies, which are mostly concentrated above 600 m. The Darién highlands remain poorly studied and threats to their conservation are increasing. Therefore, effective measures are needed, particularly in Colombia, where the sole protected area in the region currently covers forests only below 600 m.

The Darién comprises a system of humid lowlands dissected by mountain ranges and isolated massifs of moderate elevation, at the junction between Central and South America on the Colombia–Panaman border (Fig 1)—the so-called 'Darién Gap'. The region has played a significant role in the biogeography and diversification of the Neotropics, serving as a route for or barrier to the exchange of Central and South American faunas during the Tertiary and Pleistocene (Simpson 1950, Mayr 1964, Haffer 1970, Smith & Klicka 2010). This interchange and isolation are evidenced by several lowland birds and contact zones between taxa with origins in Central America, the Chocó, Nechí, Magdalena Valley and Amazonia (Haffer 1967a,b). Likewise, several highland bird species from the Talamanca Mountains and West Andes of Colombia meet in the Darién. Some are recognised as subspecies or represent separate evolutionary lineages (Wetmore 1965, 1968, 1973, Wetmore *et al*. 1984, Miller *et al*. 2007, Cadena & Cuervo 2010, Gutiérrez-Pinto *et al*. 2012). Some authors have proposed the existence of isolated forest refuges on the slopes of several massifs in the region (e.g. Cerro Pirre, Cerro Tacarcuna south to Los Saltos–El Limón and northern Baudó Mountains) during recent geological history (Haffer 1967, Hernández-Camacho *et al*. 1992) as drivers of the high degree of avian endemism and population differentiation.

Current knowledge of Darién avifauna is incomplete (BirdLife International 2014) and mainly based on historical collections and observations, with better documentation of lowland birds due to easier access (Rodríguez 1982, Hilty & Brown 1986, Ridgely & Gwynne 1989, Bayly *et al*. 2014, Hruska *et al*. 2016). In particular, the avifauna of the Gulf of Urabá, north-east of the Colombian Darién, has been studied in greater detail (Haffer 1959, 1967a,b, Bran-Castrillón *et al*. 2014). In contrast, the Darién highland avifauna has been less studied, although better documented on the Panamanian side, with expeditions to massifs such as Cerro Pirre, Alturas de Nique, Cerro Tacarcuna and its spur Cerro Malí (Wetmore 1965, 1968, 1973, Wetmore *et al.* 1984, Robbins *et al*. 1985, Ridgely & Gwynne 1989, Hruska *et al*. 2016), Altos de Quía (Wetmore & Galindo 1972), Serranía de Jungurudó (Angehr *et al*. 2004), Serranía de Majé (Angehr & Christian 2000) and the foothills of Cerro Piña (Miller *et al*. 2011), the last two of which are both isolated massifs north of the Serranía de Jungurudó. In Colombia, Cerro Tacarcuna has been the only Darién massif visited: H. E. Anthony and D. S. Ball in 1915 to the eastern slope of Alto Tacarcuna (Chapman 1917, Haffer 1959, Participantes de la Alianza Biomap 2006), L. Gualdrón *et al*. to Alto Barrigonal (*c*.1,400 m) in 1980 (specimens at Instituto Alexander von Humboldt, Villa de Leyva) and Pearman (1993) who ascended to 1,250 m in the headwaters of the río Tigre. Recent expeditions to the Serranía del Darién were conducted by J. Zuluaga-Bonilla in January 2007 to Cerro La Nevera (08°30’N, 77°26W; *c*.475–775 m), municipality Acandí, dpto. Chocó; and by JMR-O & T. Walschburger in November 2008 to the headwaters of the río Tanelita at Cerro Tacarcuna (08°13’N, 77°16W; *c*.1,250–1,400 m), Comunidad Eyákera, municipality Unguía, dpto. Chocó (Ruiz-Ovalle *et al*. 2014). Olaciregui *et al*. (2016) visited the Serranía de Abibe south-east of the Gulf of Urabá. Despite these new data, the paucity of field studies and the complex topography of the Colombian Darién makes this region one of the least biologically documented in the country (Rangel 2004, Arbeláez-Cortés 2013). It is expected that several bird species will be found on the Colombian side, representing range extensions from Panama and / or the Andes, some of them new species for the country and even South America.

Here, we present the results of an expedition to the Colombian slope of Cerro Tacarcuna in August 2010. We present a list of bird species recorded, several of which represent noteworthy range extensions, or additional records of poorly known species (e.g. endemics) from the Darién highlands of Colombia. Finally, we discuss the need for protection of the foothills and highlands of the Colombian Darién.

Methods

Three main mountain ranges run parallel from the eastern Isthmus of Panama to north-west Colombia (Fig. 1). On the Pacific slope, the Serranía de Jungurudó at 1,200 m ranges from its northern outlier, Cerro Sapo, south to the headwaters of the río Jaqué, and is connected to the Cordillera de Juradó and Altos de Aspavé. To the east, this serranía is separated from the Serranía de Pirre by *c*.30 km of lowlands in the valleys of the ríos Balsas and Juradó (Angehr *et al*. 2004). The Serranía de Pirre (1,550 m) extends further south to Alturas de Nique and Cerro Quía, and via a relatively high range connects to the Serranía de los Saltos (300–600 m) (Haffer 1970, Angehr *et al*. 2004). Nearly 50 km of lowlands separate the Pirre ridge from the Serranía del Darién on the Caribean coast (Robbins *et al*. 1985). This range rises to 1,875 m at Cerro Tacarcuna and extends north to the Serranía de San Blas in Panama, termining abruptly to the south-west at the Gulf of Urabá (Haffer 1970). Almost 100 km of humid lowlands of the Atrato Valley separate the Serranía del Darién from Serranía de Abibe (2,200 m), a northern spur of the West Andes of Colombia. The lower río Atrato drains into the Gulf of Urabá, forming an extensive delta covered by mangrove, riverine vegetation and flooded plains (Haffer 1970, Bran-Castrillón *et al*. 2014).

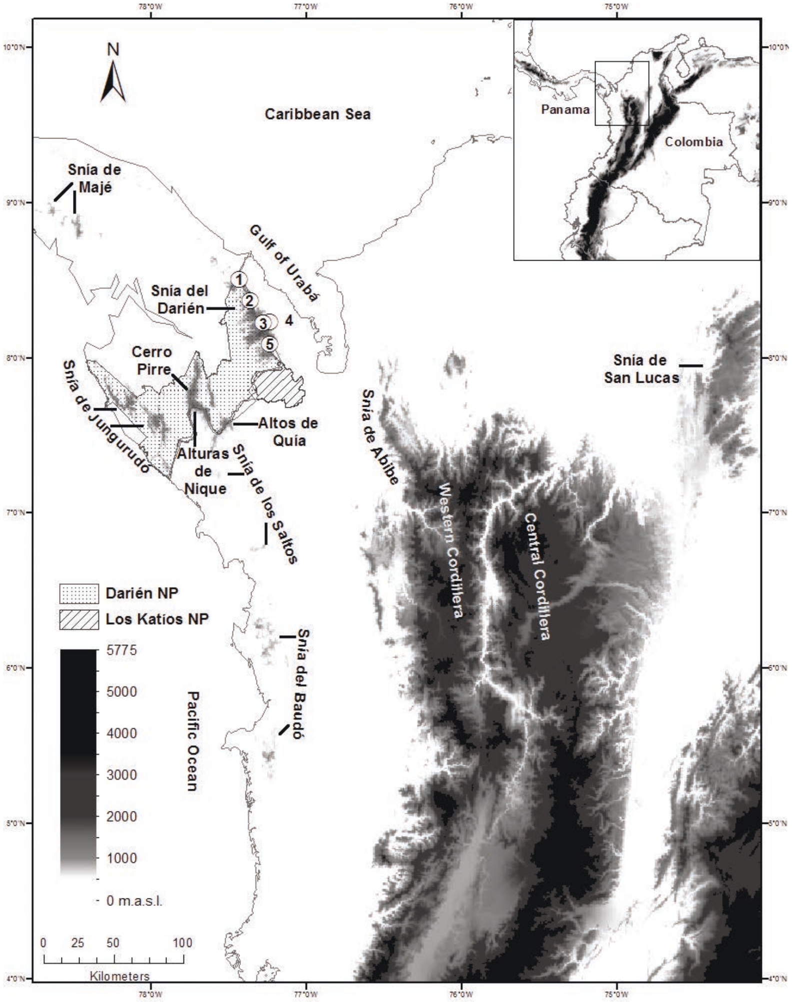

Figure 1. Map of north-western South America and eastern Panama showing the location of the Darién and the major geographical features mentioned in the text. Land above 600 m is indicated in grey to black. Circles represent historical and recent localities, including our study site in the Serranía del Darién: 1 = Cerro La Nevera (475–775 m), municipality Acandí, dpto. Chocó; 2 = Alto Barrigonal (1,400 m), municipality Acandí, dpto. Chocó; 3 = Cuchilla del Lago (1,150 m), Corregimiento de Balboa, municipality Unguía, dpto. Chocó; 4 = headwaters of the río Tanelita (1,250–1,400 m), Comunidad Eyákera, municipality Unguía, dpto. Chocó; and 5 = headwaters of the río Tigre (1,250 m), municipality Unguía, dpto. Chocó.

We conducted field work along the ridge known as Cuchilla del Lago, Corregimiento de Balboa, municipality Unguía, dpto. Chocó, Colombia (08°13'49"N, 77°14'08"W; 1,150 m). The area lies in the headwaters of the río Bonito, on the east slope of the Cerro Tacarcuna (Fig. 1). We accesed Cuchilla del Lago by opening a trail in primary forest upslope from the left bank of the río Bonito (*c.*450 m), close to a property currently occupied by the Toro family. Based on our observations, the transition from wet to cloud forests on this part of Cerro Tacarcuna starts at *c.*900 m. Vegetation at our campsite comprised primary forest with a dense understorey and closed canopy 4–8 m tall, with many epiphytes and palms. Climate in this region is classified as partially dry according to annual precipitation (730–2,025 mm) and humidity (factor: -25–112), compared with wetter and more humid zones in southern Chocó (Poveda-M. *et al.* 2004).

Three observers made visual and aural records along two transects, between 05.45 h and 18.00 h on 4–7 August 2010. The first transect comprised *c.*300 m along the ridge at 1,150 m, which permitted us to sample different primary habitats (understorey, canopy facing the ridges and natural clearings). The second transect was at 980–1,150 m and followed the trail we opened to reach the campsite. Simultaneously, two of us undertook *c.*288 mist-net hours (12 × 2 m; 36 mm mesh) along the first transect, mainly between 06.00 h and 14.00

h. In addition, two observers made sound-recordings using Sony MiniDisc and Zoom-H4 digital recorders with Sennheiser ME-67 shotgun microphones. Recordings are deposited at www.xeno-canto.org (see Results). We collected some specimens that were mist-netted and others using a Gamo air rifle. Study skins are deposited in the ornithological collection of the Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá. Muscle tissue samples from each specimen were preserved in 95% Ethanol and deposited at Banco de Tejidos, Universidad de los Andes, Bogotá.

Results

We recorded 84 species in the cloud forest belt at 900–1,150 m. An additional 11 forest species were recorded at 450–900 m (Appendix 1). Of these, significant new distributional data or range extensions are presented for 27 species. Most (16) were expected to occur on the Colombian slope of Cerro Tacarcuna, given that they have been recorded on the Panamanian slope of Cerro Tacarcuna and adjacent Cerro Malí. However, seven species represent range extensions from other Darién massifs in Panama, the Serranía de San Blas, the Chocó lowlands, Serranía de Abibe and / or Western and Central Andes of Colombia. Another four records correspond to rare and poorly known species in Colombia, but previously known from Cerro Tacarcuna.

BARRED HAWK *Morphnarchus princeps*
Adult perched at 4–5 m near the campsite on 8 August 2010. Previously known from the Darién highlands on Cerro Pirre at 1,100–1,500 m (Wetmore 1965, Robbins *et al*. 1985) and Cerro Tacarcuna at 1,380 m (Sullivan *et al.* 2009), as well as locally on the Pacific slope of the West Andes from Quibdó south and in other Andean cordilleras (Hilty & Brown 1986).

RUSSET-CROWNED QUAIL-DOVE *Geotrygon goldmani*
Recorded by voice almost daily at 1,150 m near our campsite, but apparently in smaller numbers or was less vocal than Violaceous Quail-Dove *G. violacea*. Known from several localities in Panama, at Cerro Sapo (900 m), Cerro Pirre (900–1,600 m), Cerro Malí and Cerro Tacarcuna (1,450 m; Wetmore 1968), and recently the Serranía de Jungurudó (Angehr *et al*. 2004) and Cerro Piña (*c*.1,100 m; Miller *et al*. 2011). In Colombia, it is known only from the headwaters of the río Cutí on Cerro Tacarcuna and the río Juradó (*c*.90 m) in Chocó (Hilty & Brown 1986).

VIOLACEOUS QUAIL-DOVE *Geotrygon violacea*
One at 1,100 m vocalising from a 2 m-high perch. Known from the lower northern slopes of Cerro Pirre above Cana and El Real, and Cerro Sapo in Panama (Wetmore 1968, Ridgely & Gwynne 1989). In Colombia, known from a few records in the northern Central Andes and Serranía de San Lucas (Hilty & Brown 1986, Salaman *et al*. 2002).

BARE-SHANKED SCREECH-OWL *Megascops clarkii*
A pair recorded daily at 1,150 m (XC184848). Both individuals were perched in the midstorey (4–6 m) inside forest and usually started to vocalise at dusk. An adult male sound-recorded and collected (ICN 38187, XC184846) near the base camp on 7 August 2010. Hilty & Brown (1986) mentioned a specimen for Colombia, however, ours seems to representing the first confirmed Colombian record (Participantes de la Alianza Biomap 2006). The individual showed moderate body, wing and tail moult, with relatively large testes (left 5.0 × 1.7 mm). Stomach contents included parts of beetles (Coleoptera). *M. clarkii* is rare in Panama, with records at 1,080–2,100 m (Ridgely & Gwynne 1989). Previously known from Cerro Malí

(1,450 m), the crest of the Cerro Tacarcuna ridge (1,460 m, in both Panama and Colombia) and Cerro Pirre (Wetmore 1968) where it is rare to uncommon at 1,000–1,500 m (Robbins *et al*. 1985).

VIOLET-CAPPED HUMMINGBIRD *Goldmania violiceps*
Two females mist-netted at 1,150 m, of which one was collected (ICN 38179; Fig. 2). The specimen had an enlarged ovary (5.4 × 2.4 mm) with follicles averaging 0.3 mm, and no moult. Another four specimens (ICN 37362–65) were collected by JMR-O in November 2008 at the río Tanelita (*c*.1,400 m), *c*.4 km west of our study site (Fig. 1). Known from the foothills (600–1,200 m) of central and eastern Panama to Cerro Malí and Cerro Tacarcuna (Wetmore 1968, Ridgely & Gwynne 1989). In Colombia, previously known only from the headwaters of the río Cutí at Cerro Tacarcuna near the Panama border (Hilty & Brown 1986).

RED-HEADED BARBET *Eubucco bourcierii*
A male following a mixed-species canopy flock near our campsite. Although known in Panama from the foothills and highands of Cerro Pirre, Cerro Quía, Cerro Malí and Cerro Tacarcurna (*c*.550–1,450 m; Wetmore 1968, Robbins *et al*. 1985, Ridgely & Gwynne 1989), this is the first confirmed record in the Colombian Darién (Hilty & Brown 1986). Recorded in the northern Central Andes, Serranía de San Lucas and the adjacent West Andes (Salaman *et al*. 2002, McMullan & Donegan 2014).

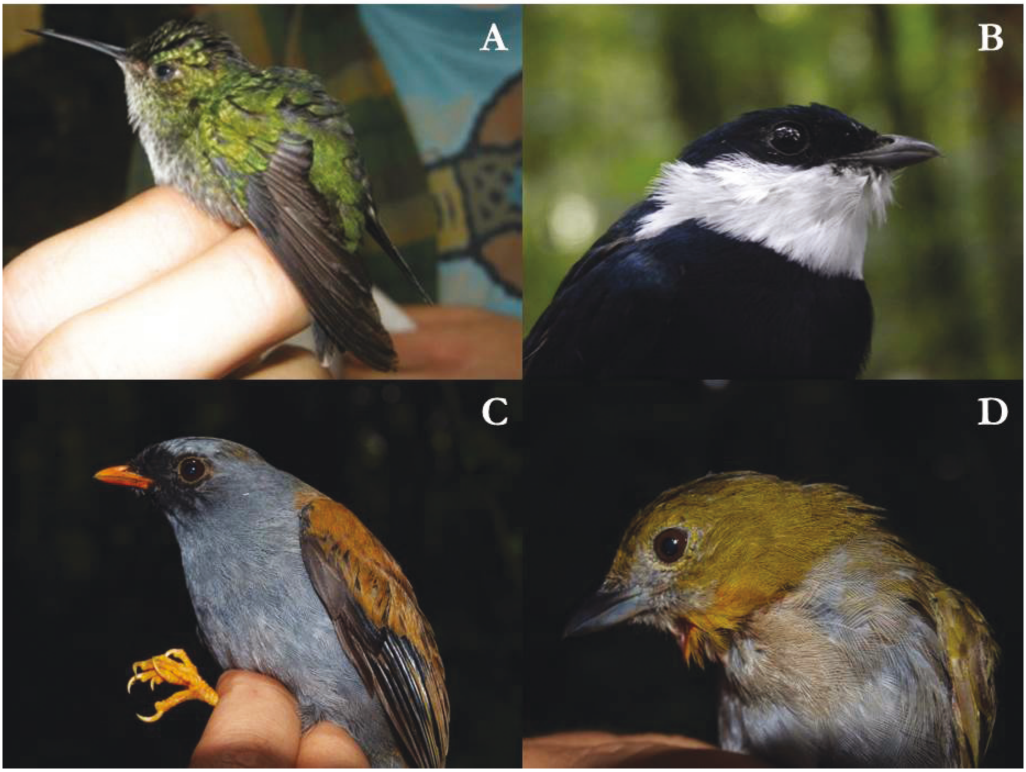

Figure 2. Restricted-range and noteworthy birds from Cerro Tacarcuna: (A) female Violet-capped Hummingbird *Goldmania violiceps*; (B) male White-bibbed Manakin *Corapipo leucorrhoa*; (C) Varied Solitaire *Myadestes coloratus*; (D) Yellow-throated Chlorospingus *Chlorospingus flavigularis* (J. M. Ruiz-Ovalle)

Figure 3. Ventral, dorsal and lateral views of adult male *Scytalopus* tapaculos in the Darién highlands and adjacent Western Andes of Colombia, from left to right: Nariño Tapaculo *S. vicinior* (ICN 31208), Alto de Pisones, 8 km north-west Jegüadas, municipality Mistrató, dpto. Risaralda, 6 June 1992; Tacarcuna Tapaculo *S. panamensis* (ICN 38181), Cuchilla del Lago, Corregimiento de Balboa, municipality Unguía, dpto. Chocó, 6 August 2010; and Chocó Tapaculo *S. chocoensis* (ICN 37480), Reserva Natural Río Ñambí, Corregimiento de Altaquer, municipality Barbacoas, dpto. Nariño, 11 October 2009 (J. E. Avendaño)

ZELEDON'S ANTBIRD *Myrmeciza zeledoni*

Observed in mixed-species flocks following army-ant swarms with Spot-crowned Antvireo *Dysithamnus puncticeps*, Chestnut-backed Antbird *Poliocrania exsul*, White-cheeked Antbird *Gymnopithys leucaspis*, Ocellated Antbird *Phaenostictus mcleannani* and Black-headed Antthrush *Formicarius nigricapillus*. On 6 August 2010, an adult male was foraging with a juvenile displaying a yellow gape, suggesting that it had fledged recently. Previously known in Panama on Cerro Pirre (*c*.500–1,400 m) and Cerro Tacarcuna (*c*.730–1,040 m; Robbins *et al*. 1985, Ridgely & Gwynne 1989, Donegan 2012a), with records in Colombia from adjacent ridges such as Serranía de Abibe (1,500 m), Serranía de Baudó (*c*.900 m), the Chocó lowlands and adjacent West Andes (Hilty & Brown 1986, Donegan 2012a, Olacerigui *et al*. 2016).

