

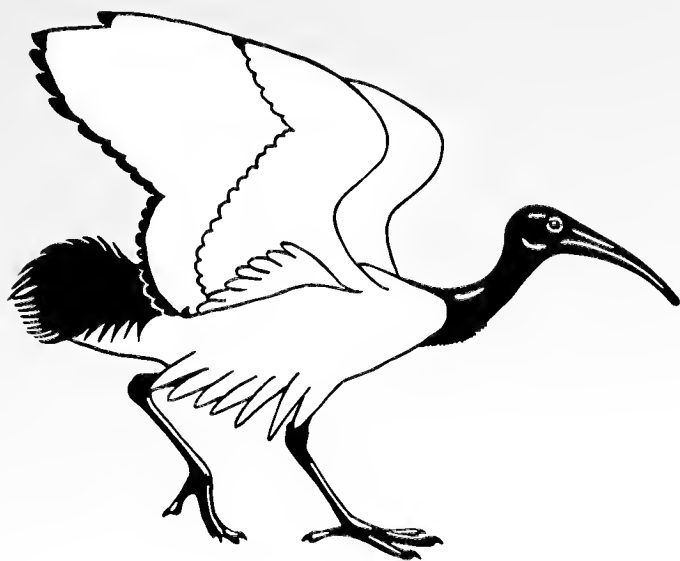
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Bulletin of the British Ornithologists' Club

NATURAL HISTORY
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Volume 134 No. 1
March 2014

FORTHCOMING MEETINGS

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

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

Evening meetings are 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.marketaverns.co.uk/the_barley_mow.html or ask the Chairman for directions.

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

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

25 February 2014—6.30 pm—Richard Porter—*Birds of Socotra: populations and distribution*

Abstract: The Socotra archipelago lies in the Arabian Sea, c.350 km south of the Yemen mainland. Ecologically heavily influenced by the dry south-west monsoon that batters the islands in May–September, it boasts high endemism in plants, reptiles, insects and birds, which I will summarise. Whilst its avifauna is species-poor, with just 42 regular breeders, 11 are endemic, making it the richest area of avian endemism in the Middle East (along with the highlands of south-west Arabia). From 1999 to 2011, I have been engaged in mapping the distribution and determining the populations of the breeding species and I will present some of my findings. I will also talk briefly about the migrants that visit the islands and recent taxonomic studies that have added Socotra Buzzard *Buteo socotraensis*, Abd Al Kuri Sparrow *Passer hemileucus* and Socotra Golden-winged Grosbeak *Rhychostruthus socotranus* to the species list. My talk will end with my thoughts on future research and conservation.

Biography: Richard Porter has had a continuing involvement in bird research and conservation in the Middle East since 1966, when he spent the autumn studying soaring bird migration over the Bosphorus. Whilst his early exploits were largely in Turkey, since 1979 most of his visits have been to Yemen, particularly Socotra, and Iraq, where he is the bird and conservation adviser to Nature Iraq. Richard, who is author of *Birds of the Middle East*, advises BirdLife International on their Middle East programme.

20 May 2014—5.30 pm—Annual General Meeting, followed at 6.30 pm by Guy Kirwan—*Cuban birds at home and abroad, in the field and museum*

Abstract: This talk will provide an introduction to the birds of the largest Caribbean island, Cuba, which despite boasting the most speciose avifauna in the West Indies supports fewer endemics than either Hispaniola or tiny Jamaica. Nevertheless, depending on taxonomy, at least seven avian genera occur only on Cuba, as well as the world's smallest bird, Bee Hummingbird *Mellisuga helenae*, while the country might yet prove to be the last bastion of one of the planet's most iconic birds, Ivory-billed Woodpecker *Campephilus principalis*. Despite >150 years of ornithological exploration, our knowledge of Cuban birds is still advancing comparatively rapidly, especially with respect to their ecology and conservation, largely via the efforts of a few dedicated researchers, both Cuban and foreign. My talk will focus on the taxonomy, ecology and conservation of some of the most special of Cuba's birds, as well as providing an introduction to travel in what was very briefly part of the British Empire!

Biography: Guy Kirwan has been a regular visitor to the Greater Antilles since the mid-1990s and is a co-author of a forthcoming checklist to Cuban birds. He is a freelance ornithologist and editor, notably of *Bull. Brit. Orn. Cl.*, with strong interests in avian taxonomy and the breeding biology of birds in the New World tropics. A Research Associate at the Field Museum of Natural History in Chicago, he recently joined the BOU's Taxonomic Subcommittee and currently works for Lynx Edicions on the HBW Alive project.

23 September 2014—6.30 pm—Dr Andrew Gosler—*Ethno-ornithology*

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

A one-day meeting in the Flett Theatre, Natural History Museum, South Kensington, London SW7 5BD starting at 10.30 am. Details to be announced

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Bulletin of the BRITISH ORNITHOLOGISTS' CLUB

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CLUB ANNOUNCEMENTS

Chairman's message

Since 2003 and the publication of the *The birds of Morocco*, the BOC and the BOU have jointly published the Checklist series and other books (e.g. *The bird atlas of Uganda*). However, following a thorough review of its activities, the BOU has decided to withdraw from the publication of such titles with immediate effect. All BOU and joint BOU/BOC titles may of course still be purchased via the BOU website: www.bou.org.uk or from the BOU office, P.O. Box 417, Peterborough PE7 3FX, UK.

The BOC Committee remains of the view that Checklists fit naturally with the Club's aims and objectives, and make an important contribution to ornithological studies. Consequently, it is committed in principle to their continued publication and is now considering in detail the practicalities of undertaking this task as sole publisher, including discussion with the BOU and Dr David R. Wells, Checklist Commissioning Editor. The aim is to seek to resolve the many outstanding issues and to establish our intensions in time for the AGM in May. In the meantime any views and or comments would be gratefully received by David Wells or myself.

Chris Storey

Annual General Meeting

The Annual General Meeting of the British Ornithologists' Club will be held in the upstairs room at The Barley Mow, Horseferry Road, Westminster, London SW1P 2EE, at 5.30 pm on Tuesday 20 May 2014.

Agenda

1. Apologies for absence
 2. Minutes of the Annual General Meeting held on 21 May 2013 (see *Bull. Brit. Orn. Cl.* 133: 165–166, and the BOC website).
 3. Receive and consider the Chairman's Review, the Trustees' Report and the Accounts for 2013 (these will be available in the room before the start of the meeting).
 4. The Bulletin Editor's report—Mr G. M. Kirwan.
 5. Election of Officers. The Committee proposes that:
 - i. Dr R. P. Prÿs-Jones be re-elected as *Hon. Secretary*
 - ii. Mr D. J. Montier be re-elected as *Hon. Treasurer*No other changes to the Committee are proposed as all other members are eligible to serve at least one more year in office.
 6. Any other business, of which advance notice has been given.
-

Gerlof Fokko Mees (1926–2013)

Gerlof Mees, former bird curator at the Rijksmuseum van Natuurlijke Historie (RMNH) at Leiden, Netherlands, was born into a well-off family in Bloemendaal, Netherlands. Both his parents had a keen interest in natural history, and Gerlof was stimulated to study birds by them and by his uncle Jan Verwey, founder of Dutch research into bird migration and ethology. After completing secondary school, he started to study biology in Leiden, but this was soon interrupted by a stay on Java (1946–49) as part of the Dutch forces in the Indonesian independence war. His scarce spare time was spent birdwatching, and problems identifying the local white-eyes *Zosterops* brought him into contact with George Junge, then bird curator at RMNH. Junge permitted Mees to study the white-eyes in his care, and Gerlof also learned the practical work of a museum department. Though he specialised in fish research (thought to be more likely to produce employment than birds), Gerlof visited Trinidad & Tobago when still a student and collected birds during an eight-month stay in 1953/54, reporting on these together with his mentor (Junge & Mees 1958). Between May 1955 and July 1957 he was an assistant at RMNH, working in both the bird and fish departments. He obtained his doctorate in 1956. His study on white-eyes resulted in a thesis on the Indo-Australian *Zosteropidae* (Mees 1957). However, fishes still held his interest and Mees was appointed a curator at the Western Australian Museum in Perth in 1958 mainly for his fame as an ichthyologist. There he continued

to work on Zosteropidae, but (with fishes) also on Australian larks and owls, and on the birds of the West Pilbara and Kimberley areas. He described several new taxa for Western Australia and, moreover, met his future wife, Veronica. After Junge's death in 1962 Gerlof was appointed bird curator at RMNH and the family moved to Leiden in 1963.