TACARCUNA TAPACULO *Scytalopus panamensis*

Common in dense understory of primary forest at 1,040–1,150 m, where at least five vocal individuals were heard daily along a 300 m-transect. Individuals were often seen foraging alone, mainly at ground level up to *c*.0.5 m. Most were on slightly steep and humid slopes, close to fallen trunks and thickets. An adult male was attracted by its own song using playback, and collected, on 6 August 2010 (ICN 38181; Fig. 3). This is the first specimen for Colombia, although Pearman's (1993) sound recordings published in Krabbe & Schulenberg (1997) mean that it is already treated as a confirmed species for the country. It had small gonads (left testis 1.8 × 0.4 mm), but a fresh incubation patch and symmetric moult on its second primary. Our observations and previous studies on the Serranía del Darién suggest that *S. panamensis* is the only tapaculo on the Cerro Tacarcuna–Malí and adjacent slopes at 1,050–1,500 m (Wetmore 1972, Hilty & Brown 1986). We did not find Chocó Tapaculo *S. chocoensis*, which has been recorded on Cerro Pirre (1,350–1,475 m) and Serranía de Jungurudó (*c*.800–1,000 m) (Angehr *et al*. 2004), and along the Pacific foothills of the West Andes in Colombia and Ecuador, where it occurs at 250–1,250 m (Krabbe & Schulenberg 1997). The vocalisations of *S. panamensis* are hardly known (Krabbe & Schulenberg 1997, 2003). We recorded one call type (XC184857–58, 184860) and its primary song (XC184864, 184866, 184868). The call of *S. panamensis* is a rapid series of 5–6 up-downstrokes, lasting 0.6–0.8 seconds, and repeated every 1.5–4.0 seconds for up to 13.0 seconds, with a max. frequency of 4.0 ± 0.4 kHz (mean and standard deviation, respectively; Fig. 4A). Krabbe & Schulenberg (1997) suggested some similarity between the calls of *S. panamensis* and *S. chocoensis* (Fig. 4B) based on a tape-recording by Pearman (1993). However, the call of *S.*

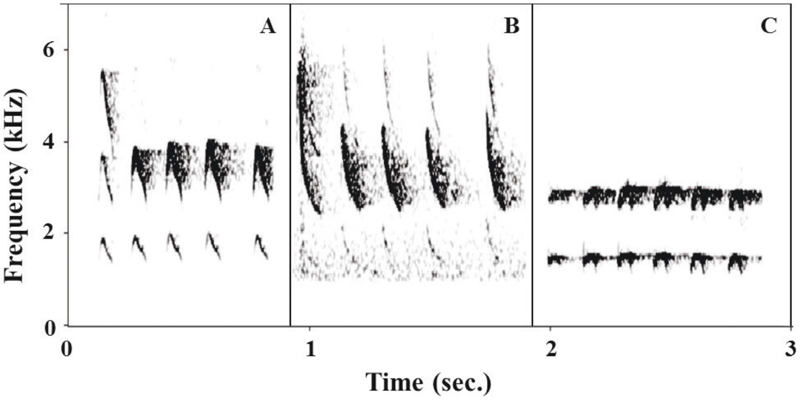

Figure 4. Calls of *Scytalopus* tapaculos from Darién and the West Andes of Colombia: (A) Tacarcuna Tapaculo *S. panamensis* natural vocalisation (XC184857, J. E. Avendaño), Cuchilla del Lago, Corregimiento de Balboa, municipality Unguía, dpto. Chocó; (B) Chocó Tapaculo *S. chocoensis* natural vocalisation (BSA 11716; Álvarez *et al*. 2007), Tambito Nature Reserve, municipality El Tambo, dpto. Cauca, Colombia; (C) Nariño Tapaculo *S. vicinior* natural vocalisation (BSA 30763; Álvarez *et al*. 2007), Las Nubes Nature Reserve, municipality Jericó, dpto. Antioquia. Note the distinctive frequency bandwidth and note shape in *S. panamensis*. Spectrograms were created using Syrinx v2.6h (Burt 2006) applying the same parameters except for adjusting brightness to improve note resolution.

chocoensis has a mean higher variation in frequency (the difference between max. and min. frequencies; 2.0 ± 0.4 kHz, *n* = 6 vs. 1.2 ± 0.2 kHz, *n* = 3) and comprises sharp notes. The call of Nariño Tapaculo *S. vicinior* (Fig. 4C) also differs from that of *S. panamensis* in its mean lower max. frequency (3.2 ± 0.2 kHz, *n* = 7) and note shape (e.g. length of stroke 'tails'). A natural song of *S. panamensis* was a 16.2-second series of 0.05–0.06-second up-downstroke notes delivered at 3.7 notes / second on average. During playback responses (Fig. 5A), the song was prolonged and faster (lasting 18.8–32.1 seconds and delivered at 4.5–4.7 notes / second, *n* = 2). Note shape is similar to that of some individuals of *S. chocoensis* (Fig. 5B–C), and differs from the downstroke notes of *S. vicinior* (Fig. 5D). It also is faster paced than *S. chocoensis*, but slower than *S. vicinior*. Thus, *S. panamensis* appears to be a vocal and morphologically distinct taxon (Fig. 3), although it overlaps in some vocal attributes with *S. vicinior* and *S. chocoensis*, suggesting that they are closely related. Vocalisations referenced herein are detailed in Appendix 2.

BLACK-HEADED ANTTHRUSH *Formicarius nigricapillus*

Solitary individuals, or with mixed-species flocks, observed following army-ant swarms above 1,000 m at our study site. Previously recorded in the Chocó lowlands at Nuquí north to Bahía Solano (D. Calderón-F. pers. comm.), the río Jurubidá on the Pacific coast (Haffer 1967a, Hilty & Brown 1986) and Serranía de Abibe (D. Calderón-F. pers. comm.). The closest locality in Panama is Nusagandi, western San Blas (Ridgely & Gwynne 1989). Black-faced Antthrush *F. analis* inhabits the Urabá region and the Atrato Valley, but the contact zone between the two species was not previously known. Haffer (1967a) suggested the Alto del Buey area (1,810 m), in the Serranía del Baudó, as a possible contact zone. However, one record of Black-faced Antthrush on the Panamanian slope of Cerro Tacarcuna at 1,180 m (Sullivan *et al*. 2009), plus an aural record below 800 m at our study site suggests possible contact in the foothills of Cerro Tacarcuna, where the species possibly replace each other elevationally. Specimen collection will be necessary to test Haffer's hypothesis that the two species may hybridise in a narrow zone within this region.

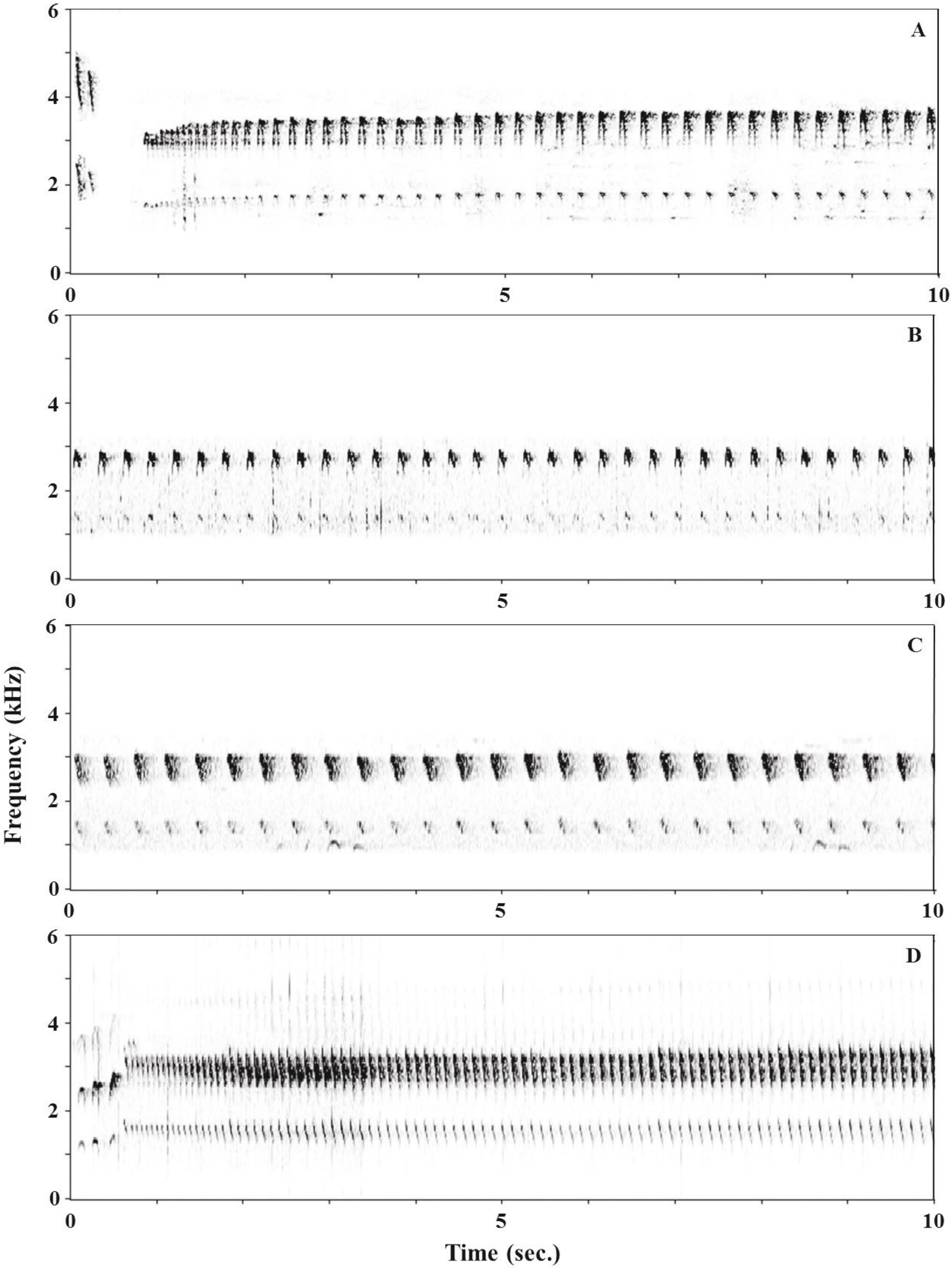

Figure 5. Primary songs of *Scytalopus* tapaculos from Darién and the Andes of Colombia and Ecuador: (A) Tacarcuna Tapaculo *S. panamensis* song after playback (XC184866, J. E. Avendaño), Cuchilla del Lago, Corregimiento de Balboa, municipality Unguía, dpto. Chocó, Colombia; (B) Chocó Tapaculo *S. chocoensis* natural song (LNS 40016, T. S. Schulenberg), El Placer, prov. Esmeraldas, Ecuador; (C) *S. chocoensis* natural song (XC60678, K. Allaire), Cerro Pirre, prov. Darién, Panama; (D) Nariño Tapaculo *S. vicinior* natural song (BSA 15041, Álvarez *et al*. 2007), Corregimiento de Bitaco, municipality La Cumbre, dpto. Valle del Cauca, Colombia.

SPOTTED WOODCREEPER *Xiphorhynchus erythropygius*
Singles or pairs observed daily in mixed-species flocks in the midstorey and subcanopy. Previously known in Panama from Cerro Pirre (1,580 m), Cerro Malí (1,450 m; Robbins *et al*. 1985, Wetmore 1972) and Serranía de Majé (*c*.1,150–1,250; Angehr & Christian 2000). Adjacent records in Colombia are from the Serranía del Baudó, ríos Atrato and Truandó (Participantes de la Alianza Biomap 2006), the Pacific slope of the West Andes (Hilty & Brown 1986), Serranía de Abibe (Olaciregui *et al*. 2016), the northern Central Andes (Cuervo *et al*. 2008b) and Serranía de San Lucas (Donegan 2012b).

BROWN-BILLED SCYTHEBILL *Campylorhamphus pusillus*
Observed and tape-recorded (XC184875) at 1,150 m. Previously known in Panama from Cerro Tacarcuna (1,250 m), Cerro Malí (1,460 m), Cerro Pirre (1,000–1,600 m), Cerro Quía (760 m; Wetmore 1972, Robbins *et al*. 1985) and Serranía de Majé (*c*.1,150–1,250 m; Angehr & Christian 2000). In Colombia, known from Serranía de Abibe (Olaciregui *et al*. 2016), the northern West Andes at Frontino (Hilty & Brown 1986) and the northern Central Andes (Cuervo *et al*. 2008b). Our record confirms the species' presence on the Colombian slope of the Tacarcuna massif.

SCALY-THROATED FOLIAGE-GLEANER *Anabacerthia variegaticeps*
Singles in canopy-level mixed-species flocks also containing Red-faced Spinetail *Cranioleuca erythrops* and several *Tangara* species. The nearest localities to our record are Cerro Flores in eastern Chiriquí, Panama (Ridgely & Gwynne 1989), and near Carmen de Atrato, Antioquia (D. Calderón-F. pers. comm.) and Serranía de Abibe at the northern extremity of the West Andes, Colombia (Olaciregui *et al*. 2016). Taxonomy of Middle and South American populations of this species is controversial, with some authors suggesting that *A. v. temporalis* of the West Andes should be recognised as a separate species from Middle American populations (Remsen *et al*. 2016). Specimens from the Darién will be crucial to resolve species limits in the group.

BEAUTIFUL TREERUNNER *Margarornis bellulus*
One on 5 August at 1,025 m, investigating vine tangles and epiphytes 4–5 m above ground. Its presence in Colombia was based on mainly habitat continuity and geographic proximity to known localities in adjacent Panama, e.g. Cerro Pirre (1,375–1,580 m), Cerro Malí (*c*.1,400–1,450 m) and Cerro Quía (900 m; Wetmore 1972, Ridgely & Gwynne 1989, Renjifo *et al*. 2002) and recently Serranía de Majé (1,150 m; Angehr *et al*. 2004). However, a 'Bogotá' specimen was recently reported (Verhelst-Montenegro 2015). Our record extends the species' range to Cerro Tacarcuna, and is the first confirmed locality for Colombia and South America (Remsen *et al*. 2016).

RUFOUS-BROWED TYRANNULET *Phylloscartes superciliaris*
Singles or pairs were seen within mixed-species flocks in the canopy. Previously known on the Panamanian side of Cerro Tacarcuna and Cerro Malí (1,060 m; Wetmore 1972, Ridgely & Gwynne 1989). In Colombia, this little-known bird has been recorded recently in the West Andes (Cuervo *et al*. 2003), Central Andes (Salaman *et al*. 2002, Cuervo *et al*. 2008a) and Serranía de San Lucas (Donegan 2012b), with historical records in the East Andes in dpto. Santander (Hilty & Brown 1986).

PIRATIC FLYCATCHER *Legatus leucophaius*

Heard at 450 m beside the río Bonito. This record extends the species' range to the Gulf of Urabá, closing a gap between Cerro Pirre (600–1,000 m; Robbins *et al.* 1985), the Chocó lowlands and northern West Andes (Hilty & Brown 1986, Olaciregui *et al*. 2016). This is a widespread species of lowland habitats that has possibly colonised the region due to the expansion of modified environments.

WHITE-BIBBED MANAKIN *Corapipo leucorrhoa*

Very common at 1,150 m where six males and four females were mist-netted (Fig. 2). Panamanian records are available from Cerro Pirre, Cerro Tacarcuna (575–1,250 m) and Cerro Quía (730 m) (Wetmore 1972, Ridgely & Gwynne 1989). The nearest localities in Colombia are the humid northern slopes of the West and Central Andes (Hilty & Brown 1986). The very similar White-ruffed Manakin *C. altera*, which also occurs on Cerro Tacarcuna and Cerro Malí, is present on adjacent mountains such as Cerro Pirre (1,050–1,375 m), Cerro Sapo, Jaqué (Wetmore 1972) and Serranía de Jungurudó (Angehr *et al*. 2004), as well as probably south along the Pacific coast to Serranía del Baudó (Hilty & Brown 1986). These taxa appear to be separate species based on their sympatry in this region, which is probably related to differences in the structure of their outer primaries, which may affect their respective displays (Ridgely & Gwynne 1989, Remsen *et al*. 2016). However, lek behaviour has been studied only in *C. altera* (Hilty & Brown 1986, Remsen *et al.* 2016).

OCHRACEOUS WREN *Troglodytes ochraceus*

Singles or pairs seen daily, foraging in the midstorey and subcanopy (3–4 m) at 1,150 m. They searched for insects within dense mosses and bromeliads, climbing vine tangles and inspecting dead, curled leaves trapped by vines, as part of mixed-species flocks formed mainly of tanagers and furnariids, although the wren also foraged and vocalised in the absence of other species. Two song types (XC184885, 184890) and one call (XC184888) were sound-recorded. These match recordings from Chiriquí province in Panama (Fig. 6) and clearly differ from vocalisations of Mountain Wren *T. solstitialis*, which occurs in the West Andes. This wren ranges from Costa Rica to Panama where it has been recorded on Serranía de Majé (*c*.1,150–1,490 m; Angehr & Christian 2000), Cerro Pirre (*c*.1,000–1,580 m; Robbins *et al*. 1985), and Cerro Malí (*c*.1,460 m; Wetmore *et al*. 1984). Our records confirm the species' presence in Colombia and South America for the first time (Donegan *et al*. 2016, Remsen *et al*. 2016).

VARIED SOLITAIRE *Myadestes coloratus*

One to three were heard daily and sound-recorded (XC184927). Singles took fruits from shrubs in the understorey at 1,100–1,150 m. An adult male was collected on 7 August 2010 (ICN 38185; Fig. 2); stomach contents included fruit and insect parts. The specimen had abundant moult in the body, wing and tail, and small testes (left 3.0 × 1.1 mm), which agrees with an immature collected on 29 August 1996 on Serranía de Majé (Angehr & Christian 2000). An additional specimen (ICN 37358) was collected by JMR-O in November 2008 at río Tanelita (*c*.1,400 m), on the east slope of Cerro Tacarcuna. This Darién highland endemic is known in Panama from Cerro Pirre (1,500–1,600 m), Alturas de Nique, Cerro Quía (900 m), Cerro Malí (1,400–1,600) (Ridgely & Gwynne 1989, Wetmore *et al*. 1984), and recently from Serranía de Majé (*c*.1,250–1,500 m) and Serranía de Jungurudó (*c*.1,000 m) (Angehr & Christian 2000, Angehr *et al*. 2004). Despite its broad distribution across isolated massifs in the Darién, and the apparent lack of phenotypic differentiation (Angehr & Christian 2000,

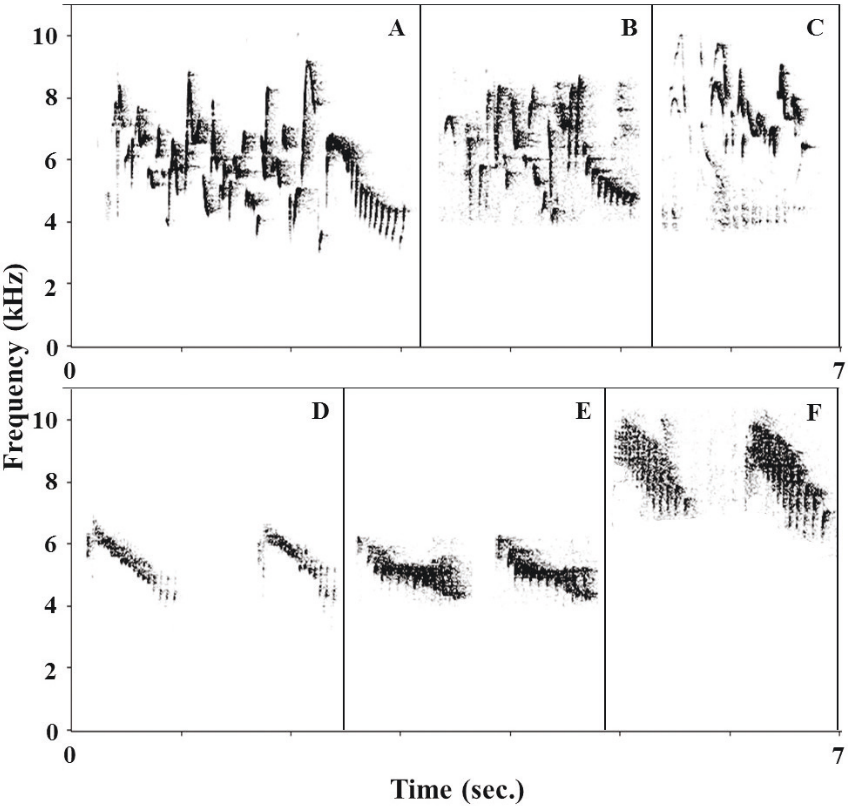

Figure 6. Songs and calls of *Troglodytes* wrens from Panama, Darién and the Andes of Colombia: (A) Ochraceous Wren *T. ochraceus* natural song (XC31764, A. Spencer), 2,300 m, Sendero Los Quetzales, prov. Chiriquí, Panama; (B) *T. ochraceus* natural song (XC184885, J. E. Avendaño), Cuchilla del Lago, Corregimiento de Balboa, municipality Unguía, dpto. Chocó, Colombia; (C) Mountain Wren *T. solstitialis* natural song (BSA 22470, Álvarez *et al*. 2007), Ibanasca, Corregimiento de Juntas, municipality Ibagué, dpto. Tolima, Colombia; (D) *T. ochraceus* natural call (XC94688, W. Adsett), 1,650 m, Cerro Colorado, Comarca Ngobe–Bugle, Panama; (E) *T. ochraceus* natural call (XC184888, J. E. Avendaño), Cuchilla del Lago, Corregimiento de Balboa, municipality Unguía, dpto. Chocó, Colombia; (F) *T. solstitialis* natural call (XC27530, N. Krabbe), Páramo de Frontino, dpto. Antioquia, Colombia.