The rich Indonesian collections at RMNH now formed the main subject of Mees' work, resulting in very thorough publications on the birds of Bangka, the Moluccas, Misool, southern New Guinea and Java. Moreover, he made collecting trips to Nigeria, Guyana, Zimbabwe and (especially) Suriname, often with Veronica, while he also oversaw the acquisition of large bird collections for RMNH from Turkey, Mexico, Taiwan, Kenya, Tanzania and Flores, resulting in further major papers and several revisions and shorter notes. His distributional notes or reviews of Andaman sparrowhawks, Chinese Crested Tern *Sterna bernsteini*, Large-tailed Nightjar *Caprimulgus macrurus*, Common Cuckoo *Cuculus canorus* and Whiskered Tern *Chlidonias hybrida* are meticulously detailed. His publication list numbers c.100 articles on birds, but his list of papers on fishes is also long.

Mees' luxury work room at RMNH, surrounded by shelves with 3,000 bird books and complete series of >200 bird journals with a central desk covered by long rows of bird skins, jars with fishes, and piles of reprints and manuscripts made a lasting impression on most visitors, especially as Gerlof often seemed disturbed when one dared to enter his room. However, visitors with serious interests were always pleasantly provided with books and articles, and given free access to the collections, though they perhaps would still feel themselves rather uneasy because Gerlof often would debate the failure of the political system in the Netherlands at the same time. It was wonderful to see Mees find his way among the 50,000 mounted birds and 200,000 skins and clutches to pick out a special item, especially as large parts of the collections were not yet databased. Within the museum staff he was admired because of his deep knowledge on the history of the collections and of nomenclatorial questions, but some people felt ambiguous towards him. For instance, though fluent in at least four languages, as an employee of a Dutch museum Mees often insisted in writing in his native language when publishing in RMNH journals, using a rather old-fashioned style. As a result, editors of journals, being some of his fellow curators, had to translate his lengthy manuscripts into English, during which small errors frequently crept in. Mees tended to blame his colleagues for this, although his own proof-reading could have prevented the mistakes. Also, he still worked periodically on fishes, even though these had a curator of their own.

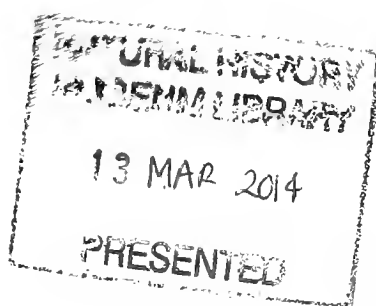
Mees retired in 1991 to Western Australia with Veronica, where their children had already settled. Until his death, he maintained a deep interest in ornithology, and despite living in the outback he published several papers and notes, in part with help of friends in Leiden who sent him literature. The change from the research institute RMNH into the public museum with research facilities Naturalis Biodiversity Center and its move within Leiden was followed by him with much interest. In his last years, failing eyesight largely hindered further research, much to his regret. He died peacefully on 31 March 2013. He will be remembered for *Monarchia sacerdotum* Mees, 1973, from Flores, and in *Caprimulgus meesi* Sangster & Rozendaal, 2004.