Angehr *et al*. 2004), populations of *M. coloratus* on Cerro Pirre are genetically distinct from those of Serranía de Majé (Miller *et al*. 2007).

BLACK-AND-YELLOW TANAGER *Chrysothlypis chrysomelas*

A common and noisy member of mixed-species flocks at the campsite (1,150 m) where a family group of 3–4 individuals was seen daily, foraging in the canopy and feeding at least one fledgling. This group was often accompanied by other tanagers, *Chlorospingus* species, woodcreepers and tyrant flycatchers. Previously known in Panama on Cerro Tacarcuna (625–725 m), Cerro Sapo, Cerro Pirre, Cerro Quía (Ridgely & Gwynne 1989, Wetmore *et al*. 1984) and Serranía de Majé (Angehr & Christian 2000). Our records represent the third confirmed records for Colombia and South America. Previous records from Colombia are a female specimen (ICN 37353) collected by JMR-O in November 2008 at río Tanelita (*c*.1,400 m), on the east slope of Cerro Tacarcuna (Ruiz-Ovalle *et al.* 2014); and one observed by J. Zuluaga-Bonilla on Cerro La Nevera (*c*.475–775 m), *c*.37 km north-west of our study site in January 2007 (Fig. 1).

BLUE-AND-GOLD TANAGER *Bangsia arcaei*

Singles recorded daily at 1,150 m accompanying midstorey and subcanopy mixed-species flocks comprising insectivores and frugivores such as Slaty Antwren *Myrmotherula schisticolor*, Red-faced Spinetail, Olivaceous Woodcreeper *Sittasomus griseicapillus*, Ochraceous Wren, Speckled Tanager *Tangara guttata*, Bay-headed Tanager *T. gyrola*, Silver-throated Tanager *T. icterocephala*, Black-and-yellow Tanager, Yellow-throated Chlorospingus *Chlorospingus flavigularis* and Tawny-capped Euphonia *Euphonia anneae*. This species ranges across the Caribbean slope from Costa Rica (400–1,200 m; Stiles & Skutch 1989) south to Panama (300–1,050 m), with the easternmost record from Cerro Brewster in western San Blas (Ridgely & Gwynne 1989, Wetmore *et al*. 1984). Our record represents the second for Colombia, following two specimens (ICN 37361, 37372) collected in November 2008 between 1,250 m and 1,400 m at río Tanelita, on the east slope of Cerro Tacarcuna (Ruiz-Ovalle *et al*. 2014).

BAY-HEADED TANAGER *Tangara gyrola*

Common in canopy-level mixed-species flocks. Previously known in Panama from Serranía de Majé, Cerro Sapo, Cerro Pirre, Cerro Malí, Cerro Tacarcuna (Wetmore *et al*. 1984) and Serranía de Jungurudó (Angehr *et al*. 2004). This record extends the species' range to the Colombian slope of the Cerro Tacarcuna. Adjacent records from Colombia are from Serranía de Abibe, the West Andes and northern Central Andes (Hilty & Brown 1986, Cuervo *et al*. 2008b, Olaciregui *et al*. 2016).

EMERALD TANAGER *Tangara florida*

Rare in canopy-level mixed-species flocks. Previously known in Panama from Cerro Pirre (Robbins *et al*. 1985), Cerro Tacarcuna (Wetmore *et al*. 1984) and Serranía de Jungurudó (Angehr *et al*. 2004); and Serranía de Abibe, south to El Carmen de Atrato in the West Andes of Colombia (Sullivan *et al*. 2009, Olaciregui *et al*. 2016). The Pacific slope subspecies is *T. f. auriceps*, whereas the nominate occurs on the Caribbean slope from Costa Rica to Panama. We were unable to collect specimens, consequently the subspecies in the Serranía del Darién is unknown, although it has been considered to represent an intermediate population (Haffer 1967a, Wetmore *et al*. 1984).

TACARCUNA CHLOROSPINGUS *Chlorospingus tacarcunae*

One of the commonest constituents of mixed-species flocks in the midstorey and subcanopy at 1,150 m (XC184939), moving in family groups of 4–5 individuals and frequently accompanied by Yellow-throated Chlorospingus *C. flavigularis*, which was more abundant. Both *Chlorospingus* appear to be core members of mixed-species flocks mainly comprised by Spotted Woodcreeper, Red-faced Spinetail, Green Manakin *Cryptopipo holochlora*, Scale-crested Pygmy Tyrant *Lophotriccus pileatus*, Rufous-browed Tyrannulet, Ochraceous Wren, Slate-throated Redstart *Myioborus miniatus*, Silver-throated Tanager, Black-and-yellow Tanager and Tawny-capped Euphonia. During our field work, a fledging was observed begging for food from an adult on 6 August 2010, which is consistent with previous observations of nest construction and immatures that suggest the species' breeding season probably begins in late February and extends to the middle of the year (Wetmore *et al*. 1984, Angehr & Christian 2000, Christian 2001). JMR-O collected one (ICN 37351) in November 2008 at 1,400 m at río Tanelita, on the east slope of Cerro Tacarcuna, representing the first specimen for Colombia. These are the only confirmed records in Colombia (*cf*. Donegan *et al*. 2011) of a species whose presence in the country had been suggested based on Panamanian records from Cerro Tacarcuna (1,230–1,440 m) and Cerro Malí (1,410 m) (Wetmore *et al*. 1984, Hilty & Brown 1986, Ridgely & Gwynne 1989).

YELLOW-THROATED CHLOROSPINGUS *Chlorospingus flavigularis*
Observed regularly in mixed-species flocks with Tacarcuna Chlorospingus (see above). A fledgling was observed begging for food and an adult and juvenile mist-netted on 5 August 2010. The adult had brown irides and a buff breast (Fig. 2) matching descriptions of *C. f. hypophaeus*, which occurs in Bocas del Toro to Veraguas in Panama, in contrast to the grey eyes and breast of *C. f. marginatus* on the Pacific slope of the West Andes (Isler & Isler 1999). A specimen (ICN 37354), which also agrees with *C. f. hypophaeus*, was collected by JMR-O in November 2008 at 1,400 m on the río Tanelita, east slope of Cerro Tacarcuna. These records confirm this subspecies' presence on Cerro Tacarcuna and in Colombia for the first time. Its nearest locality is Cerro Brewster in western San Blas (Ridgely & Gwynne 1989). In Colombia the species occurs north to the upper río Sinú (Hilty & Brown 1986) and was recently recorded in Serranía de San Lucas (Donegan 2012b).

CHESNUT-CAPPED BRUSH FINCH *Arremon brunneinucha*
Fairly common in the understorey above 1,000 m. Previously recorded on most massifs on the Panamanian side, on Cerro Pirre, Cerro Quía (900 m), Cerro Tacarcuna, Cerro Malí (1,400 m) (Wetmore *et al.* 1984), Serranía de Majé and Serranía de Jungurudó (Angehr & Christian 2000, Angehr *et al*. 2004). Adjacent Colombian records are from the West Andes (Hilty & Brown 1986), the northern Central Andes (Cuervo *et al*. 2008b) and Serranía de San Lucas (Salaman *et al*. 2002).

SOOTY-FACED FINCH *Arremon crassirostris*
Status in Colombia and South America uncertain (Donegan *et al*. 2011, Remsen *et al*. 2016). Although we did not record the species, we report here two specimens collected in the foothills of Cerro Tacarcuna, at Alto Barrigonal, in June 1980. Both specimens, a male and female (IAvH-A 3164, 3174; Fig. 7) exhibit the conspicuous white malar stripe and yellow patch on the central underparts typical of the species. Based on these specimens, Rodríguez (1982) listed the species for Los Katíos National Park, as subsequently Hilty & Brown (1986) did for Colombia. On 1 December 2008 an unsexed specimen (ICN 37368) was collected by JMR-O & T. Walschburger at río Tanelita (1,408 m), on the east slope of Cerro Tacarcuna. These records remove any doubts concerning the species' presence in Colombia and South America (Remsen *et al*. 2016).

HEPATIC TANAGER *Piranga flava*
A male in a mixed-species canopy flock at the campsite. Panamanian records are from Darién province (Ridgely & Gwynne 1989), Serranía de Majé (Angehr & Christian 2000) and Cerro Pirre (Robbins *et al*. 1985). Nearest Colombian records are from the Pacific slope of the West Andes, in Serranía de Abibe south (Hilty & Brown 1986, Olaciregui *et al.* 2016).

Discussion

Despite field work during the last century, the Darién highland avifauna continues to be poorly known. Among the new distributional records here, ten relate to little-known and restricted-range species from the Darién highlands (Russet-crowned Quail-Dove, Bare-shanked Screech Owl, Violet-capped Hummingbird, Tacarcuna Tapaculo, Beautiful Treerunner, Ochraceous Wren, Varied Solitaire and Tacarcuna Chlorospingus) and foothills (Blue-and-gold and Black-and-yellow Tanagers), which represent 40% of the endemic species reported in the region (Fig. 8A). In addition, four species previously known from Panama were recorded for first time in the Darién highlands of Colombia. Two of these (Scaly-throated Foliage-gleaner and Ochraceous Wren) inhabit cloud forests of the West

Figure 7. Lateral views of specimens of Sooty-faced Finch *A. crassirostris* (A–B) collected on the Colombian slope of Cerro Tacarcuna, compared to a specimen of Olive Finch *A. castaneiceps* (C) from the West Andes of Colombia: (A) male IAvH-A 3164 and (B) female IAvH-A 3174, from Alto Barrigonal, dpto. Chocó, Colombia; (C) male IAvH-A 8315 from Reserva Natural Río Ñambí, municipality Barbacoas, dpto. Nariño, Colombia (S. Sierra)

Andes and the Chiriquí highlands, respectively, whereas the remaining species (Black-headed Antthrush and Yellow-throated Chlorospingus) occur in the foothills of adjacent ranges such as San Blas and Serranía del Baudó. These range extensions, plus another also presented here, are indicative of the poorly known avifauna of the region.

Our field work produced the first specimens of Bare-shanked Screech Owl, Violet-capped Hummingbird, Tacarcuna Tapaculo and Varied Solitaire for Colombia. Another eight records represented the first or second specimen records of subspecies endemic to the Darién highlands (e.g. *Phaethornis guy coruscans*, *Catharus f. fuscater*, *Basileuterus tristriatus tacarcunae*) and foothills (*Schiffornis veraepacis acrolophites*, *Chlorospingus flavigularis hypophaeus*). Clearly, the Darién requires further ornithological work to improve our taxonomic, geographic and temporal representation of several poorly known species in bird collections (Cuervo *et al*. 2008). Sound-recording also yielded the first record of Tacarcuna Tapaculo song, and documented the vocalisations on the Colombian side of endemic taxa such as Bare-shanked Screech Owl, Ochraceous Wren, Varied Solitaire and Tacarcuna Chlorospingus.

Our preliminary list includes 84 species from the cloud forest belt at 900–1,150 m. Although this inventory is probably far from complete, the combination of visual and aural observations, supplemented by sound-recordings and mist-netting enabled us to assemble a representative inventory swiftly. These complementary methodologies have been recommended as the most appropriate for rapid and efficient inventories of tropical forests (Parker 1991, Salaman & Donegan 1998, Stiles & Bohórquez 2000). More species will be added as further field work is conducted and higher elevations are explored in the Tacarcuna range. For example, Robbins *et al*. (1985) recorded 186 species on Cerro Pirre at 1,000–1,500 m, although species richness (244) was concentrated in the foothills (600–1,000 m).

Nearby lowland ecosystems are currently protected in Colombia within Los Katíos National Park, which covers 72,000 ha at 50–600 m, with 412 bird species recorded (Rodríguez 1982). This park is connected to Darién National Park in Panama (579,000 ha). Highland and lowland Darién endemics are of conservation concern, especially because eight species are currently considered nationally threatened in Colombia (Renjifo *et al*. 2002). Moreover, the elevational distribution of most Darién endemics is concentrated above 600 m, based on the midpoints of each species' range (Fig. 8A). Exceptions are the rare Spiny-faced Antshrike *Xenornis setifrons* and Yellow-green Tyrannulet *Phylloscartes flavovirens*. For highland species, 15 of 16 reach their lower elevational limit at or above 600 m, whereas foothill species attain their upper elevational limit above 600 m. This elevational distribution shown by the endemic avifauna of Darién draws attention to the need to protect the highlands, especially in Colombia where Los Katíos National Park covers forests only below 600 m.

To conserve species endemic to the Darién highlands, one option would be to extend Los Katíos National Park through the Serranía del Darién to the Panamanian border. However, we suggest that a conservation unit, besides including the Serranía del Darién, also should cover the better-preserved Central and Pacific serranías of Pirre and Jungurudó, and the adjacent massifs (Cerro Quía, Alturas de Nique, Altos de Aspavé, Cordillera de Juradó). These mountains harbour six endemics not known to occur in the Serranía del Darién, which has ten endemics confined to it (Fig. 8A). Protecting this area will also conserve high endemism at the subspecies level as the Darién avifauna includes at least 24 endemic subspecies, 21 of them mainly found above 600 m (Fig. 8B). However, endemism could be higher because this region is the contact zone for three well-differentiated lowland faunas, the Pacific coast, Darién and Sinú regions (Haffer 1959), and several endemic subspecies

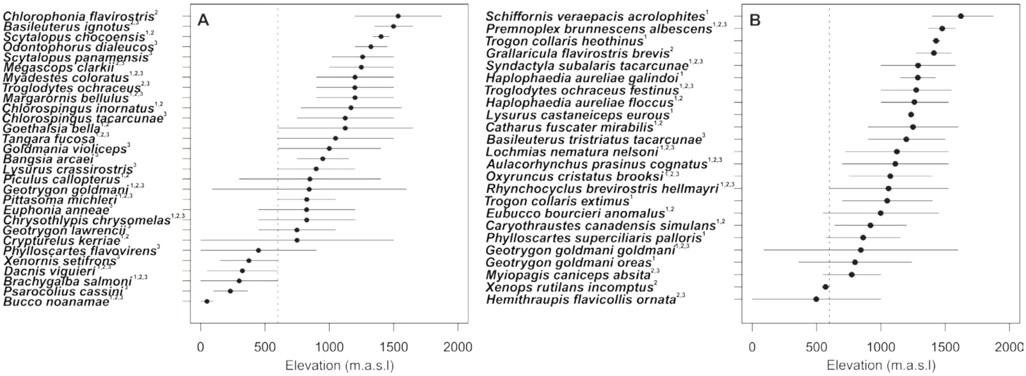

Figure 8. Elevational and geographic distribution of 29 restricted-range species (A) and 24 restricted-range subspecies (B) in the Darién lowlands and highlands. Taxa ranges (horizontal bars) are ordered according to their elevational midpoint (black dots). Note that most taxon ranges are concentrated above 600 m as shown by the vertical dashed line. Taxon names are followed by one or more superscripts indicating geographic distribution. ^{1}Pacific: Serranía de Jungurudó, Cerro Sapo and Serranía de Majé. ^{2}Central: Serranía de Pirré, Cerro Quía and Alturas de Nique. ^{3}Caribbean: Serranía del Darién including Cerro Tacarcuna and Cerro Malí. Data from Wetmore (1965, 1968, 1973), Wetmore *et al*. (1984), Robbins *et al*. (1985), Hilty & Brown (1986), Ridgely & Gwynne (1989), Pearman (1993), Angehr & Christian (2000) and Angehr *et al*. (2004).

could potentially represent distinctive species (e.g. *Basileuterus tristriatus tacarcunae*; Donegan 2014). Finally, protection of the Darién could guarantee the conservation of one of the major congregatory zones for Nearctic migratory birds in the Americas (Bayly *et al*. 2014).

Currently, the main threats to the Darién lowland and highland ecosystems are habitat loss and fragmentation due to cattle ranching and large-scale agriculture (e.g. banana plantations), which have accelerated in recent decades in Panama and Colombia (Rangel-C. 2004, Angehr *et al*. 2004, Sánchez-Cuervo & Aide 2013). Moreover, critical habitats for threatened species such as the Darién highlands could be especially vulnerable to climate change because of the small ranges and isolation of their endemic populations. Indeed, most of those species whose 'climate envelope' is projected to disappear in Colombia due to climate change are confined to isolated mountains or regions with well-defined geographic barriers. For example, in the Darién, optimal habitat for Violet-capped Hummingbird is projected to disappear by 2050 (Velásquez-Tibatá *et al*. 2013). We hope that this study will encourage further biological exploration of the region, and more importantly, draw the attention of environmental agencies and local conservationists as to the need for effective monitoring and implementation of conservation action in the Colombian Darién. Establishing a large bi-national protected area would represent a significant step towards the preservation of one of the most interesting biogeographical regions in the Neotropics (Haffer 1970).

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References:

Álvarez, M., Caro, V., Laverde, O. & Cuervo, A. M. 2007. *Guía sonora de los Andes colombianos*. CDs. Instituto Alexander von Humboldt, Bogotá & Cornell Lab of Ornithology, Ithaca, NY.

Angehr, G. R. & Christian D. G. 2000. An ornithological survey of the Serranía de Majé, an isolated mountain range in eastern Panama. *Bull. Brit. Orn. Cl*. 120: 173–178.

Angehr, G. R., Christian, D. G. & Aparicio, K. M. 2004. A survey of the Serranía de Jungurudó, an important isolated mountain range in eastern Panama. *Bull. Brit. Orn. Cl*. 124: 51–62.

Arbeláez-Cortés, E. 2013. Knowledge of Colombian biodiversity: published and indexed. *Biodiver. Conserv*. 22: 2875–2906.

Bayly, N. J., Cárdenas-Ortiz, L., Rubio, M. & Gómez, C. 2014. Migration of raptors, swallows and other diurnal migratory birds through the Darien of Colombia. *Orn. Neotrop*. 25: 63–71.

BirdLife International. 2014. Endemic Bird Area factsheet: Darién lowlands and highlands. www.birdlife.org (accessed 27 April 2014).

Bran-Castrillón, C., Gaviria-Zapata, C. & Parra, J. L. 2014. Avifauna de los hábitats de la desembocadura del Río Atrato (Turbo, Antioquia). *Orn. Colombiana* 14: 94–111.

Burt, J. 2006. Syrinx version 2.6h. www.syrinxpc.com.

Cadena, C. D. & Cuervo, A. M. 2010. Molecules, ecology, morphology, and songs in concert: how many species is *Arremon torquatus* (Aves: Emberizidae)? *Biol. J. Linn. Soc*. 99: 152–176.

Cuervo, A. M., Cadena, C. D. & Parra, J. L. 2006. Seguir colectando aves en Colombia es imprescindible: un llamado a fortalecer las colecciones ornitológicas. *Orn. Colombiana* 4: 51–58.

Cuervo, A. M., Stiles, F. G., Cadena, C. D., Toro, J. L. & Londoño G. A. 2003. New and noteworthy bird records from the northern sector of the Western Andes of Colombia. *Bull. Brit. Orn. Cl*. 123: 7–24.

Cuervo, A. M., Pulgarín, P. C. & Calderón-F., D. 2008a. New distributional bird data from the Cordillera Central of the Colombian Andes, with implications for the biogeography of northwestern South America. *Condor* 110: 526–537.

Cuervo, A. M., Pulgarín, P. C., Calderón-F., D., Ochoa-Quintero, J. M., Delgado-V., C. A., Palacio, A., Botero, J. M. & Múnera, W. A. 2008b. Avifauna of the northern Cordillera Central of the Andes, Colombia. *Orn. Neotrop*. 19: 495–515.

Chaparro-Herrera, S., Echeverry-Galvis, M. Á., Córdoba-Córdoba, S. & Sua-Becerra, A. 2013. Listado actualizado de las aves endémicas y casi-endémicas de Colombia. *Biota Colombiana* 14: 113–150.

Chapman, F. M. 1917. The distribution of bird-life in Colombia. *Bull. Amer. Mus. Nat. Hist*. 36: 1–729.

Christian, D. G. 2001. Nests and nesting behavior of some little known Panamanian birds. *Orn. Neotrop*. 12: 327–336.

Donegan, T. M. 2012a. Geographical variation in Immaculate Antbird *Myrmeciza immaculata*, with a new subspecies from the Central Andes of Colombia. *Bull. Brit. Orn. Cl*. 132: 3–40.

Donegan, T. M. 2012b. Range extensions and other notes on the birds and conservation of the Serranía de San Lucas, an isolated mountain range in northern Colombia. *Bull. Brit. Orn. Cl*. 132: 140–161.

Donegan, T. M. 2014. Geographical variation in morphology and voice of Three-striped Warbler *Basileuterus tristriatus*. *Bull. Brit. Orn. Cl*. 134: 79–109.

Donegan, T. M., Quevedo, A., McMullan, M. & Salaman, P. 2011. Revision of the status of bird species occurring or reported in Colombia 2011. *Conserv. Colombiana* 15: 4–21.

Donegan, T., Verhelst, J. C., Ellery, T., Cortés-Herrera, O. & Salaman, P. 2016. Revision of the status of bird species occurring or reported in Colombia 2016 and assessment of BirdLife International's new parrot taxonomy. *Conserv. Colombiana* 24: 12–36.

Gutiérrez-Pinto, N., Cuervo, A. M., Miranda, J., Pérez-Emán, J. L., Brumfield, R. T. & Cadena, C. D. 2012. Non-monophyly and deep genetic differentiation across low-elevation barriers in a Neotropical montane bird (*Basileuterus tristriatus*; Aves, Parulidae). *Mol. Phyl. & Evol*. 64: 156–165.

Haffer, J. 1959. Notas sobre las aves de la región de Urabá. *Lozania (Acta Zool. Colombiana)* 12: 1–49.

Haffer, J. 1967a. Speciation in Colombian forest birds west of the Andes. *Amer. Mus. Novit*. 2294: 1–57.

Haffer, J. 1967b. Some allopatric species pairs of birds in north-western Colombia. *Auk* 84: 343–365.

Haffer, J. 1970. Geologic-climatic history and zoogeographic significance of the Uraba region in northwestern Colombia. *Caldasia* 10: 603–636.

Hernández-Camacho, J. I., Hurtado, A., Ortiz, R. & Walschburger, T. 1992. Origen y distribución de la biota suramericana y colombiana. Pp. 55–104 *in* Halffter, G. (ed.) *La diversidad biológica de Iberoamérica I*. *Acta Zool. Mexicana* vol. especial.

Hilty, S. L. & Brown, W. L. 1986. *A guide to the birds of Colombia*. Princeton Univ. Press.

Hruska, J. P., Dzielski, S. A., Van Doren, B. M. & Hite, J. M. 2016. Notes on the avifauna of the northern Serranía de Pirre, Panama. *Bull. Brit. Orn. Cl*. 136: 224–242.

Isler, M. L. & Isler, P. R. 1999. *The tanagers: natural history, distribution, and identification*. Second edn. Smithsonian Institution Press, Washington DC.

Krabbe, N. & Schulenberg, T. S. 1997. Species limits and natural history of *Scytalopus* tapaculos (Rhinocryptidae), with descriptions of the Ecuadorian taxa, including three new species. Pp. 47–88 *in* Remsen, J. V. (ed.) *Studies in Neotropical ornithology honoring Ted Parker*. *Orn. Monogr*. 48.

Krabbe, N. & Schulenberg, T. S. 2003. Family Rhinocryptidae (tapaculos). Pp. 748–787 *in* del Hoyo, J., Elliott, A. & Christie, D. A. (eds.) *Handbook of the birds of the world*, vol 8. Lynx Edicions, Barcelona.

Mayr, E. 1964. Inferences concerning the Tertiary American bird faunas. *Proc. Natl. Acad. Sci. USA* 51: 280–288.

Miller, M. J., Bermingham, E. & Ricklefs, R. E. 2007. Historical biogeography of the New World solitaires (*Myadestes* spp.). *Auk* 124: 868–885.

Miller, M. J., Weir, J. T., Angehr, G. R., Guitton, P. & Bermingham, E. 2011. An ornithological survey of Piñas Bay, a site on the Pacific coast of Darién Province, Panama. *Bol. Soc. Antioqueña Orn*. 20: 29–38.

Olaciregui, C., Quevedo, A., González, F. & Barrera, L. F. 2016. Range extensions and noteworthy records of birds from the Serranía de Abibe, north-west Colombia. *Bull. Brit. Orn. Cl*. 136: 234–262.

Participantes de la Alianza Biomap. 2006. Base de datos Darwin: proyecto BioMap base de datos de distribución de la avifauna Colombiana. www.biomap.net (accessed 20 December 2013).

Parker, T. A. 1991. On the use of tape recorders in avifaunal surveys. *Auk* 108: 443–444.

Pearman, M. 1993. Some range extensions and five species new to Colombia, with notes on some scarce or little known species. *Bull. Brit. Orn. Cl*. 113: 66–75.

Poveda-M., I. C., Rojas, C. A., Rudas-Lleras, A. & Rangel-C., J. O. 2004. El Chocó biogeográfico: ambiente físico. Pp. 1–22 *in* Rangel-C., J. O. (ed.) *Colombia diversidad biótica*, vol. 4. Unibiblos, Bogotá.

Rangel-C., J. O. 2004. Amenazas a la biota y a los ecosistemas del Chocó biogeográfico. Pp. 841–866 *in* Rangel-C., J. O. (ed.) *Colombia diversidad biótica*, vol. 4. Unibiblos, Bogotá.

Remsen, J. V., Areta, J. I., Cadena, C. D., Jaramillo, A., Nores, M., Pacheco, J. F., Pérez-Emán, J., Robbins, M. B., Stiles, F. G., Stotz, D. F. & Zimmer, K. J. 2016. A classification of the bird species of South America. www.museum.lsu.edu/~Remsen/SACCBaseline.html.

Renjifo, L. M., Franco-Maya, A. M., Amaya-Espinel, J. D., Kattan, G. H. & López-Lanús, B. 2002. *Libro rojo de aves de Colombia*. Instituto de Investigación de Recursos Biológicos Alexander von Humboldt & Ministerio del Medio Ambiente, Bogotá.

Ridgely, R. S. & Gwynne, J. A. 1989. *A guide to the birds of Panama with Costa Rica, Nicaragua and Honduras*. Second edn. Princeton Univ. Press.
Robbins, M. B., Parker, T. A. & Allen, S. A. 1985. The avifauna of Cerro Pirre, Darién, Panama. Pp. 198–232 *in* Buckley, P. A., Foster, M. S., Morton, E. S., Ridgely, R. S. & Buckley, F. G. (eds.) *Neotropical ornithology*. *Orn. Monogr*. 36.
Rodríguez, J. V. 1982. *Aves del Parque Nacional Natural Los Katíos*. INDERENA, Bogotá.
Ruiz-Ovalle, J. M., Hurtado-Guerra, A. & Zuluaga-Bonilla, J. 2014. *Bangsia arcaei* y *Chrysothlypis chrysomelas* (Aves: Thraupidae): nuevas especies para Suramérica y la Serranía del Darién en Colombia. *Orn. Colombiana* 14: 130–135.
Salaman, P. & Donegan, T. M. 1998. *Colombia '98 expedition to Serranía de los Churumbelos: preliminary report*. Colombian EBA Project Rep. Ser. 1.
Salaman, P., Donegan, T. M. & Cuervo, A. M. 2002. New distributional bird records from Serranía de San Lucas and adjacent Central cordillera of Colombia. *Bull. Brit. Orn. Cl*. 122: 285–303.
Sánchez-Cuervo, A. M. & Aide, T. M. 2013. Identifying hotspots of deforestation and reforestation in Colombia (2001–2010): implications for protected areas. *Ecosphere* 4: 1–21.
Simpson, G. G. 1950. History of the fauna of Latin America. *Amer. Sci*. 38: 361–389.
Smith, B. T. & Klicka, J. 2010. The profound influence of the Late Pliocene Panamanian uplift on the exchange, diversification, and distribution of New World birds. *Ecography* 33: 333–342.
Stattersfield, A. J., Crosby, M. J., Long, A. J. & Wege, D. C. 1998. *Endemic Bird Areas of the world: priorities for biodiversity conservation*. BirdLife International, Cambridge, UK.
Stiles, F. G. & Bohórquez, C. I. 2000. Evaluando el estado de la biodiversidad: el caso de la avifauna de la Serranía de las Quinchas, Boyacá, Colombia. *Caldasia* 22: 61–92.
Stiles, F. G. & Skutch, A. F. 1989. *A guide to the birds of Costa Rica*. Cornell Univ. Press, Ithaca, NY.
Sullivan, B. L., Wood, C. L., Iliff, M. J., Bonney, R. E., Fink, D. & Kelling, S. 2009. eBird: a citizen-based bird observation network in the biological sciences. *Biol. Conserv*. 142: 2282–2292.
Velásquez-Tibatá, J., Salaman, P. & Graham, C. H. 2013. Effects of climate change on species distribution, community structure, and conservation of birds in protected areas in Colombia. *Reg. Environ. Change* 13: 235–248.
Verhelst-Montenegro, J. C. 2015. New subspecies records from Colombia based on museum specimens. *Not. Orn. Columbianae* 1: 1–8.
Wetmore, A. 1965. *The birds of the Republic of Panama*, pt. 1. Smithsonian Institution, Washington DC.
Wetmore, A. 1968. *The birds of the Republic of Panama*, pt. 2. Smithsonian Institution, Washington DC.
Wetmore, A. 1972. *The birds of the Republic of Panama*, pt. 3. Smithsonian Institution, Washington DC.
Wetmore, A. & Galindo, P. 1972. Additions to birds recorded in Panama. *Proc. Biol. Soc. Wash*. 85: 309–312.
Wetmore, A., Pasquier, R. F. & Olson, S. L. 1984. *The birds of the Republic of Panama*, pt. 4. Smithsonian Institution Press, Washington DC.

Addresses: Luis Miguel Renjifo, Depto. de Ecología y Territorio, Facultad de Estudios Ambientales y Rurales, Pontificia Universidad Javeriana, Bogotá, Colombia, e-mail: lmrenjifo@javeriana.edu.co. Augusto Repizo, Profesional de Apoyo, Parque Nacional Natural El Tuparro, Vichada, Colombia, e-mail: augustorepizo@gmail.com. Juan Miguel Ruiz-Ovalle, Fundación Ecotrópico, Calle 127C #5A-74, Bogotá, Colombia, e-mail: susande.juanmiguel@gmail.com. Sergio Ocampo, Fundación Ecológica Gabriel Arango Restrepo, Calle 66 #23B-10, Manizales, Colombia, e-mail: sergiofundegar@gmail.com. Jorge Enrique Avendaño, Laboratorio de Biología Evolutiva de Vertebrados, Universidad de los Andes, Bogotá, Colombia, e-mail: jorgeavec@gmail.com

Appendix 1

Birds recorded in the Cerro Tacarcuna foothills (450–900 m) and at our study site (900–1,150 m) on 4–7 August 2010. Types of record: V = visual, A = aural, T = sound-recorded, C = trapped, S = specimen. No. of individuals captured in parenthesis. *Colombian near-endemic (Chaparro *et al*. 2013). Taxonomy follows Remsen *et al*. (2016).

Family / English name	Scientific name	Foothills	Study site
TINAMIDAE			
Little Tinamou	*Crypturellus soui*	A	
CRACIDAE			
Crested Guan	*Penelope purpurascens*		V
Great Curassow	*Crax rubra*	V	
ODONTOPHORIDAE			
Tawny-faced Quail	*Rhynchortyx cinctus*	S	

Family / English name	Scientific name	Foothills	Study site
ACCIPITRIDAE			
Barred Hawk	*Morphnarchus princeps*		VA
Black Hawk-Eagle	*Spizaetus tyrannus*	A	A
White Hawk	*Pseudastur* cf. *albicollis*		V
COLUMBIDAE			
Short-billed Pigeon	*Patagioenas nigrirostris*		A
Russet-crowned Quail-Dove	*Geotrygon goldmani**		AT
Violaceous Quail-Dove	*Geotrygon violacea*		VAT
CUCULIDAE			
Squirrel Cuckoo	*Piaya cayana*		A
STRIGIDAE			
Bare-shanked Screech Owl	*Megascops clarkii*		VATS
Mottled Owl	*Ciccaba virgata*		AT
TROCHILIDAE			
White-tipped Sicklebill	*Eutoxeres aquila*		C (1)
Stripe-throated Hermit	*Phaethornis striigularis*		V
Green Hermit	*Phaethornis guy*		VCS (3)
Tooth-billed Hummingbird	*Androdon aequatorialis**		C (3)
Greenish Puffleg	*Haplophaedia aureliae**		CS (2)
Green-crowned Brilliant	*Heliodoxa jacula*		C (1)
Bronze-tailed Plumeleteer	*Chalybura urochrysia*		C (2)
Crowned Woodnymph	*Thalurania colombica*	V	
Rufous-tailed Hummingbird	*Amazilia tzacatl*		
Violet-capped Hummingbird	*Goldmania violiceps*		CS (2)
TROGONIDAE			
Slaty-tailed Trogon	*Trogon massena*		AT
Black-throated Trogon	*Trogon rufus*		A
MOMOTIDAE			
Broad-billed Motmot	*Electron platyrhynchum*	VA	
Rufous-capped Motmot	*Baryphthengus ruficapillus*		A
CAPITONIDAE			
Red-headed Barbet	*Eubucco bourcieri*		V
RAMPHASTIDAE			
Black-mandibled Toucan	*Ramphastos ambiguus*		VAT
Emerald Toucanet	*Aulacorhynchus prasinus*		VA
PICIDAE			
Olivaceus Piculet	*Picumnus olivaceus*	A	
Smoky-brown Woodpecker	*Picoides fumigatus*		VA
PSITTACIDAE			
Saffron-headed Parrot	*Pyrilia pyrilia**		A
Mealy Parrot	*Amazona farinosa*		AT
Red-and-green Macaw	*Ara chloropterus*		A
THAMNOPHILIDAE			
Black-crowned Antshrike	*Thamnophilus atrinucha*	A	VA
Plain Antvireo	*Dysithamnus mentalis*		VATC (1)
Spot-crowned Antvireo	*Dysithamnus puncticeps*		V
Slaty Antwren	*Myrmotherula schisticolor*		VA
Chestnut-backed Antbird	*Poliocrania exsul*		VA
Zeledon's Antbird	*Hafferia zeledoni*		VAT
Bicoloured Antbird	*Gymnopithys bicolor*		VAT (1)

Family / English name	Scientific name	Foothills	Study site
Ocellated Antbird	*Phaenostictus mcleannani*		VAT
RHINOCRYPTIDAE			
Tacarcuna Tapaculo	*Scytalopus panamensis**		VATS
FORMICARIIDAE			
Black-faced Antthrush	*Formicarius analis*	A	
Black-headed Antthrush	*Formicarius nigricapillus*		VAT
FURNARIIDAE			
Olivaceus Woodcreeper	*Sittasomus griseicapillus*		V
Long-tailed Woodcreeper	*Deconychura longicauda*		V
Plain-brown Woodcreeper	*Dendrocincla fuliginosa*		VAT
Wedge-billed Woodcreeper	*Glyphorhynchus spirurus*		VC (1)
Spotted Woodcreeper	*Xiphorhynchus erythropygius*		VAT
Brown-billed Scythebill	*Campylorhamphus pusillus*		VAT
Streak-headed Woodcreeper	*Lepidocolaptes souleyetii*		A
Plain Xenops	*Xenops minutus*		V
Scaly-throated Foliage-gleaner	*Anabacerthia variegaticeps*		V
Lineated Foliage-gleaner	*Syndactyla subalaris*		VAT
Beautiful Treerunner	*Margarornis bellulus**		V
Red-faced Spinetail	*Cranioleuca erythrops*		V
TYRANNIDAE			
Rufous-browed Tyrannulet	*Phylloscartes superciliaris*		V
Olive-striped Flycatcher	*Mionectes olivaceus*		AC (3)
Scale-crested Pygmy Tyrant	*Lophotriccus pileatus*		VAT
White-throated Spadebill	*Platyrinchus mystaceus*		VATC (1)
Smoke-coloured Pewee	*Contopus fumigatus*		A
Tufted Flycatcher	*Mitrephanes phaeocercus*		VATS
Dusky-capped Flycatcher	*Myiarchus tuberculifer*		AV
PIPRIDAE			
White-bibbed Manakin	*Corapipo leucorrhoa**		VAC (10)
Green Manakin	*Cryptopipo holochlora*		VC (1)
TITYRIDAE			
Russet-winged Schiffornis	*Schiffornis stenorhyncha**		VACS (1)
TROGLODYTIDAE			
Scaly-breasted Wren	*Microcerculus marginatus*	A	A
Ochraceous Wren	*Troglodytes ochraceus*		VAT
White-headed Wren	*Campylorhynchus albobrunneus**		VA
Sooty-headed Wren	*Pheugopedius spadix**		VA
White-breasted Wood Wren	*Henicorhina leucosticta*	A	
Grey-breasted Wood Wren	*Henicorhina leucophrys*		VAT
Song Wren	*Cyphorhinus* cf. *phaeocephalus*		A
TURDIDAE			
Varied Solitaire	*Myadestes coloratus*		VATCS
Slaty-backed Nightingale-Thrush	*Catharus fuscater*		VACS
THRAUPIDAE			
Blue-and-gold Tanager	*Bangsia arcaei*		V
Speckled Tanager	*Tangara guttata*		V
Green-naped Tanager	*Tangara fucosa*		V
Bay-headed Tanager	*Tangara gyrola*		V
Emerald Tanager	*Tangara florida*		V
Silver-throated Tanager	*Tangara icterocephala*		V

Family / English name	Scientific name	Foothills	Study site
Black-and-yellow Tanager	*Chrysothlypis chrysomelas*		V
Bananaquit	*Coereba flaveola*		C (1)
EMBERIZIDAE			
Tacarcuna Chlorospingus	*Chlorospingus tacarcunae*		VAT
Yellow-throated Chlorospingus	*Chlorospingus flavigularis*		VATC (2)
Chestnut-capped Brush Finch	*Arremon brunneinucha*		VAC (3)
CARDINALIDAE			
Hepatic Tanager	*Piranga flava*		V
PARULIDAE			
Buff-rumped Warbler	*Myiothlypis fulvicauda*		VA
Three-striped Warbler	*Basileuterus tristriatus*		VACS (1)
Slate-throated Redstart	*Myioborus miniatus*		VAT
FRINGILLIDAE			
Tawny-capped Euphonia	*Euphonia anneae*		VAC (1)

Appendix 2

Sound-recordings used in vocal comparisons of *Scytalopus* tapaculos (see text). Sound collections: BSA = Colección de Sonidos Animales of Instituto Alexander von Humboldt; XC = xeno-canto.org; ML = Macaulay Library. Songs: Tacarcuna Tapaculo *S. panamensis* (XC184864, XC184866, XC184868); Chocó Tapaculo *S. chocoensis* (XC119663, XC85493, XC60679); Nariño Tapaculo *S. vicinior* (XC58880, XC82587, BSA 15041). Calls: *S. panamensis* (XC184857-58, XC184860); *S. chocoensis* (ML 25770, ML 25839, ML 25843, ML 60326, XC8049, BSA 11716); *S. vicinior* (XC51263, XC89856, XC102391, XC121576, XC128511, BSA 19470, BSA 30763).

First record of River Warbler *Locustella fluviatilis* and additional records for Plain Nightjar *Caprimulgus inornatus* and Lesser Masked Weaver *Ploceus intermedius* in Djibouti

by Carla J. Dove, Jacob Saucier, James F. Whatton, Brian Schmidt &
Houssein R. Roble

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Summary.—Three species, River Warbler *Locustella fluviatilis*, Lesser Masked Weaver *Ploceus intermedius* and Plain Nightjar *Caprimulgus inornatus*, are further documented as occurring in Djibouti, via observation and specimen records obtained during two brief surveys in 2014 and 2016. Two specimens of River Warbler represent the first records in Djibouti. These reports underscore the need for more detailed and long-term surveys of this ornithologically under-studied part of the Horn of Africa.

During spring 2014 and winter 2016, brief biodiversity surveys were conducted in and near Camp Lemonnier (11º32′30″N, 43º10′00″ E; 5 m elevation), a US Navy Expeditionary Base in Djibouti (north-east Africa), to provide preliminary biological inventories for this military installation. The surveys involved visual observations and specimen documentation for avian, herpetological, mammalian, botanical and entomological species found on the military installation and the vicinity immediately surrounding Camp Lemonnier, including the shoreline of the Gulf of Aden and the old French airfield at Chabelley. We obtained >1,200 vertebrates representing approximately 126 species of birds, 24 species of amphibians and reptiles and 18 species of mammals. We also collected approximately 49 species of plants and thousands of insects. All of the specimens are housed in the Smithsonian Institution's National Museum of Natural History in Washington, DC. Here we describe new and noteworthy avian species documented during these brief surveys.