Main publications of Gerlof F. Mees

1946. Courtship feeding of Willow-Warbler. *Brit. Birds* 39: 280.
1957. A systematic review of the Indo-Australian Zosteropidae (pt. I). Ph.D. thesis. Univ. of Leiden.
1958. The avifauna of Trinidad and Tobago. *Zoöl. Verhand.* 37: 1–172 (with G. C. A. Junge).
1961. A systematic review of the Indo-Australian Zosteropidae (pt. II). *Zoöl. Verhand.* 50: 1–168.
1961. An annotated catalogue of a collection of bird skins from West Pilbara, Western Australia. *J. Roy. Soc. West. Austral.* 44: 97–143.
1964. A revision of the Australian owls (Strigidae and Tytonidae). *Zoöl. Verhand.* 65: 1–62.
1965. The avifauna of Misool. *Nova Guinea, Zool.* 31: 139–203.
1969. A systematic review of the Indo-Australian Zosteropidae (pt. III). *Zoöl. Verhand.* 102: 1–390.
1970. On some birds from southern Mexico. *Zoöl. Meded.* 44: 237–245.
1970. Birds of the Inyanga National Park, Rhodesia. *Zoöl. Verhand.* 109: 3–74.
1970. Notes on some birds from the island of Formosa (Taiwan). *Zoöl. Meded.* 44: 287–304.
1971. Systematic and faunistic remarks on birds from Borneo and Java, with new records. *Zoöl. Meded.* 45: 225–244.
1972. Die Vögel der Insel Gebe. *Zoöl. Meded.* 46: 69–89.
1974. Additions to the fauna of Suriname. *Zoöl. Meded.* 48: 55–67.
1975. Identiteit en status van *Sterna bernsteini* Schlegel. *Ardea* 63: 78–86.
1977. Geographical variation of *Caprimulgus macrurus* Horsfield (Aves, Caprimulgidae). *Zoöl. Verhand.* 155: 1–47.

1977. The subspecies of *Chlidonias hybridus* (Pallas), their breeding distribution and migration (Aves, Laridae, Sterninae). *Zoöl. Verhand.* 107: 1–64.
1979. Die Nachweise von *Cuculus canorus* L. im Indo-Australischen Raum. *Mitt. Zool. Mus. Berlin* 55, *Suppl. Ann. Orn.* 3: 127–134.
1979. Verspreiding en getalssterkte van de Witwangstern, *Chlidonias hybridus* (Pallas), in Europa en Noord-Afrika. *Zoöl. Bijdragen* 26: 3–63.
1980. The sparrow-hawks (*Accipiter*) of the Andaman Islands. *J. Bombay Nat. Hist. Soc.* 77: 371–412.
1982. Bird records from the Moluccas. *Zoöl. Meded.* 56: 91–111.
1982. Birds from the lowlands of southern New Guinea (Merauke and Koembe). *Zoöl. Verhand.* 191: 1–188.
1986. A list of the birds recorded from Bangka Island, Indonesia. *Zoöl. Verhand.* 232: 3–176.
1991. Bemerkungen über *Acrocephalus caffer* (Sparman) in der Tahiti-Gruppe (Aves, Sylviidae). *Proc. K. Ned. Akad. Wet., Ser. C* 94: 243–256.
1994. *The birds of Surinam*. Second edn. Vaco, Paramaribo. [Thoroughly updated version of Haverschmidt's original work of 1968.]
1996. Geographical variation in birds of Java. *Publ. Nuttall Orn. Cl.* 26: 1–119.
2006. The avifauna of Flores. *Zoöl. Meded.* 80(3): 1–261.

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Some black-and-white facts about the Faeroese white-speckled Common Raven *Corvus corax varius*

by *Hein van Grouw*

Received 24 April 2013

SUMMARY.—The white-speckled raven, a colour aberration of the Faroese Raven *Corvus corax varius* Brünnich, 1764, has occurred in the Faroe Islands since at least the Middle Ages. It has been described in many publications, and was a desired object for collectors of curiosities, especially in the 18th and 19th centuries. Early in the 20th century (1902) the last white-speckled individual was seen in the Faeroes, leaving only about two dozen specimens in museum collections. Although often referred to as albino, the aberration causing the white feathers is not albinism but leucism.

Common Raven *Corvus corax* Linnaeus, 1758, has a circumpolar distribution in the Northern Hemisphere. In addition to nominate *C. c. corax*, ten subspecies have been described, including the slightly larger *C. c. varius* Brünnich, 1764, which is endemic to the Faeroes and Iceland. The white-speckled variant of *C. c. varius* was known only from the Faeroes. Salomonsen (1934a) discussed whether white-speckled birds might also have occurred in Iceland, as claimed by Olaus Magnus (1555), but doubted this for several reasons. It is unknown when the mutation first arose, but Ole Worm already had two specimens in his Museum Wormianum in Copenhagen, both collected before 1650 (Worm 1655).

By 1767 Ascanius had written that the white-speckled variant was not a separate species but a variety of Common Raven. However, in later descriptions both Vieillot (1817) and Wagler (1827) referred to it as a distinct species, giving rise to an ongoing debate concerning its taxonomic status.

Salomonsen (1934) described the presumed inheritance of white-speckled plumage based on historical records of the colours of pairs and their offspring. His study suggested a recessive inheritance for the black-and-white pattern, which is a form of leucism (van Grouw 2012, 2013). Recessive genes can be inherited invisibly via many generations before two birds, both carrying the recessive gene, mate, making the white-speckled gene visible in their offspring. Therefore, if this was indeed a recessive gene, it is difficult to be sure whether it has been lost, through time, since the last white-speckled bird was seen, or whether it might still occur in some individuals.

A remarkable bird, occurring in small numbers in a remote place, will inevitably be targeted by collectors. Both live birds and mounted specimens of the white-speckled raven were sent to museums and collectors of curiosities throughout Europe from the 17th century, although many specimens were subsequently lost or destroyed. Only 26 specimens remain in museums (van Grouw & Bloch in press).

Based on the numerous reports in the literature, one can acquire a fairly good idea of the population size of the Faroese raven through time. It is obvious that it was very common until c.1850. Svabo (1783) mentioned 'large flocks', Landt (1800) stated that it was a well-known 'bird of prey', Graba (1830) saw many in 1828, and Atkinson (1989) said the same in 1833. Both Holm (1848) and Müller (1862) regarded the raven as common but Feilden (1872) saw fewer than expected. Annandale (1905) observed hardly any and, although the population

thereafter increased again, in 1930 Salomonsen (1931) still saw only small numbers, as did Ferdinand (1947) later. Bloch also observed few ravens in 1963, but in 1974 she noted a remarkable increase (Bloch *et al.* 2010). By 1981 at least 117 breeding pairs were counted on the Faeroes and the population was estimated at 150–350 pairs (Bloch & Sørensen 1984: 59). The recovery was mainly due to food supplies at waste sites of fish factories and incineration plants (Bloch 1981, Bloch & Sørensen 1984). Despite a legal requirement, introduced in 1988, for waste sites to be covered, limiting food for the ravens, the estimated number of breeding pairs in the Faeroes is currently c.500 (J.-K. Jensen pers. comm.).

The sharp decline in numbers on the Faeroes after 1850 was mainly due to the increase in the islands' human population, combined with the local beak tax still in force (Bloch 2012). The Faeroese National Archive contains lists from all six districts, covering most of the period 1742–1934, during which the annual number of ravens destroyed appears to have been c.150–250 (Bloch 2012). Around 1900 the population apparently reached its lowest ebb and the white-speckled variant became extinct.

The white-speckled mutation

Although the terms albino and partial albino are frequently used for the white-speckled ravens (Hartert & Kleinschmidt 1901, Sage 1962), the mutation causing the black-and-white pattern is a form of leucism. Leucism, from the Greek *Leukos* = white, can be defined as the partial or total lack of melanin in feathers (and skin) (van Grouw 2012, 2013). The lack of melanin is due to the congenital and heritable absence of pigment cells from some or all of those skin areas where they would normally provide the growing feather with colour. Depending on the type of leucism, the amount of white can vary from just a few feathers (= partial leucistic) to all-white individuals, which always possess colourless skin as well. Partially leucistic birds can have a normal-coloured bill and legs depending on where the colourless patches occur. However, leucistic birds always have pigmented eyes. To properly understand the nature of leucism it is necessary to know something of feather pigmentation first.

Melanins are the commonest pigments in birds and play a major role in the coloration of feathers, skin and eyes. They comprise two main types: eumelanin and pheomelanin, which differ in colour, chemical composition and pigment granule structure (Fox & Vevers 1960). Eumelanin produces black, grey and brown feathers, and eye and skin colour, while pheomelanin only occurs in feathers, and determines colours from deep reddish brown to pale buff. In all *Corvus* species only eumelanin is present, but for convenience it will simply be referred to as melanin hereafter.