New country record

RIVER WARBLER *Locustella fluviatilis*
Breeds in central and eastern Europe east to south-west Siberia and north-west Kazakhstan, and is a long-distance migrant to the southern African countries of Zambia, Malawi, Botswana, Zimbabwe, Mozambique and northern South Africa, probably migrating via narrow routes through the Middle East and north-east Africa (Pearson 2006). Ash & Atkins (2009) and Redman *et al*. (2011) listed it as an uncommon passage migrant in the central Rift Valley in September–November and April–May but did not list any records for Djibouti. Two specimens were obtained during the spring 2014 survey. On 11 May 2014, a male (USNM 647876) was found dead on the ground under a small sapling between the armoury building and the religious chapel at Camp Lemonnier. The specimen was prepared as a skeleton (feathers saved), body mass was 20.7 g, the stomach was empty, and heavy fat was noted at the time of preparation. The testes were minute (2 × 1 mm). Another specimen (USNM 647822) was collected on 13 May 2014 on the beach near Camp Lemonnier. Prior to collection, the bird was observed skulking inside a small isolated bush among the sand dunes. This specimen was prepared as a study skin with a partial skeleton. The bird was

a male (testes; left = 3 × 2 mm, right = 2 × 2 mm) and the skull was 25% pneumatized. The preparation notes record extremely heavy fat and body mass was 24.6 g.

We did not record any additional River Warblers during the winter 2016 (1 February–2 March 2016) survey. DNA barcoding (Hebert *et al*. 2003) was conducted on USNM 647822 and the resulting mtCOI sequence was run through a BLAST search (December 2015). The top hit was GQ482077 (*L. fluviatilis*), with 100% pairwise identity and 99.7% query coverage. The mtCOI sequences for this specimen is deposited in GenBank (KU722455). Morphologically, the streaked breast and pale-tipped undertail-coverts separate this species from the closely related Savi's Warbler *L. luscinioides* which has been recently recorded in Djibouti (Hering *et al*. 2015). Heavy fat reserves and reduced testes size on both specimens indicates that these individuals were migrants.

Additional country records

PLAIN NIGHTJAR *Caprimulgus inornatus*

Currently listed as vagrant with just two observations from Djibouti (Redman *et al*. 2011) but we recorded the species as fairly common in 2014. It is considered a fairly common resident in north-west Somalia, with one record much further east (Ash & Miskell 1998) and is a rather uncommon breeding resident in parts of Ethiopia (Ash & Atkins 2009). We observed this species sporadically on the coastal side of Camp Lemonnier on several different occasions, and once during a visit to Decan Wildlife Refuge. The species was common in the Ambouli River drainage and at Chabelley, an old French airfield *c*.24 km south-east of Camp Lemonnier (Arta Region). A specimen (USNM 647811) was collected from a group of Plain Nightjars that were crowding around a spotlight at night, on 7 May 2014, near Chabelley (11º31′10″N, 43º10′00″E; 85 m elevation). The specimen was prepared as a study skin with a partial skeleton saved. Body mass was 52.9 g with light fat and no moult. The skull was completely pneumatized, no bursa was present and the testes measured 9 × 8 mm (left) and 10 × 8 mm (right). Stomach contents comprised large insects including five grasshoppers (Orthoptera) and a wasp (Hymenoptera). Another sighting of the species, on 2 October 2015, from Camp Lemonnier is available on eBird (P. Kaestner; http://ebird.org/ebird/view/checklist/S25404346). We did not observe the species during the 2016 survey. The specimen record and our observations indicate that the species may be more seasonally common than thought, with more detailed observations being warranted to further document the status of Plain Nightjar in Djibouti.

LESSER MASKED WEAVER *Ploceus intermedius*

A male was mist-netted on 5 February 2016 at Camp Lemonnier in an area of *Prosopis* sp. scrub near the east end of the installation. The bird (USNM 653247) was photographed (Fig. 1) and prepared as a skeleton (feathers saved) because it represents the only osteological specimen of the species in the Smithsonian collection. The testes were not enlarged (2 × 1 mm), there was no bursa present, the skull was 100% pneumatized, and the bird was undergoing head and scattered body moult. Body mass was 18.1 g and trace fat was observed. Ash & Atkins (2009) indicated that the species is known (without evidence of breeding) from a cluster of tetrads close to the Djibouti border in Ethiopia, from where its distribution extends mainly along the Rift Valley. Ash & Miskell (1998) reported a breeding pair in northern Somalia among a colony of Rüppell's Weavers *P. galbula* and our bird was mist-netted with several of the last-named species. We only observed this single individual during the winter survey of 2016. Prior to this, Welch & Welch (1992) observed a male building a nest on 26 March 1987 near the small town of Às ʿEla (11º00′N, 42º06′E;

Figure 1. Male Lesser Masked Weaver *Ploceus intermedius*, Camp Lemonnier, Djibouti, 5 February 2016, in the late stages of definitive moult showing orange-chestnut hindcrown feathers and diagnostic creamy-white eye (Carla J. Dove)

255 m elevation) in far southern Dikhil Region (132 km south-west of Djibouti City near the border with Ethiopia) and Laurent (1990) reported three nests on 28 December 1989 at the same location. Ours is the first specimen record of Lesser Masked Weaver for Djibouti, and is morphologically consistent with nominate *P. i. intermedius* in having an orange-chestnut hindcrown and yellow nape (Fig. 1).

The date of collection (5 February) and the fact the bird was an adult (skull ossified) male moulting from non-breeding (eclipse) into breeding (nuptial) plumage may shed light on the status of the species in Djibouti. In most dimorphic Ploceidae, the male does not moult into breeding plumage until at least two years of age at which point they alternate between breeding and non-breeding plumages (Fry & Keith 2004). One of the males (USNM 247367) in the Smithsonian's collection from Sadi Malk (near modern-day Awash, Ethiopia, *c.*450 km south-west of Camp Lemonnier) was collected on 31 January 1912, during the Child's Frick Expedition, by Edgar Mearns and exhibits less advanced adult plumage on the head and throat than our specimen.

The species is presumed resident where it occurs, and details of movements away from breeding areas are not well described. The greatest recorded distance travelled by a ringed individual was 74 km in South Africa (Craig 2010). Craig (2010) considered the species to be a wet-season visitor to South Sudan (rainy season mainly May–October), but given the distance it is unlikely that our specimen was headed there. In Ethiopia it is a locally very common breeding resident (Ash & Atkins 2009).

Unless it is discovered to be a longer distance migrant in the future, this specimen further documents this species presence in or very near Djibouti and underscores the need to better document the movements and breeding status of Lesser Masked Weaver.

Our surveys of Camp Lemonnier in 2014 and 2016 were very brief and represent only two short seasonal snapshots of the area's biodiversity. However, our observations indicate that the area is under-studied and in need of additional surveys over longer time periods to more completely document the biodiversity of Djibouti. Given the rapid growth of this region in the Horn of Africa for military and commerce purposes, detailed biodiversity surveys should be a priority before critical conservation areas are designated for development.

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References:

Ash, J. S & Atkins, J. D. 2009. *Birds of Ethiopia and Eritrea*. Christopher Helm, London.

Ash, J. S. & Miskell, J. E. 1998. *Birds of Somalia*. Pica Press, Robertsbridge.

Craig, A. 2010. Lesser Masked Weaver (*Ploceus intermedius*). Pp. 161–162 *in* del Hoyo, J., Elliott, A. & Christie, D. A. (eds.) *Handbook of the birds of the world*, vol. 15. Lynx Edicions, Barcelona.

Fry, C. H. & Keith, S. (eds.) 2004. *The birds of Africa*, vol. 7. Christopher Helm, London.

Hebert, P. D. N., Cywinska, A., Ball, S. L. & deWaard. J. R. 2003. Biological identifications through DNA barcodes. *Proc. Roy. Soc. Lond. B: Biol. Sci*. 270: 313–321.

Hering, J., Hering, H. & Rayaleh, H. A. 2015. First records for Djibouti of Hottentot Teal *Anas hottentota*, Yellow Bittern *Ixobrychus sinensis*, Savi's Warbler *Locustella luscinioides* and Mangrove Reed Warbler *Acrocephalus scirpaceus avicenniae*. *Bull. Afr. Bird Cl*. 22: 78–82.

Laurent, A. 1990. Catalogue commentè des oiseaux de Djibouti. Unpubl. ms. Djibouti Office Nat. Tourisme.

Pearson, D. J. 2006. River Warbler *Locustella fluviatilis*. P. 614 *in* del Hoyo, J., Elliott, A. & Christie, D. A. (eds.) *Handbook of the birds of the world*, vol. 11. Lynx Edicions, Barcelona.

Redman, N., Stevenson, T. & Fanshawe, J. 2011. *Birds of the Horn of Africa*. Second edn. Christopher Helm, London.

Welch, G. R. & Welch, H. J. 1992. *Djibouti III – migrant raptor count*. Privately published.

Addresses: Carla J. Dove, Smithsonian Institution, Division of Birds, NHB E-600, MRC 116, P.O. Box 37012, Washington, DC 20013, USA, e-mail: dovec@si.edu. Jacob Saucier, Smithsonian Institution, Division of Birds, NHB E-607a, MRC 116, P.O. Box 37012, Washington, DC 20013, USA, e-mail: saucierj@si.edu. James F. Whatton, Smithsonian Institution, Division of Birds, NHB E-601, MRC 116, P.O. Box 37012, Washington, DC 20013, USA, e-mail: whattonj@si.edu. Brian Schmidt, Smithsonian Institution, Division of Birds, NHB E-605, MRC 116, P.O. Box 37012, Washington, DC 20013, e-mail: schmidtb@si.edu. Houssein R. Roble, Environment and Sustainable Development Ministry of Housing, Urban Planning and Environment, BP 2091, Republic of Djibouti, Africa, e-mail: housseinrirach@yahoo.fr

Dr William H. James 1852–76: medical doctor and naturalist

by Graham R. Fulton

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Summary.—Dr William Hughes James (1852–76), commonly known as Dr James, was an American citizen, originally from Virginia, USA. He travelled with William Macleay's *Chevert* Expedition to New Guinea in 1875, assuming dual roles as the ship's surgeon and as a collector / taxidermist. The expedition collected in northern Queensland, the Torres Strait Islands and New Guinea. At the conclusion of the expedition Dr James returned to New Guinea and continued collecting, and while doing so he was murdered by natives. While many of his specimens were never recorded against his name, at least 99 birds, three mammals and some invertebrates were. They are now in the Natural History Museum, Tring, and the Macleay Museum, Univ. of Sydney. Very little has ever been published about Dr James despite his participation in an important and historic international expedition. This paper presents what is known based on published and unpublished sources.

Dr W. H. James was an American medical doctor who turned his hand to collecting natural history specimens. His full name of William Hughes James and his year of birth were sourced via his archive at the Univ. of Virginia Library (Anon. 2016). He was commonly and affectionately known simply as Dr James. Born in Loudon County, Virginia (Anon. 1877a) he studied medicine at Baltimore for a year before pecuniary difficulties necessitated he join his uncle's medical practice to receive further training[1]. His collecting career lasted from 28 May 1875 to 23 August 1876—one year, two months and 26 days[2] (Anon. 1876a). He was speared and killed while on a boat in Hall Sound, adjacent to Yule Island, New Guinea, on 23 August 1876 (Anon. 1876a,b). He was evidently a young man with a thirst for travel and adventure: travelling first from east to west across the USA before venturing to Australia and then to New Guinea. His short-lived career as a naturalist / collector was conducted on the fringe of the known world, where he penetrated into the unknown—an occupation fraught with inherent dangers and alas his life was taken too soon.

USA

Dr James travelled to Nevada in the western USA from his home in Virginia, before he travelled to Australia and New Guinea. Information about Dr James' life on the west coast of the USA (Nevada and San Francisco) came to light after his death. His death brought a cluster of newspaper reports of varying veracity. For example, *The Pioche Weekly Record* stated that he was 'seeking for gold diggings' when 'eaten by cannibals' (Anon. 1877b); *The Iola Register* published that he 'was with an exploring party from Melbourne' and devoured on 'becoming separated' (Anon. 1877c); while a headline in the *Sacramento Daily Union* had adopted Dr James as a local, 'A San Franciscan … sacrificed and devoured by the cannibals' (Anon. 1877d). The most informative newspaper article providing his movements on the west coast of the USA was published in the *Staunton Spectator*, based in his home state of Virginia. It was in the form of a letter from the Attorney-General of Nevada, Mr John R. Kittrell, to Miss Mary Baldwin (Anon. 1877e). Miss Baldwin was the principal of the Augusta Female Seminary, later renamed the Mary Baldwin College (and now the Mary Baldwin University).

> 'Miss Baldwin:—Some three or four years ago there came to this State from Virginia—I forget what county—a young physician by the name of W. H. James… He was about twenty-two or twenty-three years of age… His first place of residence was at Pioche; thence he removed to White Pine county, and for a while worked at a mine or mill, performing manual labor at a mining camp known as Robinson District … Leaving there he went to Cherry Creek in the last named county and resumed the practice of his profession with but partial success, I believe, in the Fall of 1874 he became a candidate on the Democratic ticket for a seal in the Nevada Legislature to represent White Pine county in the Assembly. He failed to be elected, and shortly after the election, went to San Francisco, where I met him either in November or December of that year, 1874. He was then endeavoring to procure employment with the Pacific Mail Steamship Company as Surgeon or Assistant Surgeon to sail between the ports of San Francisco and Panama, and succeeded in the undertaking' (Anon. 1877e).

Dr James resided at Pioche, Nevada, where he ran a medical practice with a Dr Rogers, and their place of business was situated at Mrs Stanton's house on Main Street (Anon. 1877b). Dr James' move to White Pine County came about with the discovery of silver there. The 'silver rush' to that location is historically and colloquially known as White Pine Fever (Hall 1994). No record was found of his running for the state legislature in Nevada. Searches of Nevada legislators did not reveal his name and would not if he had not been elected. Regional newspapers also yielded no results, perhaps because they were reporting on a general election during the autumn of 1874.[3] Dr James secured a position aboard the steamer *MacGregor*, from San Francisco to Sydney, although he apparently lost this position during the voyage (see below).

Sydney, Australia

In Australia, Dr James is best known for his involvement with the *Chevert* Expedition staged in 1875 and the offshoot expeditions that followed. The *Chevert* Expedition was the first scientific expedition to leave Australia for foreign shores, and was headed and fully funded by Sir William Macleay, founder of the Macleay Museum (Fletcher 1929, Fulton 2012).

Dr James arrived in Sydney on 11 January 1875 from San Francisco aboard the RMS *MacGregor*, which had departed San Francisco on 8 December 1874 (Anon. 1875a). According to New South Wales government records, he arrived as a saloon passenger and not as crew (State Records Authority NSW 2016). Moore & Mullins (2012) stated that he had joined the *MacGregor* as ship's surgeon but during the passage he had lost this position and needed to turn to the US Consul in Sydney for assistance. On 14 March 1877, in a letter from the US Consul, J. H. Williams, to the Assistant Secretary of State, John L. Cadwalader, the Consul stated: 'Dr James arrived here some two years ago, as Surgeon of a Steamer from San Francisco, and was (in my opinion) dishonestly left here, without friends or means … He was a very promising young man and if he had lived would, without doubt have done credit to himself and to his country.'[4]

The US Consul referred him to Dr Alfred Roberts[4] who was a consulting surgeon at Sydney Infirmary and a trustee of the Australian Museum (Rutledge 1976). Roberts in turn encouraged him to apply to William Macleay. He was hired by William Macleay on 19 April 1875 as ship's surgeon for the *Chevert* Expedition to New Guinea.

Chevert Expedition (Australia–New Guinea)

William Macleay hired Dr James as ship's surgeon for the *Chevert* Expedition. The position had been advertised after his good friend Dr James Cox, medical doctor and conchologist, pulled out about a month before departure. On 19 April 1875, Macleay wrote in his private journal, 'I engaged a Surgeon for the *Chevert* today, a Dr James an American. He is strongly recommended by [Dr Alfred] Roberts and he seems to be willing to make himself useful to the expedition. He is to take lessons in skinning birds from Masters.'[2]

Dr James attended Elizabeth Bay House, where Macleay lived and the expedition was based, and took lessons in skinning birds from George Masters. His first lesson was on a heron, probably a White-faced Heron *Egretta novaehollandiae*, skinned on 21 April. Apparently the taxidermy went well and Dr James was invited to practice again two days later when he and Masters each prepared a Silver Gull *Chroicocephalus novaehollandiae*. At the same time Dr James attended his first patient of the expedition Jimmy Rotumah, one of the Polynesian seamen, and prescribed some medicine; Jimmy was suffering from scrofula, a tuberculosis infection of the lymph nodes in the neck.[5]

The *Chevert* Expedition got underway on 18 May 1875. The *Chevert* sailed from Port Jackson (Sydney Harbour) and began collecting at sea. The first reported animal collected by Dr James was an Allied Rock-wallaby *Petrogale assimilis*, on Palm Island, which became the species' holotype. He shared the honours with George Masters, Edward Spalding and an unnamed Nyawaygi guide (Fulton 2016a). Dr James quickly proved an eager and useful addition to the collecting parties as they cruised along the Great Barrier Reef stopping at various islands. His name crops up in Macleay's personal journal frequently, demonstrating his involvement with the expedition, for example: Dr James found a huge tumulus (incubation mound) of a megapode, Orange-footed Scrubfowl *Megapodius reinwardt*, on Palm Island; he shot a pitta on Fitzroy Island, although it was too damaged to be of any value and was discarded; at sea, near Cape Sidmouth, he attended patients of a passing steam launch the *Darwin* who were suffering from malaria[5].

Macleay was impressed by the diligence of the American, Dr James. He wrote the following account in his journal on 16 June 1875: 'The doctor went out early this morning to lie in wait for a pair of White-bellied Sea-Eagles [*Haliaeetus leucogaster*], which frequent the point of land opposite the ship and though not successful in getting a shot at them, he displayed an amount of patient determination and endurance much to be admired. He did not move from his hiding place till sunset.'[2]

This occurred at Cape Grenville where James had collected what we now recognise as a new subspecies of Grey Shrike Thrush *Colluricincla harmonica superciliosa*. Masters considered it a species in his 1875 publication naming it *Colluricincla superciliosa* and adding: 'one specimen only, of this very distinct species, was shot at Cape Grenville by Dr James' (Masters 1875). Macleay also wrote in his 1875 newspaper article that Dr James was 'a most enthusiastic sportsman, was always ready to join in any and every excursion' (Macleay 1875b). No doubt Dr James collected many more specimens than are attributed to him.

When the expedition reached the Somerset outpost near the northernmost tip of Australia, Macleay found many of the indigenous locals had succumbed to disease. To his horror he saw attenuated bodies lying unburied on the ground about the outpost. He immediately sent Dr James to investigate the cause of the 'extraordinary mortality'[2]. James reported the epidemic as measles (Liddell 1996, Stride 2016). Masters and Dr James are reported as collecting many birds here, albeit most without detail. Of those specifically secured by Masters and James were a fine male Magnificent Riflebird *Lophorina magnificus* along with another younger male and three younger females (Fletcher 1929: 249, Fulton

2012). On 20 June Masters and Dr James collected many small birds that Macleay described as 'desirable specimens', among them a quite distinct and brightly coloured female Mangrove Golden Whistler *Pachycephala melanura*[5]. Masters quickly noticed that this bird was more robust than the type seen earlier at Cape Grenville, so he named it *Pachycephala robusta*; he stated that it was shot in dense mangroves and that it was the only one seen (Masters 1875). Before leaving Somerset for the Torres Strait Islands and New Guinea, Macleay reported in a letter to a Sydney newspaper that Dr James had shot and collected a fine specimen of Short-tailed Spotted Cuscus *Spilocuscus maculatus* (Anon. 1875b).

Dr James is not specifically mentioned in connection with any further *Chevert* collections after Somerset. His name appears occasionally, telling us that his position as a collector and ship's doctor had not changed. He spent one night with Lawrence Hargrave in the small steam launch when it was bumped by a crocodile, at the mouth of the Katow (now Binaturi) River. He treated the Polynesian man, Jimmy Rotuma, until he finally died from scrofula. He had been treating him throughout the expedition.[2] Dr James is remembered as a significant member of the *Chevert* Expedition not least due to his dual roles as ship's surgeon and collector / taxidermist.

Dr James returns to New Guinea

The *Chevert* Expedition ended too soon for some of the expeditioners who staged their own offshoot expedition and returned to New Guinea: Dr James was among this small group. They were drawn predominately from the *Chevert* and also comprised William Petterd, Felix Knight, Lawrence Hargrave and Kendall Broadbent (Anon. 1875c). Broadbent had been collecting for himself and Count Castelnau at the Norman River on the western side of the Gulf of Carpentaria[8]. He had sold some of his birds to Macleay at Somerset on the *Chevert*'s return journey when he met the expeditioners[5]. It was only then that he became associated with the *Chevert* Expedition (Castelnau & Ramsay 1876). The offshoot group was to join Octavius Stone aboard the London Missionary Society's steamer the SS *Ellangowan* and return to New Guinea (Anon. 1875d).