Melanin is produced by specialised cells in the skin referred to as melanin cells or melanocytes, which develop from melanoblasts formed in the 'neural crest' – the embryonic spinal cord. Normally, melanoblasts migrate at an early embryonic stage to the mesodermal layers of the skin. Finally incorporated in the skin and feather follicles, melanoblasts develop into melanocytes to provide the feather cells with melanin (Crawford 1990).

The migration process is genetically determined and any (inheritable) change can affect the final distribution of the melanoblasts. If, due to a mutation, the melanoblasts are unable to migrate from the neural crest to the skin, there will be no melanocytes present to produce melanin, resulting in a completely un-pigmented (white) bird with pink skin. However, the eyes are not red (the crucial difference from albinos). The embryonic origin of eye pigments partially differs from that of the rest of the body; eye pigments are formed mainly from the outer layer of the optic cup (Lamoreux *et al.* 2010) and as leucism affects only the migration of melanoblasts originating from the neural tube it has no influence on eye pigmentation with an optic cup origin.

In addition to being all white, leucistic birds can be partially white, with colourless feathers adjacent to normal ones. The pied appearance can be caused by a delay in the migration of the melanoblasts from the neural tube to the skin (Wagener 1959, Wendt-Wagener 1961). Because of the delay, some melanoblasts reach certain parts of the body where the skin is too far developed to incorporate them, resulting in these parts lacking colour. Another possibility is that, from the outset, insufficient melanoblasts develop in the neural crest and therefore not all parts of the body are provided with pigment cells (Daneel & Schumann 1961, 1963).

The white in leucistic birds is often patchy and bilaterally symmetrical due to the way melanoblasts migrate to the rest of the body, leaving certain areas without pigmentation. The white pattern is already present in juvenile plumage and the amount of white does not change with age. The commonest form of leucism affects pigment in body parts furthest from the neural crest: the face, the 'hand' of the wings, the feet and belly. This form caused the white-speckled plumage of Faroese ravens.

Although this form of leucism is commonest and occurs in many bird species (Fig. 4), leucism in general is uncommon. A far more widespread cause for the lack of pigment in feathers is progressive greying (van Grouw 2012, 2013) but this is not discussed further here.

Presumed inheritance and leucism in related species

The black-and-white pattern in ravens was uniform and symmetrical, following the pattern of the commonest form of leucism in birds; absence of pigment in the body parts furthest from the pigment cells' origin (Figs. 1–2). The total area of affected skin parts may differ, with smaller or larger white patches as a result, but generally the head and throat are white, as are the belly, primaries and primary-coverts, and claws. In extreme cases almost the entire wings are white, and the white throat extends to the belly breaking the black pectoral band.

Depending on where in the face pigment is lacking, the melanins in the eyes may be absent too, resulting in only those pigments that formed in the optic cup being visible. These appear to be much paler as, according to Graba (1830), who examined two freshly shot white-speckled ravens, the eyes were grey greenish-white (*'Iris graugrünlichweiss'*). In other species, e.g. Rook *Corvus frugilegus* and Greylag Goose *Anser anser*, bluish-white eyes occur in leucistic individuals.

Different genes in birds result in this leucistic pattern. In Mallard *Anas platyrhynchos* it is due to a dominant gene, while in Japanese Quail *Coturnix japonica* it is recessive. It is partially dominant in Helmeted Guineafowl *Numida melcagris*: if the gene is present just once (heterozygous) the bird will possess the white pattern, while the presence of two genes (homozygous) produces an all-white bird. The same is true in Zebra Finch *Poephila guttata* (Fig. 3), although in this case another recessive gene is the cause.

Nothing is known with certainty concerning inheritance in genus *Corvus*. It has not been recorded in ravens except in the Faeroes (van Grouw 2012). Nor is it known to have occurred in Carrion Crow *Corvus corone*, but is found very rarely in Hooded Crow *C. cornix* and Jackdaw *C. monedula*. In Rook, however, it is reasonably frequent, though in some cases only a small patch of white feathers is present on the chin, occasionally with 1–2 white claws. Given that Rooks lose most of their facial feathering on reaching adulthood, leucism is probably under-recorded. A juvenile leucistic Rook was described as a separate species by Sparman (1786), who named it *Corvus clericus* (Latin for priest) on account of its white 'bib' (Fig. 8). There is, however, considerable variation in the white chin's size and, the larger it is, the more likely it is to be accompanied by white primaries and claws. More extreme

1



2



Figure 1. Drawing of a life-like white-speckled Common Raven *Corvus corax* in flight (Katrina van Grouw)

Figure 2. White-speckled Common Raven *Corvus corax* specimen in the Überseemuseum Bremen, Germany (UMB 3800), collector and collection date unknown, but probably pre-1870 (Gabriele Warnke)



cases follow the same pattern as in Common Raven (Fig. 5).

According to Salomonsen (1934) the inheritance of leucism in Common Raven was recessive, based on different crossings mentioned in the literature: two black parents may produce white-speckled offspring (Ascanius 1767, Graba 1830, Holm 1848, Müller 1862) and a white-speckled crossed with black may also yield white-speckled young (Graba 1830, Holm 1848, Müller 1862). In all cases white-speckled ravens hatched only when black parents were heterozygous (= carrying the allele for white-speckled once). Unfortunately, no records are available of crossings between two white-speckled birds. Based on these pairings, provided they are correct, straightforward recessive inheritance for white-speckled appears to be true. However, that this genetic variety was lost during the period that the variants were hunted to extinction, c.110 years ago, is in contrast to the recessive trait. Many black ravens in the Faeroes must have been heterozygous for leucism and the gene would be carried for many generations after the last white-speckled bird was seen. Sooner or later two heterozygous individuals would presumably have paired, producing white-speckled offspring. However, during the last century no pied ravens have been reported, but this might be explained by the severe decline in the population as a whole in the second half of the 19th century.

5a



5b



Figure 3. Comparable leucism in different bird species: above, Bengalese finch *Lonchura domestica*; bottom, Zebra Finch *Poephila guttata* (Pieter van den Hooven)

Figure 4. Comparable leucism in different bird species: Common Moorhen *Gallinula chloropus*, Durham, UK, January 2010 (Glen Roberts)

Figure 5. Leucistic Ravens *Corvus frugilegus*: left, juvenile, State Darwin Museum Moscow (SDM OF61) (Igor Fadeev); right, adult, formerly at Zoological Museum Amsterdam (ZMA 54604, now at NBC Naturalis) (Hein van Grouw)

As there are no reliable estimates of the proportions of white-speckled ravens and black ones, it is impossible to calculate the presumed gene frequency in a specified timeframe. However, with some assumptions we can acquire an impression of how common the allele for white-speckled could have been. Given that ravens were still common in the mid 1800s (Holm 1848, Müller 1862), we might assume that the pre-1850 population comprised *c.*120 breeding pairs (240 individuals). White-speckled individuals were not uncommon then (Graba 1830), so let us assume they comprised 10% of the population (24 birds). Of the 216 black birds a percentage were heterozygous. Knowing that the mutation had been present for centuries and that white-speckled individuals were breeding, it is plausible that 50% carried the allele for white-speckled (108 birds). Symbolising black as A and white-speckled as a, the number of genotypes in the population were: 108 AA, 108Aa and 24 aa, i.e. 45% did not carry the white-speckled gene (AA), 45% were carriers (Aa) and 10% were white-speckled (aa), thus the white-speckled gene was present in 55% of the raven population.

If we consider all white-speckled individuals eliminated, the a-allele in single form is still present in 50% of the population; that is, 108 pairs of black ravens (216 individuals; 108 AA and 108 Aa). In this scenario, four different crosses are possible and all equally probable (AA × AA = 100% AA; AA × Aa = 50% AA and 50% Aa; Aa × AA = 50% AA and 50% Aa; Aa × Aa = 25% AA, 50% Aa and 25% aa). Expressed as a percentage, the genotype of the offspring of these 108 pairs is: 56.25% black and lacking the gene for white-speckled (AA); 37.5% black and carrying the gene for white-speckled (Aa) and 6.25% white-speckled (aa). By removing the white-speckled individuals, a-gene frequency will be reduced, but if the population is sufficiently large the gene will still be present. However, the natural process of genetic drift can cause loss of certain alleles, especially in small populations.