Dr James had been the first person to formally propose a return expedition to William Macleay in a letter dated 7 August 1875[7]. This was before the termination of the *Chevert* Expedition while it was collecting on Darnley Island. At this time, Macleay in consultation with Captain Edwards had relinquished the planned exploration of the Fly River and accepted to head to the eastern side of the Gulf of Papua and thereafter terminate the expedition early.[5] Dr James' letter indicates that he forwarded the concept of a return expedition in the form of a business venture, in which Macleay might finance the return to New Guinea for half of the collections made. Dr James wrote:

> 'Mr. Macleay Esteemed Sir.
>
> Begging your indulgence for a few moments I will premise this communication by stating in brief that it contains a business proposition which I have every reason to believe you will feel interested in and which can be defined more explicitly by letter than by word of mouth...
>
> I have no idea of attempting this enterprise alone. I have presented the subject to another member of this expedition hoping that he would consult to join me…
>
> Mr Petterd is to whom I refer…
>
> What we propose is this:– To remain on New Guinea not less than 18 months nor more than 3 years…To proceed to Port Moresby for beginning operations. …Port Moresby is easy of access, offers facilities for communications and the reception of supplies, and

> at the same time constitutes a point not far removed from the mountain range and interior…
>
> …in order to prosecute this work with every prospect of success, we require influence and a certain amount of pecuniary assistance… we ask assistance upon the following conditions:– that we spare no effort to reach the interior of Papua:– that we devote at least 18 months to the trial:– that we make collections from every department of natural science for which we have the material:– and that of the entire collections you shall receive half. —Yours most faithfully, W. H. James.[7]

Dr James' collections were not sent to Macleay, and Macleay did not finance their return to New Guinea[5]. Instead, Macleay did offer some ammunition to the returning expeditioners (French & Petterd 1875).

William Petterd wrote two letters just prior to the commencement of the offshoot expedition, dated 17 and 23 September 1875 and sent to his uncle Mr. T. A. Reynolds and Mr French of the Melbourne Botanic Gardens respectively; both were subsequently published in newspapers. The following is a summary:

> 'Dr. James, Mr. Knight, and myself, return from here to New Guinea per mission steamer *Ellangowan*, collecting on our own account, and as I have lost the result of years of toil, I come to the conclusion of losing my life, or turning up trumps. The steamer is to land us at Port Moresby, on the south eastern coast of New Guinea, and from there we will try and penetrate into the interior, and ascend Mount Owen Stanley (13,000 feet high), or perish in the attempt. Of course the natives are hostile, and fevers abound, but we are all young, and, I flatter myself, foolish, and daring enough for anything… So now for 'death or glory… Our party will be the first English speaking expedition that has attempted to penetrate into the interior. I say English speaking, for our doctor is an American, consequently if any good result follows our attempt, America will share the honour… You will doubtless think this an unnecessary and dangerous, if not foolish, affair, but my inclinations are that way, so I may as well indulge in my natural propensities, and someone must go first… If things go well we anticipate stopping some years in New Guinea, so that in all probability I will never again return to civilisation —Yours, &c., W. F. Petterd' (Petterd 1875a,b).

Dr James also wrote a letter that was forwarded to *The Sydney Morning Herald* by Dr Alfred Roberts and subsequently published as follows:

> 'Sirs,—The enclosed extracts from a letter I recently received from Dr. James, the surgeon of the *Chevert*, will probably interest your readers. The energy and courage with which Dr James and his plucky companions have entered upon their difficult enterprise is worthy of all praise, and will certainly command our best wishes… Although the party is small and its means are limited there is every reason to hope that, with steady perseverance this off-shoot of the Macleay expedition will lead to important discoveries, as well as enrich our collections of natural history.—Alfred Roberts. 16 October 1875' (James & Roberts 1875).
>
> Extracts of Dr James' letter dated 18 September 1875.
>
> 'Instead of returning to Sydney with the *Chevert*, I am preparing to return to New Guinea with the twofold purpose of exploring as much as possible, and for making a scientific collection'.

> 'To assist me in this project I have two associates—a Mr Petterd, who is one of our present [*Chevert*] expedition, and a thoroughly competent collector and taxidermist, with a Mr Knight who is a fine bushman, a strong energetic young man, and somewhat of a botanical collector. The latter belongs to Sir William Macarthur's party.' [Dr James is referring to MacArthur's botanical collectors who accompanied the *Chevert* (Fulton 2016b). Felix Knight joined the *Chevert* Expedition in August 1875, at Darnley Island.[2]]
>
> 'We are making preparations entirely upon our own limited resources, and though at first sight it may appear foolhardy, yet, upon considering the circumstances, our prospect is a very flattering one.'
>
> 'We hope by going vigorously to work, be able to within three months to make sufficient collection to send off to Sydney, that through it we may not only receive a small amount of working capital, but interest some gentlemen of means and lovers of natural science sufficiently to induce them to lend us assistance to continue our investigations and collections' (James & Roberts 1875).

The returning expeditioners financed their own return and were transported in the missionary steamer *Ellangowan* (Anon. 1875c). Petterd wrote to French who in turn sent the letter to *The Queenslander* newspaper. Petterd wrote:

> 'We have a good fit-out, fine arms, rations, and some kanakas. We intend to collect everything. Of course we risk our lives from sickness, and the natives are not of the most trustworthy disposition. This affair is organised entirely independent of Mr. Macleay, from our own slender resources, kindly assisted by Captain Onslow, R.N., and Reedy (Sir W. Macarthur's man). Every man on the ship has made us some little present from friendship, and to start us on our perilous journey. Mr. Macleay is going to give us some ammunition, so that considering we are young men ready for anything, if the gods favour us we must do something' (French & Petterd 1875).

The offshoot expedition breaks up

The offshoot expedition broke up before it even started collecting. Various newspaper reports inform us that this little band of expeditioners split by stages, with the fragments going in different directions. No doubt the heat and humidity combined with infections and fever proved challenging for these determined explorers. Lawrence Hargrave's personal diary gave the first hint of disharmony within the small group. Hargrave was a young man of 25 at the time, and inclined to openly express his frustrations in his private diary. This entry, made while still at Somerset and dated 26 September to 10 October 1875, states: 'The doctor, Petterd and I are stopping with Broadbent, the doctor sulky and seems useless for roughing it.'[6]

By 23 October the correspondent for *The Queenslander* informs us that the party had broken into two or three small groups. 'The *Chevert* offshoot expedition were conveyed across by this little craft [across Torres Strait to New Guinea aboard the *Ellangowan*] consisting of Dr. James, Mr. Knight, Mr. Petterd, and Mr. Hargraves. Besides this party, Mr. O. C. Stone, a gentleman lately from England, athirst for adventure, and Mr. Broadbent, a taxidermist, took passage for the same almost unknown region. They all land at Port Moresby, and strike out from there in directions which suit their fancy, and feet, most' (Anon. 1875c).

William Petterd, publishing his memoir of the New Guinea explorations in May 1876, mentioned the break up and named the remaining members of his party. 'The small party organised on the *Chevert* having collapsed, I joined that of a Mr Stone… Our party consisted of Messrs. Stone, Broadbent, Hargraves and myself (Petterd 1876).' [Dr James and Felix Knight were absent from this list.]

Petterd was discussing the period after arriving at Port Moresby before leaving on their various quests. More news by the *Brisbane Courier's* correspondent at Somerset, dated 26 November 1875 states: 'Dr. James and Mr. Knight, spoken of in my last, are quartered on Yule Island, having forsaken Port Moresby, with the description of it being no place for collecting. 'Bareness and sterility describe the country,' writes Dr. James privately to myself. The other portion of the *Chevert* people… Mr. Hargrave, Mr. Stone, and Mr. Petterd are quartered, I understand, at Port Moresby, as also Mr. Broadbent, and will strike out from there when opportunity offers.'

Hargrave's diary provides some exact dates: on 31 October 1875 he wrote: 'In the afternoon Petterd and Knight said Dr James was disgusted with their partnership and thought they did not treat him with sufficient respect Ha! Ha!'

Hargrave's petulance and youth are again clearly evident in his diary entry. By the next day Hargrave confirmed that Dr James and Knight planned to shift to Yule Island aboard the *Ellangowan* and had loaded their traps aboard that day. They steamed out on Friday 5 November 1875[6].

A wait of nearly four months followed (until 13 March 1876) for more news of Dr James, when again Dr Alfred Roberts wrote in *The Sydney Morning Herald*. Roberts informs that food and supplies were sent as relief to those of the *Chevert* Expedition who continued in New Guinea, with most falling to Dr James and Mr Knight. This letter can be summarised:

> 'Sir,—In December last a few gentlemen kindly subscribed a small fund to purchase stores for the relief of Dr. James and his companions or companion, and I have sent an expenditure statement of the collection for insertion in your paper…
>
> The utilisation of the fund was entrusted to Captain Onslow and myself, and every article purchased was carefully selected by us…
>
> In a long letter which I received from Dr James by the last mail, he states that nearly all the stores had arrived safely, and had proved most acceptable. He and his companion had, it appears, become much reduced in strength and seriously ill, before they received them, but had picked up remarkably after a few days improved diet.
>
> It is much to be regretted that Mr Knight (Dr James' companion) has been compelled to return to Sydney, for the restoration of his health, and I fear the want of companionship will prove a heavy trial to Dr James during the present hot and unhealthy season.
>
> Mr. Knight visited me upon his arrival, and, I am glad to say, will soon be well again. During conversation with him, I ascertained that all the articles sent proved to be of a useful character, but he thought a supply of beads would have been very useful for trading purposes… Mr Knight especially mentioned that the preserved meat sent by the Sydney Meat Preserving Company was of a very superior character in every way, and that with care, they were able to keep an opened tin until the third day.
>
> I am, yours, faithfully, Alfred Roberts' (Roberts 1876).

Octavius Stone called on Dr James and Felix Knight on Yule Island, in February. He had not seen them since the conclusion of the *Chevert* Expedition when he had helped ferry them across to Port Moresby. He wrote: 'Both looked mightily changed in appearance since they landed there three months before. Then they were in the most robust health, but now they were so emaciated, and altered by attacks of fever and ague, and insufficient nourishment in consequence of having run short of provisions, that at first sight I scarcely recognised them. In addition to fever, his assistant was suffering from a large sore on the calf of his leg, caused by knocking it against a mangrove root, the severity of which had increased daily, until it had become serious' (Stone 1880).

Stone gave some supplies to Dr James and he dined with him on the island 'in a new grass house he [Dr James] had just completed.' Afterward Stone conveyed Felix Knight to Somerset (Stone 1880). Dr James was seen again in June by Andrew Goldie in transit from Somerset to New Guinea aboard the *Ellangowan*; Dr James disembarked at Yule Island (Moore & Mullins 2012).

Following Knight's departure Dr James entered a partnership with a Swede, Carl Thorngren, to collect zoological and other specimens (King 1909). Thorngren had arrived much earlier in the Torres Strait, in 1871–72. He had been working with the mission ketch *John Knox*, which conveyed the first batches of the London Missionary Society's teachers to New Guinea. His crew had deserted him and he had sold the *John Knox*, bought the seven-ton cutter *Mayri* and subsequently joined Dr James (Wetherell & Abel 1998, Moore & Mullins 2012).

Death of Dr James

Dr James was speared and killed on 23 August 1876, on board the *Mayri* near Yule Island, by natives from mainland New Guinea. News broke in Sydney in late September (Anon. 1876c) and details were published in October. The police magistrate at Somerset, Mr Henry M. Chester, wrote to Dr Alfred Roberts who in turn forwarded the letter to the *Sydney Morning Herald*. Chester wrote:

> 'Dear Sir.—It becomes my painful duty to announce to you the death, on the 23rd August, of Dr. James, late of the *Chevert*, in whom you were interested. It appears that he had lately joined Mr. Charles Thorngren who owned a boat called the *Mayri*, and they had gone together in the boat to the mainland opposite Yule Island with a crew of seven natives of islands in Torres Straits. The survivors give the following account of the catastrophe:—
>
> Just before daylight two canoes full of New Guinea men were seen approaching the boat. The crew called Thorngren, and asked for firearms, but he, thinking they were merely coming to trade, refused to give them. While Dr. James and Thorngren were trading a native suddenly struck the latter with a club, smashing his skull and knocking him overboard. Dr. James shot one man with his revolver, but was almost immediately thrust through with a spear and killed. The boat's crew got their guns, and succeeded in beating off their assailants after two of their number had been speared. They say they shot about ten of the New Guinea men. They dived for the body of Thorngren, but, the water being muddy, they were unable to recover it. They then got under way, and that evening buried the body of Dr. James on a sandbank' (Chester 1876).

In October 1876, Alfred Roberts received Dr James' final letters, of which he only shared a small part with *The Sydney Morning Herald*. Roberts' extracts highlighted Dr James' optimism, although with the knowledge of Dr James' death the optimism conveyed a melancholy note.

> 'SIR,—I received the enclosed letter by the steamship *Somerset* yesterday; it tells its own sad tale. Three letters from Dr. James, written at different times, and his will were

> enclosed with it. From the latter it is evident that he had reason to be, and was, very sanguine of material success in his undertaking. The natives of Yule Island, where he had established a home, welcomed him warmly upon his return from Somerset, and rendered him every assistance; he had already visited some new localities, and among them "Aroi," the natives of which speak a different language or dialect. At this place he secured five specimens of the new bird of paradise, two being males in full plumage. The concluding paragraph of his last letter is as follows:—'My health is good at present, the weather fine, and, the prospect of my remaining in good health favourable…By the time I write again I hope to have accomplished something worth telling' (Roberts 1876).

A letter from Dr James to his sister Emma survives in the Univ. of Virginia Library. It was written more than a year before his death and provides a glimpse into his thoughts while aboard the *Chevert*. Dr James' letter allows us to engage with both the times and the unusual locality. It permits us to gain a sense of his mind as he reaches out to a larger world; such a context enables us to deepen our engagement with the spirit of exploration in that remote place and time.

> 'Darnley Island, Torres Strait, July – 31 – 1875.
>
> My Dear Sister,
>
> This letter is a strange locality from which to date a letter. A small mountainous island situated between North Australia and New Guinea, inhabited by savages so low in the scale of humanity that they are scarcely beyond the use of the "Palm leaf"…
>
> Oh! with what unspeakable pleasure I look forward to the time when after arriving at home again, I shall call you again all up around the cheerful old hearth in the sitting room, and whilst the familiar ticking of the faithful old clock marks the flight of time, read to you… of my tour and adventures in that strange and almost unknown island where the glorious Bird of Paradise, arrayed in all its gaudy plumage reigns king of the avifauna…
>
> If you are an old maid when I return, not a thing will you get. So there's a great inducement to make a change. That's a change which – by the way – I shouldn't object to myself, if I were once more within the friends of dear old Loudon. I think it would be a very consoling change – a change which would put a quietus upon my prodigality and wandering… With sincere affection, yours – W.H.J.'

Dr James' collections

Overall 99 birds, three mammals plus some Coleoptera and Lepidoptera (beetles and butterflies) are known to have been collected by Dr James (Table 1). Of the three known mammals, two Allied Rock-wallabies represented a new species, of which the holotype is in the Macleay Museum (Ramsay 1877, Fulton 2016a). George Masters (1875) attributed two new species of Australian birds to Dr James. These are currently recognised as the subspecies Torresian Grey Shrike-thrush *C. h. superciliosa* and Robust Mangrove Golden Whistler *P. m. robusta*; the type specimens are currently in the Australian Museum, Sydney, on loan from the Macleay Museum. Other type specimens collected by Dr James include: *Phonygammus jamesii*, holotype (Sharpe 1877: 181); *Tanysiptera microrhyncha*, three syntypes (Sharpe 1878: 311); and *Melidora collaris*, holotype (Sharpe 1878: 313). Richard Bowlder Sharpe, curator of birds at the British Museum, named *P. jamesii* in honour of Dr James. It is currently regarded as a subspecies of Trumpet Manucode *P. keraudrenii jamesii*. This

TABLE 1

Collections of Dr James. Current scientific and common names are given along with the name used by the authors when the collections were first published. Current scientific names follow del Hoyo & Collar (2014, 2016). Collection locations and dates are taken from those published by R. B. Sharpe. Transcription errors were detected in some of the collection years given by Sharpe (1878), specifically some were after Dr James' death. These are marked by an asterisk (*) and retain the month given by Sharpe; in most cases these were one year out with no reason to doubt the month; however, one was given as 1865, instead of 1875: Sharpe's *Actitis hypoleucus* (Common Sandpiper). Abbreviations: *a*, *b*, *c*, *d*, and *e* in italics denote individual specimens; and s.e. denotes the compass point south-east. Museum acronyms and locations: MM = Macleay Museum, Sydney; AM = Australian Museum (on loan from the Macleay Museum); NHMUK = Natural History Museum, Tring.

Taxa	**English name**	**Original name**	**Location & Date**
***Chevert* Expedition**			
Mammals			
Ramsay (1877), Fulton (2016a)			
Petrogale assimilis	Allied Rock-wallaby	*Petrogale assimilis*	♂ & ♀ Palm I.—2 June 1875 (MM)
Anon. (1875b)			
Spilocuscus maculatus	Spotted Cuscus	*Cuscus maculatus*	Somerset—23 June 1875 (MM)
Birds			
Masters (1875)			
Campephagidae			
Colluricincla harmonica superciliosa	Grey Shrike Thrush	*Colluricincla superciliosa*	♂ Cape Grenville—16 June 1875 (AM)
Masters (1875), Fletcher (1929)			
Campephagidae			
Pachycephala melanura robusta	Mangrove Golden Whistler	*Pachycephala robusta*	♀ Somerset—20 June 1875 (AM)
Paradisaeidae			
Lophorina magnificus	Magnificent Riflebird	*Craspedophora magnifica*	2♂ & 3♀ Somerset—25 June 1875 (MM)
Dr James New Guinea			
Sharpe (1877)			
Paradisaeidae			
Phonygammus keraudrenii jamesii	Dr James' Trumpet Manucode	*Phonygamma jamesii*	Aleya—April 1876 (NHMUK)
Sharpe (1878)			
Coleoptera and Lepidoptera	unknown	unknown	Yule Island
Anatidae			
Tadorna radjah	Radjah Shelduck	*Tadorna radjah*	*a*, *b* & *c*. Nicura—*a*. December 1875, *b*. March 1876, *c*. April 1876
Columbidae			
Chalcophaps indica	Emerald Dove	*Chalcophaps chrysochlora*	*a*. Aleya, *b*. s.e. mainland—*a*. *April 1876, *b*. 29 February 1876
Ducula mullerii	Collared Imperial Pigeon	*Carpophaga muelleri*	♂ s.e. mainland 8 miles from Yule I.—November 1875
Ducula pinon	Pinon Imperial Pigeon	*Carpophaga pinon*	Mainland e. of Yule I.—February 1876
Alopecoenas jobiensis	White-bibbed Ground Dove	*Phlogaenas jobiensis*	*a*. s.e. mainland, *b*. no label—*a*. 29 February 1876
Goura scheepmakeri	Southern Crowned Pigeon	*Goura albertisii*	*a*, *b*, *c*, *d* & *e*. s.e. mainland—*February 1873
Ptilinopus coronulatus	Coroneted Fruit Dove	*Ptilonopus coronulatus*	*a*. s.e. mainland, *b* & c. Aleya—b & c. April 1876

Caprimulgidae			
Aegotheles bennettii	Barred Owlet-Nightjar	*Aegotheles bennetti*	*a* & *b*. Aleya—April 1876
Caprimulgus macrurus	Large-tailed Nightjar	*Caprimulgus macrurus*	Yule I.—April 1876
Ardeidae			
Butorides striata	Striated Heron	*Butorides javanica*	♂ Yule I.—December 1875
Accipitridae			
Haliaeetus leucogaster	White-bellied Sea Eagle	*Haliaetus leucogaster*	♀ Yule I.—January 1876
Haliastur indus	Brahminy Kite	*Haliastur girrenera*	Mainland e. of Yule I.—February 1876
Macheiramphus alcinus	Bat Hawk	*Macheiramphus alcinus*	♀ Low Nicura—1 April 1876 (NHMUK)
Aviceda subcristata	Pacific Baza	*Baza reindwardti*	♀ s.e. mainland 8 miles from Yule I.—November 1875 (NHMUK)
Pandion cristatus	Osprey	*Pandion leucocephalus*	2 ♂ Yule I.—December 1875
Rallidae			
Megacrex inepta	New Guinea Flightless Rail	*Tigrisoma heliosylos*	mangroves of Aleya—March 1876
Porphyrio melanotus	Australian Swamphen	*Porphyrio melanopterus*	no label
Charadriidae			
Pluvialis squatarola	Black-bellied Plover	*Squatarola helvetica*	♀ Yule I.—November 1875
Scolopacidae			
Actitis hypoleucos	Common Sandpiper	*Actitis hypoleucus*	♂ Yule I.—*December 1875
Numenius madagascariensis	Eastern Curlew	*Numenius cyanopus*	♂ Yule I.—December 1875
Psittacidae			
Geoffroyus geoffroyi	Red-cheeked Parrot	*Geoffroyius aruensis*	♂ mainland—January 1876
Psittaculirostris desmarestii	Large Fig Parrot	*Cyclopsittacus cervicalis*	Eucalyptus range—February 1876
Trichoglossus haematodus	Rainbow Lorikeet	*Trichoglossus massena*	*a*. ♂ & ♀ s.e. mainland—January 1876, *b*. Eucalyptus range—February 1876
Cuculidae			
Centropus menbeki	Greater Black Coucal	*Centropus menebeki*	Aleya—April 1876
Centropus phasianinus	Pheasant Coucal	*Centropus spilopterus*	3 ♂ *a*, *b*, & *c*. Yule I.,—Nov & Dec 1876, *d*. Nicura—*December 1875
Chrysococcyx lucidus	Shining Bronze Cuckoo	*Lamprococcyx lucidus*	Aleya—April 1876
Eudynamys orientalis	Eastern Koel	*Eudynamis cyanocephala*	3 ♂ Yule I.—*December 1875
Alcedinidae			
Ceyx azureus	Azure Kingfisher	*Alcyone lessoni*	♂ s.e. mainland 8 miles from Yule I.—November 1875
Ceyx pusilla	Little Kingfisher	*Alcyone pusilla*	♂ Aleya—*April 1876
Halcyonidae			
Dacelo gaudichaud	Rufous-bellied Kookaburra	*Dacelo gaudichaudi*	♂ Nicura—November 1875
Dacelo leachii	Blue-winged Kookaburra	*Dacelo intermedius*	♂ & ♀ *a* & *b*. s.e. mainland—January 1876, *c*. ♀ Port Moresby—*November 1875
Tanysiptera galatea	Common Paradise Kingfisher	*Tanysiptera microrhyncha*	*a*. ♀ s.e. mainland 8 miles from Yule I., b & c. Aleya—a. November 1875, *b* & *c*. *April 1876 (*a*, *b* & *c* NHMUK)
Todiramphus chloris	Collared Kingfisher	*Melidora collaris*	*a*. ♂ no label, *b*. ♀ Low Aleya, *c*. ♀ s.e. mainland —*b*. February 1876, *c*. 29 February 1876 (*c* NHMUK)
Todiramphus sanctus	Sacred Kingfisher	*Halcyon sanctus*	♀ Yule I.—April 1876

Bucerotidae			
Rhyticeros plicatus	Blyth's Hornbill	*Rhytidoceros ruficollis*	*a* & *b*. Aleya—March 1876
Pittidae			
Pitta sordida	Hooded Pitta	*Pitta novaeguineae*	*a*. ♂ Aleya—*April 1876, *b*. Aleya—*April 1876
Maluridae			
Malurus alboscapulatus	White-shouldered Fairy-wren	*Malurus alboscapulatus*	♂ Nicura—December 1875
Malurus cyanocephalus	Emperor Fairy-wren	*Todopsis bonapartii*	*a*. s.e. mainland—February 1876, *b*. ♂ s.e. mainland 8 miles from Yule I.—November 1875
Meliphagidae			
Ramsayornis modestus	Brown-backed Honeyeater	*Glyciphila modesta*	♂ s.e. mainland—December 1875
Campephagidae			
Coracina melas	New Guinea Cuckooshrike	*Edoliosoma melas*	Aleya—April 1876
Pachycephalidae			
Pseudorectes ferrugineus	Rusty Pitohui	*Rectes ferruginea*	*a*. Aleya—April 1876, *b*. ♀ Nicura—December 1875 (*a* or *b* NHMUK)
Pachycephala sp.	whistler sp.	*Pachycephala* sp.	Aleya—April 1876 (NHMUK)
Oriolidae			
Oriolus szalayi	Brown Oriole	*Oriolus striatus*	♀ Port Moresby—*November 1875
Atamidae			
Cracticus cassicus	Hooded Butcherbird	*Cracticus cassicus*	*a* & *b*. Aleya—April 1876
Cracticus mentalis	Black-backed Butcherbird	*Cracticus mentalis*	♂ Nicura—December 1875 (NHMUK)
Corvidae			
Corvus orru	Torresian Crow	*Corone orru*	♂ Yule I.—November 1875 (NHMUK)
Monarchidae			
Arses telescopthalmus	Frilled Monarch	*Arses telescophthalmus*	*a*. ♂ Nicura—*December 1875, *b*. Nicura, *c*. ♀ s.e. mainland (*c* NHMUK)
Myiagra alecto	Shining Flycatcher	*Piezorhynchus nitidus*	*a* & *b*. ♂ & ♀ Yule I.—*November 1875, *c*. Yule I.—April 1876
Paradisaeidae			
Manucodia ater	Glossy-mantled Manucode	*Manucodia atra*	2♂ *a* & *b*. Yule I.—April 1876, c. ♂ s.e. mainland—January 1876
Paradisaea raggiana	Raggiana Bird-of-Paradise	*Paradisea raggiana*	♂ & ♀ Aleya—April 1876
Cisticolidae			
Cisticola exilis	Golden-headed Cisticola	*Cisticola ruficeps*	*a*. ♂ Yule I & *b*. ♀ Yule I.—*a*. November 1875, *b*. December 1875
Sturnidae			
Aplonis metallica	Metallic Starling	*Calornis viridescens*	♂ Yule I.—*November 1874
Mino dumontii	Yellow-faced Myna	*Eulabes dumontii*	♀ Aleya
Nectariniidae			
Cinnyris jugularis	Olive-backed Sunbird	*Cinnyris frenatus*	♀ s.e. mainland

Figure 1. Torresian Crow *Corvus orru* with a British Museum label and original label in Dr James' handwriting (Hein van Grouw, © Natural History Museum, London)

subspecies has been tentatively listed as the Papuan Trumpet Manucode in the BirdLife Australia subspecies list. It is listed because it occurs in the Torres Strait Islands, but other subspecies of Trumpet Manucode occur on mainland of New Guinea so this name appears inappropriate. Instead, I suggest the common name Dr James' Trumpet Manucode be adopted in Australia for this taxon.

The collections made by Dr James on his return to New Guinea were shipped to Dr Alfred Roberts in Sydney, where E. P. Ramsay reluctantly refused to act as James' agent. William Macleay saw them at Dr Roberts' house and made an offer for them that was rejected. Consequently, they were sent by Roberts to T. Higgins in London (Higgins had succeeded Samuel Stevens at Stevens' Auction House) and Higgins then sold 12 to the British Museum, with the others returned to Higgins for sale and thus probably were widely scattered. Fortunately, all those collected by Dr James were described by Sharpe (Sharpe 1877, 1878, British Museum 1906: 260, 384–385). It is possible that some of Dr James' birds and his invertebrates ended up in the Rothschild Collection, although searches of the database at the American Museum of Natural History, New York, where Rothschild's birds now reside, failed to find any birds collected at sites given by Dr James (M. LeCroy & T. Trombone *in litt*. 2016).

E. P. Ramsay's letter to Dr James, 1 January 1876:

> 'I deeply regret that some of the Trustees, Dr. Roberts for one, expressed an opinion that I could not act for you in the capacity you require—the late Curator's extraordinary proceedings have caused the Trustees to be more strict in these matters than they otherwise would have been… I cannot (according to your note) receive your specimens here for sale, but if they are sent to Dr. Roberts or anyone else in Sydney I will most willingly examine and advise you respecting them and point out as far as I know anything new or valuable among them… I regret extremely I cannot act as your agent, nothing would give me greater pleasure the examination of your treasures would be recompense enough to any naturalist…
> E. Pearson Ramsay'[9]
>
> William Macleay noted James' specimens in his personal journal.
>
> '…there were about 100 birds all badly skinned and apparently nothing new, a number of fine beetles in sand but very few species and a few badly preserved spirit specimens.' (Tuesday, 30 May 1876).[2]

> 'I offered Roberts £50 for Dr James' collection from Hall Sound. The offer was promptly declined.' (Wednesday, 31 May 1876).[2]

Twelve of Dr James specimens now reside in the Natural History Museum at Tring. R. Bowlder Sharpe originally identified and described Dr James' birds stating that there were two more new species from New Guinea, namely Common Paradise Kingfisher '*Tanysiptera microrhyncha*' (now *T. galatea*) and Collared Kingfisher '*Melidora collaris*' (*Todiramphus chloris*) (Sharpe 1878, British Museum 1906: 384–385). However, these birds were described earlier and were not new. Near the start of Sharpe's (1878) paper describing James' birds he stated, 'A melancholy interest attaches to the present collection of Dr. James; for it is at once the first, and last, that we shall receive from him.' He also noted, in contrast to Macleay's comments, that 'all the skins were very well prepared' Sharpe also noted from Dr James' notes that the specimens of invertebrates (Coleoptera and Lepidoptera) were collected on Yule Island.

Collecting locations in New Guinea

The birds that Sharpe described were collected on Yule Island and the New Guinea mainland around Hall Sound (Sharpe 1878) (Fig. 2). This general area was already known

Figure 2. Dr James' collection locations around Yule Island, New Guinea.

to Sharpe through the exploration of Signor D'Albertis and the published work of Count Salvadori and D'Albertis (1875). Sharpe gave descriptions of the collection sites, which were taken from Dr James' notes forwarded with the specimens by Dr Alfred Roberts (Sharpe 1878). The precise location of these sites has been determined by following Dr James' notes and using William Macleay's journal[2] and Lawrence Hargrave's diary[6]. Dr James' Coleoptera were collected at the north-west extremity of Yule Island (08°46'28.24"S, 146°30'40.52"E) and his Lepidoptera at an unknown location he described as 'low Yule Island in thick scrub' (Sharpe 1878).

Yule Island (08°49'05.7"S, 146°32'00.9"E) is *c*.8 km long north to south and 2 km wide east to west, with Hall Sound to the east and the Coral Sea to the west.

Aleya (08°51'34.6"S, 146°35'17.3"E) is a short salt arm (rivulet) passing through an extensive mangrove situated inside the south headland of Hall Sound.

Nicura village (08°47'49.9"S, 146°37'24.4'E) is approximately 750 m from the Ethel River, which flows into Hall Sound. Lawrence Hargrave guessed it was '3/4 mile off'[6] the Ethel River. Dr James had learned of this village when he first visited it with the *Chevert* Expedition in August 1875 (Fulton 2012). There is a village in the same location today, spelt Nicora. Beehler & Pratt (2016) noted variant spellings of Nikura and Nkora. In 1875, Nicura was the local peoples' name for both the Ethel River and the village (Bennett & D'Albertis 1875, D'Albertis 1880: 276). While Dr James collected variously around Nicura village, he gave particular mention to certain sites and one in particular: The village 'is bounded… on the east by the valley of the Nicura, which is a low swampy country, in the main, supporting a very heavy growth of scrub and forest trees. It is in the latter locality that birds abound' (Sharpe 1878).

South-east mainland (08°51'00.3"S, 146°33'56.9"E): Dr James collected specimens on the mainland south and south-east of Yule Island, from as far afield as 13 km south of Yule Island. The coordinates given here are for the southern head of Hall Sound on the New Guinea mainland. He also visited other sites, which are described in Sharpe (1878) and include: Selena a salt arm or rivulet, and Paiton a large village north of Yule Island. No collections have been found for these sites by this study.

Acknowledgements

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Notes

[1] Letter from Miss Emma James to Mrs Julian C. Jordan April 12, 1946; transcribed by D. S. Horning, 1995, transcript in Macleay Museum, Univ. of Sydney. Original letter held in Special Collections of Univ. of Virginia Library, Charlottesville, VA.

[2] William John Macleay's personal journal; transcribed by D. S. Horning, 1995, transcript in Macleay Museum, Univ. of Sydney.

[3] Pers. comm. from Jan Wolfley, Senior Assistant Librarian, Nevada Legislative Counsel Bureau, Carson City, NV.

[4] Letter from US Consul J. H. Williams to John L. Cadwalader, Assistant Secretary of State, Washington, 14 March 1877; transcribed by D. S. Horning, 1995, transcript in Macleay Museum, Univ. of Sydney. Original letter held in Special Collections of Univ. of Virginia Library, Charlottesville, VA.

[5] Unpubl. notes of the author.

[6] Private diary of Lawrence Hargrave held by the Power House Museum, Sydney.

[7] Letter from W. H. James to William Macleay 7 August 1875. Original letter held in Special Collections of Univ. of Virginia Library, Charlottesville, VA.

[8] Queensland Museum Board Minutes 1 September 1893 and 2 March 1894.

[9] Ramsay Papers ML 2278 1(2). Private Letter Book 2 1875–78 to Dr W. H. James, Somerset, Cape York, 1 January 1876.

References:
Anon. 1875a. Shipping. Arrivals. *Evening News* 12 January 1875: 2.
Anon. 1875b. The New Guinea Expedition. *Sydney Morning Herald* 27 July 1875: 5.
Anon. 1875c. Somerset. *The Queenslander* 13 November 1875: 7.
Anon. 1875d. Exploration of New Guinea. *The Argus* 13 October 1875: 6.
Anon. 1876a. Death of Dr. James. To the Editor of the Herald. *Sydney Morning Herald* 12 October 1876: 3.
Anon. 1876b. Return of the Expedition to the Fly River, New Guinea. *Sydney Morning Herald* 30 September 1876: 5.
Anon. 1876c. Murder of two persons by natives of New Guinea. *Sydney Morning Herald* 29 September 1875: 5.
Anon. 1877a. Untitled. *Staunton Spectator* Tuesday 27 February 1877: 3.
Anon. 1877b. Eaten by cannibals. *Pioche Weekly Record* 20 January 1877: 3.
Anon. 1877c. Minor notes. *Iola Register* 17 February 1877: 1.
Anon. 1877d. A San Franciscan victim of the cannibals of New Guinea. *Sacramento Daily Union* 10 February 1877: 8.
Anon. 1877e. Dr. W. H. James. *Staunton Spectator* 20 February 1877: 2.
Anon. 2016. William H. James Scientific Expedition Papers. Special Collections, Univ. of Virginia Library, Charlottesville, VA. http://search.lib.virginia.edu/catalog/u5855847 (accessed 14 April 2016).
Beehler, B. M. & Pratt, T. K. 2016. *Birds of New Guinea: distribution, taxonomy, and systematics*. Princeton Univ. Press.
Bennett, G. & D'Albertis, L. 1875. New Guinea. *Sydney Mail & NSW Advertiser* 25 December 1875: 807–809.
British Museum. 1906. *The history of the collections contained in the natural history departments of the British Museum*, vol. 2. Trustees of the Brit. Mus., London.
Castelnau, Le Comte de & Ramsay, E. 1876. Notes of a collection of birds from the Norman River, Gulf of Carpentaria, with descriptions of some new species. *Proc. Linn. Soc. NSW* 1: 379–386.
Chester, H. M. 1876. Death of Dr. James: Somerset, 26th September, 1876. *Sydney Morning Herald* 12 October 1876: 3.
D'Albertis, L. M. 1880. *New Guinea: what I did and what I saw*, vol. 1. Sampson Low, Marston, Searle & Rinington, London.
Fletcher, J. J. 1893. *The Macleay memorial volume*. Linn. Soc. of New South Wales, Sydney.
Fletcher, J. J. 1929. The Society's heritage from the Macleays. Part ii. *Proc. Linn. Soc. NSW* 54: 185–272.
French, [?]. & Petterd, W. F. 1875. Exploration of New Guinea. *The Argus* 13 October 1875: 6.
Fulton, G. R. 2012. Alexander, William Sharp, and William John Macleay: their ornithology and museum. Pp. 327–393 *in* Davis, W. E., Recher, H. F., Boles, W. E. & Jackson, J. A. (eds.) *Contributions to the history of Australasian ornithology*, vol. 2. Nuttall Orn. Cl., Cambridge, MA.
Fulton, G. R. 2016. Allied Rock-wallaby *Petrogale assimilis* Ramsay, 1877: holotype in the Macleay Museum. *Proc. Linn. Soc. NSW* 138: 57–58.
Fulton, G. R. 2016. Thomas Reedy 1842–1929: gardener for Sir William Macarthur and plant collector on the *Chevert* Expedition to New Guinea in 1875. *Cunninghamia* 16: 51–63.
Hall, S. R. 1994. *Romancing Nevada's past: ghost towns and historic sites of Eureka, Lander, and White Pine Counties*. Univ. of Nevada Press, Reno.
del Hoyo, J. & Collar, N. J. 2014. *HBW and BirdLife International illustrated checklist of the birds of the world*, vol. 1. Lynx Edicions, Barcelona.
del Hoyo, J. & Collar, N. J. 2016. *HBW and BirdLife International illustrated checklist of the birds of the world*, vol. 2. Lynx Edicions, Barcelona.
James, W. H. & Roberts, A. 1875. Further exploration of New Guinea. *Sydney Morning Herald* 30 October 1875: 6.
King, J. 1909. *W. G. Lawes of Savage Island and New Guinea*. Religious Tract Soc., London.
Liddell, R. 1996. *The savage frontier*. Liddell Publishing, Redbank.
Macleay, W. 1875. Notes on the zoological collections made in Torres Straits and New Guinea during the cruise of the Chevert. *Proc. Linn. Soc. NSW* 1: 36–40.
Macleay, W. 1875b. Voyage of the Chevert. To the Editor of the Herald. *Sydney Morning Herald* 11 October 1875: 5.
Masters, G. 1875. Zoology of the Chevert – Ornithology. Part I. *Proc. Linn. Soc. NSW* 1: 44–64.
Moore, C. & Mullins, S. 2012. Andrew Goldie's memoir: 1875–1879. Pp. 39–127 *in* Moore, C & Mullins, S. (eds.) *Andrew Goldie in New Guinea 1875–1879. Memoir of a natural history collector*. *Mem. Queensland Mus. Culture* 6.
Petterd, W. F. 1875a. Exploration of New Guinea. *The Argus* 13 October 1875: 6.
Petterd, W. F. 1875b. Exploration of New Guinea. *The Mercury* 21 October 1875: 2.
Petterd, W. F. 1876. New Guinea. [No. 3.] Port Moresby. *The Mercury* 4 May 1876: 3.

Ramsay, E. P. 1877. Description of a supposed new species of rock wallaby from the Palm Islands; on the north-east coast of Australia, proposed to be called *Petrogale assimilis*. *Proc. Linn. Soc. NSW* 1: 359–361.

Roberts, A. 1876. Death of Dr. James: to the Editor of the Herald. *Sydney Morning Herald* 12 October 1876: 3.

Roberts, A. 1876. To the Editor of the Herald. *Sydney Morning Herald* 13 March 1876: 3.

Rutledge, M. 1976. Roberts, Sir Alfred (1823–1898). *In*: *Australian dictionary of biography*, Vol. 6. Natl. Centre of Biography, Australian Natl. Univ. http://adb.anu.edu.au/biography/waterhouse-frederick-george-4805/text8009 (accessed 13 April 2016).

Salvadori, T. & D'Albertis, L. M. 1875. Catalogo di una collezione di uccelli dell' Isola Yule e della vicina costa meridionale della penisola orientale della Nuova Guinea Raccolti da L. M. D'Albertis. *Ann. Mus. Civico Storia Nat. Genova* 7: 797–839.

Sharpe, R. B. 1877. *Catalogue of the birds in the British Museum*, vol. 3. Trustees of the Brit. Mus., London.

Sharpe, R. B. 1878. Contributions to the ornithology of New Guinea. Part II—On the ornithological collections formed by the late Dr. James in southeastern New Guinea and Yule Island. *J. Linn. Soc. Lond. Zool*. 13: 305–321.

State Records Authority NSW. 2016. MacGregor, 11 January 1875, San Francisco to Sydney. http://mariners.records.nsw.gov.au/1875/01/035mac.htm (accessed 5 April 2016).

Stone, O. C. 1880. *A few months in New Guinea*. Sampson Low, Marston, Searle & Rivington, London.

Stride, P. 2016. Death and disease at Somerset, the North Queensland Government Headquarters at the top of Cape York 1864–1877. *Merit Res. J. Medicine & Medical Sci*. 4: 140–151.

Wetherell, D. & Abel, C. W. 1998. First contact mission narratives from eastern Papua New Guinea. *J. Pacific Hist*. 33: 111–116.

Address: School of Veterinary & Life Sciences, Murdoch Univ., South Street, Murdoch WA 6150, Australia; and Centre for Biodiversity and Conservation Science, Univ. of Queensland, Brisbane, Qld 4072, Australia, e-mail: grahamf2001@yahoo.com.au

Vocal comparison between Tabar Pitta *Erythropitta splendida* and New Britain Pitta *E. gazellae*

by Markus Lagerqvist, Roger McNeill & Ashley Banwell

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The taxonomy of the Red-bellied Pitta *Erythropitta erythrogaster* superspecies is currently in a state of flux. Irestedt *et al.* (2013) published a comprehensive study of the group employing molecular methods, as well as morphometric and plumage analyses. They also included sonograms for ten of the taxa. Their recommendation was to recognise 17 species, three of them in the Bismarck archipelago of Papua New Guinea: New Britain Pitta *E. gazellae* (monotypic), New Ireland Pitta *E. novaehibernicae* (including *E. n. extima*) and Tabar Pitta *E. splendida* (monotypic).

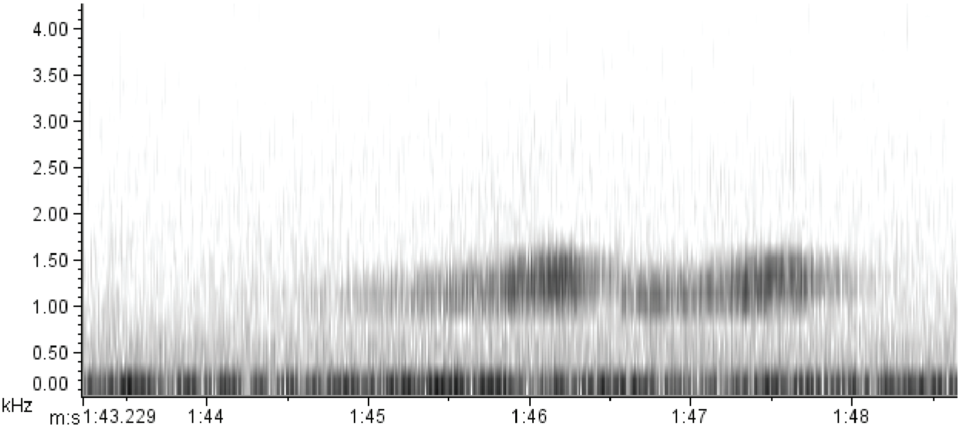
Collar *et al.* (2015) applied the criteria described in Tobias *et al.* (2010) to assign species rank to members of this complex, using morphological data alone, due to the lack of acoustic, behavioural and ecological information for many taxa. Thirteen taxa were considered species, including all three in the Bismarcks, an arrangement followed by Clements *et al.* (2016), but not by Gill & Donsker (2016), who recognised ten species, including just one in the Bismarcks, due to the lack of vocal evidence (F. Gill pers. comm.). Thus, one key to settling species limits are sound-recordings, which are lacking for several taxa. In July–August 2016 we visited Tabar Island, to search for Tabar Pitta *E. splendida*, one of the least-known taxa. We obtained several recordings of its song, which we compare here to recordings of its closest relative, New Britain Pitta *E. gazellae*, made on the same trip.

Tabar Island.—At dawn on 30 July we travelled by boat to Tabar, the main island in the Tabar group, off north-east New Ireland. On Tabar, we stayed at Tau Dikana Lodge, near Wang village, and spent the day in forest in the south of the island, during which we estimated that four pairs and six different individuals were heard in *c.*1.5 km^2, both in primary forest (02º59.295'S, 152º02.550'E) and secondary forest with an understorey dominated by ginger plants near the village (02º59.604'S, 152º02.433'E). Thus it appears fairly common within its limited range and tolerant of degraded habitat. We are unaware of other recent observations of this taxon, but G. Dutson (*in litt*. 2016) saw up to eight individuals in two hours in 1997 and estimated territory sizes as small as 4 ha in favoured areas such as patchy old growth and tall but logged forest with natural thickets of undergrowth on level terrain. We obtained high-quality sound-recordings of songs and alarm calls. Using playback, we observed multiple individuals but the birds were quite shy. Next morning we returned to the area to obtain better observations and photographic documentation. To our knowledge, these are the first-ever published photographs of *E. splendida* (Figs. 1A–B).

New Ireland.—At 11.00 h on 1 August we left Tabar by boat for New Ireland, where we spent 1.5 days. Our time there was spent mainly along the road to the Lelet Plateau. We hoped to acquire sound-recordings of *E. novaehibernicae* but we heard just two individuals calling briefly and too distant to record. We found the habitat heavily degraded, with 'good' forest only some distance from the road.

New Britain.—On 2 August we left New Ireland for a five-night stay at Walindi Plantation Resort in West New Britain, to search for New Britain Pitta. Despite being a popular site for birders visiting New Britain, there are relatively few records of the pitta and, to our knowledge, no photographs or sound-recordings have been published. During our stay, we heard at least four different individuals: one was heard briefly at Garu Wildlife

Figure 1A–B. Tabar Pitta *Erythropitta splendida*, southern Tabar Island, New Guinea, 31 July 2016 (Markus Lagerqvist)



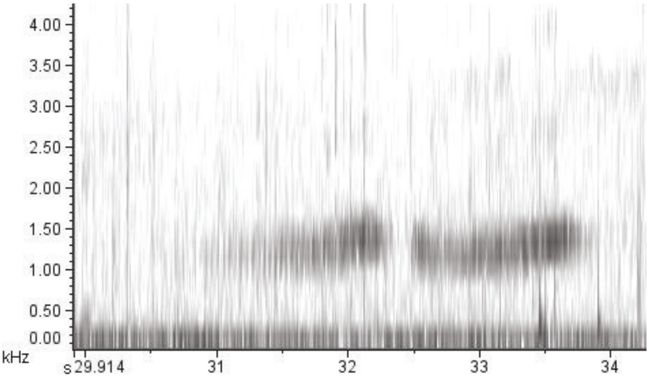


Figure 2A–B. Song phrase of Tabar Pitta *Erythropitta splendida* (above) compared to that of New Britain Pitta *Erythropitta gazellae* (left), recordings by Roger McNeill, made using a Marantz PMD661 MKII recorder and Sennheiser ME67 shotgun microphone; sonograms were produced using Raven Lite v. 2.0.0.

Management Area (05°29.106′S, 149°59.008′E), at least two in the narrow band of secondary forest near the Kulu River (e.g. at 05°32.773′S, 150°01.118′E) and one on the other side of the main river, bordering the large oil-palm plantations that dominate the area. The birds were quite vocal and we obtained good recordings of the song. Obtaining photographs or even a good view proved very difficult, as the birds appeared extremely shy and less responsive than Tabar Pitta. We managed only brief observations, including birds in flight, and no photographs.

Acoustic comparison.—For those familiar with the *Erythropitta* complex, it will be immediately apparent upon hearing the song of *splendida* or *gazellae* that they belong to the 'red-bellied pitta' complex. Compared with each other, they sound more similar than to birds from mainland New Guinea, which is unsurprising as they belong to the same phylogroup and are even more genetically similar than those birds just a few kilometres away on New Ireland (Irestedt *et al.* 2013).

Our analysis is based on 45 two-note phrases from at least five different individuals of *splendida* and 19 two-note phrases from three different *gazellae*. All recordings were made using a Marantz PMD661 MKII recorder and Sennheiser ME67 shotgun microphone. Sonograms were produced and calls analysed using Raven Lite v. 2.0.0. The recordings are available via Cornell's Macaulay Library (http://macaulaylibrary.org/). Songs of both taxa consist of a pair of 'rollercoaster' notes often repeated incessantly for several minutes. Typically, each phrase starts with a slow upward whirr speeding up as it reaches its first peak, followed by a <1-second pause, thereafter the sound whirrs again, achieving a second peak, before descending into a *c.*20-second pause before the next two-note phrase.

The main differences between Tabar and New Britain birds are the length of the two-note phrase and its pitch. On average, the individual two-note phrases of *splendida* lasted c.1 second longer than *gazellae* (c.3.9 vs. c.2.9 seconds) with a deeper, slower, more guttural start (Fig. 2A). Two-note phrases of *gazellae* were quicker, more 'breathy' and slightly higher pitched (Fig. 2B). The two-note phrases of *splendida* lasted 3.2–4.2 seconds while those of *gazellae* occupied 2.5–3.4 seconds, i.e. with an overlap around the 3.2–3.4-seconds interval). On average, notes of *splendida* peaked at 1.8 kHz vs. 1.9 kHz for *gazellae*. Comparisons were made from both 'natural' recordings and those in response to playback. The length of inter-phrase intervals varied, and our sample of *gazellae* is too small to provide any meaningful comparisons.

Based on our analysis, we conclude that there are consistent differences between the two-note phrases of *splendida* and *gazellae*. As a next step, we suggest that controlled experiments using playback are conducted to understand the significance of these differences. We also recommend that *novaehibernicae* is included in the analysis.

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References:

Clements, J. F., Schulenberg, T. S., Iliff, M. J., Roberson, D., Fredericks, T. A., Sullivan, B. L. & Wood, C. L. 2016. The eBird / Clements checklist of birds of the world: v. 2016. www.birds.cornell.edu/clementschecklist/download/

Collar, N. J., del Hoyo, J. & Jutglar, F. 2015. The number of species and subspecies in the Red-bellied Pitta *Erythropitta erythrogaster* complex: a quantitative analysis of morphological characters. *Forktail* 31: 13–23.

Gill, F. & Donsker, D. (eds.) 2016. IOC world bird list (v. 6.3). doi: 10.14344/IOC.ML.6.3.

Irestedt, M., Fabre, P.-H., Batalha-Filho, H., Jønsson, K. A., Roselaar, C. S., Sangster, G. & Ericson, P. G. P. 2013. The spatiotemporal colonization and diversification across the Indo-Pacific by a 'great speciator' (Aves, *Erythropitta erythrogaster*). *Proc Roy. Soc. B* 280: 20130309.

Tobias, J. A., Seddon, N., Spottiswoode, C. N., Pilgrim, J. D., Fishpool, L. D. C. & Collar, N. J. 2010. Quantitative criteria for species delimitation. *Ibis* 152: 724–746.

Addresses: Markus Lagerqvist, Hovås Snöbärsväg 2, lgh 1101, 436 54 Hovås, Sweden, e-mail: markus.lagerqvist@usa.net. Roger McNeill, 71 Mayfield Road, Cedar Creek, Qld 4520, Australia, e-mail: themcneills@rocketmail.com. Ashley Banwell, 13 Swaffham Road, Cockley Cley, Swaffham, Norfolk, UK, e-mail: otusbrooki@aol.com

Range extension for Buff-fronted Owl *Aegolius harrisii* in north-east Brazil and a case of *Heterochromia iridis* in Strigidae

Juan Ruiz-Esparza, José Percílio Mendonça Costa, Caroline Santos, Daniela Pinheiro Bitencurti Ruiz-Esparza, Raone Beltrão-Mendes & Stephen F. Ferrari

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Buff-fronted Owl *Aegolius harrisii* is one of 22 species of Strigidae in Brazil (Sick 1997). The species has a circum-Amazon range (Barlow & Cuello 1964, Fjeldså & Krabbe 1990, König *et al*. 1999, Barrionuevo *et al*. 2008, Ubaid *et al*. 2012) and is found from sea level to 3,800 m (Lima & Castro 1994, Marks *et al*. 1999, Bravo & Barrio 2014). In Brazil, isolated records indicate that *A. harrisii* is distributed throughout most of the east of the country (Kaminski 2009, Santos 2009, Rebelato *et al*. 2011, Ubaid *et al*. 2012, Santos *et al*. 2014). Here

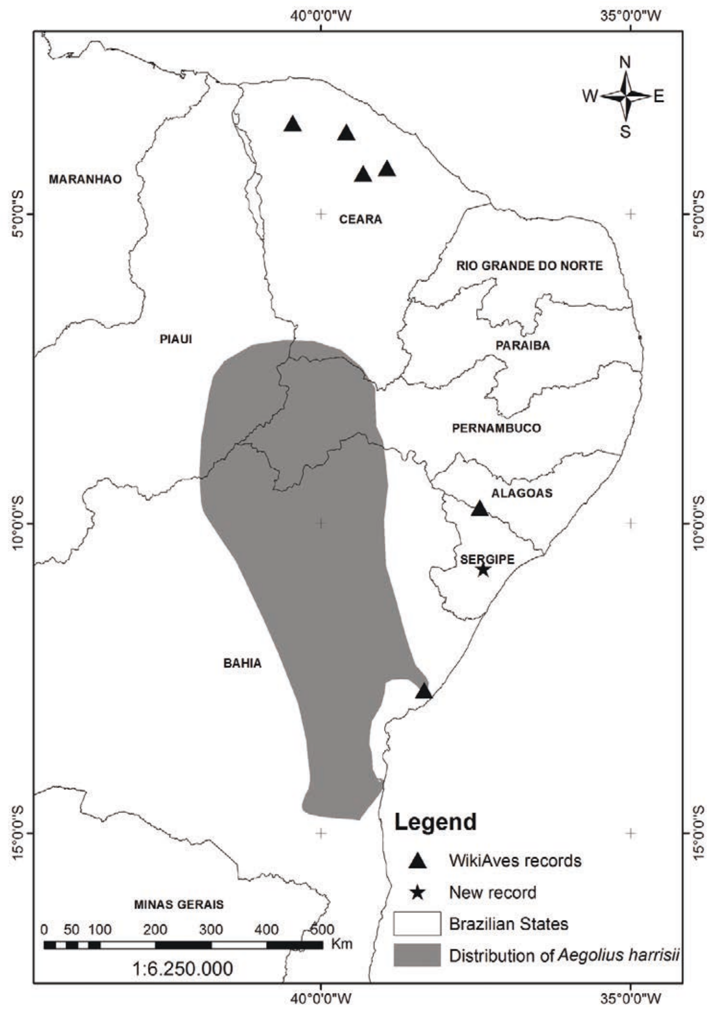

Figure 1. Present record (star) and isolated records (WikiAves 2016) of Buff-fronted Owl *Aegolius harrisii* from north-east Brazil and its current distributional polygon (in grey) following BirdLife International (2017).

we present the first record of *A. harrisii* in the state of Sergipe, extending the species' known distribution at least 100 km from the nearest localities in Alagoas and Bahia (WikiAves 2016; Fig. 1).

A Buff-fronted Owl was found near Parque dos Falcões, municipality of Itabaiana, Sergipe (10°44'S, 37°22'W) in November 2014. The local ecosystem is characteristic of the more open environments at the ecotone between Atlantic Forest and *Caatinga*. The bird was taken to the park, where it was examined and found to be in good health. We measured its wing (125 mm), total length (19.5 cm) and body mass (140 g). The owl was placed in a mobile enclosure, where it remains in quarantine, and has been registered with IBAMA, the Brazilian federal environment agency (ring no. 173).

Figure 2. *Heterochromia iridis* in Buff-fronted Owl *Aegolius harrisii* at Parque dos Falcões, Itabaiana, Sergipe, Brazil (Juan Ruiz-Esparza)

In addition, we also observed that the individual possesses an uncommon condition in birds, *Heterochromia iridis*, or different-coloured irides. The right iris is pale yellowish, whereas the left is orange-yellow (Fig. 2). *Heterochromia iridis* can occurs in more than 7% of individuals in some vertebrate species (e.g., horses, pigs and buffalo) (Gelatt *et al*. 1973, Misk *et al*. 1998), but few cases have been reported in birds and this appears to be the first pertaining to Strigidae. Given the lack of data for birds, it is unclear whether this condition relates to an inflammation, degeneration of the iris, or some other abnormality.

A. harrisii appears to be relatively rare, and is poorly known in museum collections (Studer & Teixeira 1994, Marks *et al*. 1999), which hampers systematic analysis of its biology or distribution. The available records do, however, suggest that the species is uncommon and patchily distributed (Stotz *et al*. 1996). While few records are available from north-east Brazil, mainly from Ceará (Table 1), they indicate that the species is perhaps adapted to the arid *Caatinga*, and may be a habitat generalist. The present record, together with other

TABLE 1

Records of Buff-fronted Owl *Aegolius harrisii* in north-east Brazil.

Brazilian state	**Municipality**	**No. of Records**	**Biome**	**Reference**
Alagoas	Pão de Açúcar	8	*Caatinga*	WikiAves (2016)
Bahia	Camaçarí	1	Atlantic Forest	WikiAves (2016)
Ceará	Canindé	1	*Caatinga*	WikiAves (2016)
	Guaramiranga	1		
	Itapagé	1		
	Meruoca	26		
Sergipe	Itabaiana	1	Atlantic Forest	Present study

recent records (WikiAves 2016), indicates a much more ample distribution than that given by BirdLife International (2017).

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References:
Barlow, J. C. & Cuello, J. 1964. New records of Uruguayan birds. *Condor* 66: 516–517.
Barrionuevo, C., Ortiz, D. & Capllonch, P. 2008. Nuevas localidades de Lechucita canela *Aegolius harrisii dabbenei* (Strigidae) para la Argentina. N*uestras Aves* 53: 45–47.
BirdLife International. 2017. Species factsheet: *Aegolius harrisii*. http://datazone.birdlife.org/species/factsheet/buff-fronted-owl-aegolius-harrisii (accessed 20 January 2017).
Bravo, A. G. & Barrio, J. 2014. New distribution records of the Buff-fronted Owl *Aegolius harrisii* Cassin, 1849 (Aves: Strigidae) in Peru. *Check List* 10: 156–159.
Fjeldså, J. & Krabbe, N. 1990. *Birds of the high Andes*. Zool. Mus., Univ. of Copenhagen & Apollo Books, Svendborg.
Gelatt, K. N., Rempel, W. K., Makambera, T. P. E. & Anderson, J. F. 1973. Heterochromia iridis in miniature swine. *J. Heredity* 64: 343–347.
Kaminski, N. 2009. Primeiro registro documentado de *Aegolius harrisii* para o Estado de Santa Catarina, Brasil. *Cotinga* 31: 79.
König, C., Weick, F. & Becking, J.-H. 1999. *Owls: a guide to the owls of the world*. Yale Univ. Press, New Haven, CT.
Lima, P. C. & Castro, J. O. 1994. Ocorrência e reprodução de *Aegolius harrisi* na Bahia. P. 136 *in IV Congr. Bras. Orn*. Sociedade Brasileira de Ornitologia, Recife.
Marks, J. S., Cannings, R. J. & Mikkola, H. 1999. Family Strigidae (typical owls). Pp. 76–151 *in* del Hoyo, J., Elliott, A. & Sargatal, J. (eds.) *Handbook of the birds of the world*, vol. 5. Lynx Edicions, Barcelona.
Misk, N. A., Semieka, M. A. & Fathy, A. 1998. Heterochromia iridis in water buffaloes (*Bubalus bubalis*). *Veterinary Ophthalmology* 1: 195–201.
Rebelato, M. M., Cunha, G. G., Machado, R. F. & Hartmann, P. A. 2011. Novo registro do caburé-acanelado (*Aegolius harrisii*) no Bioma Pampa, sul do Brasil. *Biotemas* 24: 105–107.
Santos, K. K., Miguel, M. & Lombardi, V. T. 2014. Novos registros do caburé-acanelado *Aegolius harrisii* (Cassin, 1849) para o Estado de Minas Gerais e comentários sobre sua biogeografia. *Atualidades Orn*. 181: 7–11.
Santos, R. E. F. 2009. Ampliação da distribuição de *Aegolius harrisii* a partir de coleta por atropelamento. *Atualidades Orn*. 147: 46–47.
Sick, H. 1997 *Ornitologia brasileira*. Ed. Nova Fronteira, Rio de Janeiro.
Stotz, D. F., Fitzpatrick, J. W., Parker, T. A. & Moskovits. D. K. 1996. *Neotropical birds: ecology and conservation*. Univ. of Chicago Press.
Studer, A. & Teixeira, D. M. 1994. Notes on the Buff-fronted Owl *Aegolius harrisii* in Brazil. *Bull. Brit. Orn. Cl*. 114: 62–63.
Ubaid, F. K., Maffei, F., Moya G. M. & Donatelli, R. J. 2012. Range extension for Buff-fronted Owl *Aegolius harrisii* in south-east Brazil. *Bull. Brit. Orn. Cl*. 132: 175–179.
WikiAves. 2016. A Enciclopédia das Aves do Brasil. www.wikiaves.com.br/mapaRegistros_cabure-acanelado (accessed 6 October 2016).

Addresses: Juan Ruiz-Esparza, Graduate Program in Development and Environment PRODEMA, Universidade Federal de Sergipe, Av. Marechal Rondon s/n, 49100-000, São Cristóvão, Sergipe, Brazil; and Nucleus of Education in Agricultural and Earth Sciences, Universidade Federal de Sergipe, Campus do Sertão, Rodovia Engenheiro Jorge Neto, km 3, Silos, 49680-000, Nossa Senhora da Glória, Brazil, e-mail: juancolorado21@hotmail.com. José Percílio Mendonça Costa, Instituto Parque dos Falcões, Itabaiana, Sergipe, Brazil. Caroline Santos, Program in Ecology and Conservation, Universidade Federal de Sergipe. Av. Marechal Rondon s/n, 49100-000, São Cristóvão, Brazil. Daniela Pinheiro Bitencurti Ruiz-Esparza, Nucleus of Education in Agricultural and Earth Sciences, Universidade Federal de Sergipe, Campus do Sertão, Rodovia Engenheiro Jorge Neto, Km 3, Silos, 49680-000, Nossa Senhora da Glória, Brazil. Raone Beltrão-Mendes & Stephen F. Ferrari, Dept. of Ecology, Universidade Federal de Sergipe, Av. Marechal Rondon s/n, 49100-000, São Cristóvão, Brazil.

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