Genetic drift is the random change in allele frequency in a population and is, along with selection, mutation and migration, a basic mechanism of evolution. These mechanisms cause changes in genotypes and phenotypes over time, and determine the degree of genetic variation within a population. In a textbook scenario, the alleles in the offspring form a representative sample of those in parents. However, in practice, certain alleles may be unrepresented in the next generation, especially if the number of offspring is low.

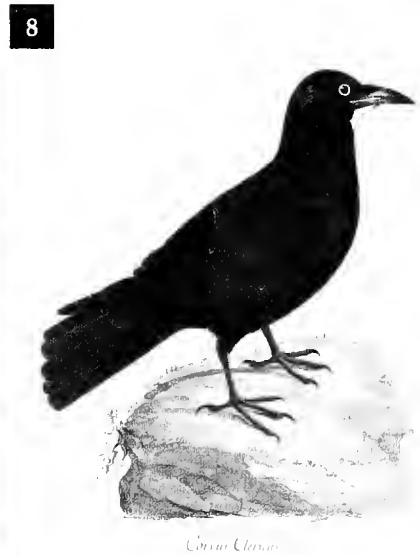


Figure 6. Diluted Common Raven *Corvus corax*, Velbastaður, 2 March 2008 (Hans Eli Sivertsen)

Figure 7. Diluted Common Raven *Corvus corax* specimen shot at Fugloy in 2008, prepared by J.-K. Jensen and donated to the Museum of Natural History, Tórshavn (Jens-Kjeld Jensen)

Figure 8. *Corvus clericus*, described by Sparrman in 1786 in *Museum Carlsonianum*, was in fact a leucistic Rook *C. frugilegus* (Harry Taylor / © Natural History Museum)

These alleles are therefore lost to subsequent generations.

The degree of loss of genetic variation (dF) is inversely proportional to the number of breeding individuals (N). The following formula illustrates the correlation between dF and N: $dF = 1 / (2N)$ (Ouborg 1988). This shows that the loss of alleles is higher in proportion to the number of breeding birds. Moreover, in small populations genetic variation decreases more rapidly. Besides that white-speckled individuals were hunted because of their value to collectors, the beak tax caused an overall decline in the raven population. In all, it is plausible that the allele for

white-speckled was recessive and was lost when the raven population reached its lowest abundance.

Last observations of white-speckled ravens

Records in the literature always referred to white-speckled or pied ravens, which were known to the Faroese people by the name Hvittravnur. Occasionally 'white' specimens may have been reported, as Debes (1673) suggested, but he also stated that 'the white ravens are not entirely white, but speckled with black feathers'. Because of their curiosity, white speckled-ravens were always highly prized. In the latter half of the 19th century especially, when the raven population was suffering intense persecution, white-speckled birds were even more severely hunted, leading to their extinction in the early 20th century. Several observations of presumed white-speckled birds were made post-1900: (1) 2 November 1902, Mykines (Andersen 1905, Salomonsen 1934), (2) autumn 1916, Velbastaður and Koltur (Ryggi 1951), (3) winter 1947 and again in late 1948, Nólsoy (Ryggi 1951), and (4) before Easter 1965, Sandvík (Nolsøe & Jespersen 2004).

In winter 1988/89, a 'white' raven was seen around Tórshavn (J.-K. Jensen pers. comm.) and again at Velbastaður throughout winter 2007/08. It was photographed on 2 March 2008 (Fig. 6), clearly revealing that it was not a white-speckled individual. In this case, and almost certainly in three of the four cases listed above, a different mutation was involved, namely dilution. Dilution is a quantitative reduction of melanins (van Grouw 2013) meaning that the number of pigment granules is reduced, but the pigment itself is unchanged. Therefore, due to the lower concentration of granules than normal, a 'weaker' or 'diluted' colour occurs. This can be compared to a photograph in a newspaper; a high concentration of black ink dots close together is perceived as black, while fewer black dots in the same-sized area appear grey. Dilution is not uncommon in Carrion Crow, Hooded Crow and Rook.

The bird at Velbastaður was last seen in April 2008, and this, or another diluted individual, later in 2008 at Suðuroy. Earlier the same year another was shot at Fugloy and donated to the Museum of Natural History in Tórshavn (Fig. 7). Additionally, in August 2008, one was at Viðareiði and two more at Fugloy. In December 2009 another was seen twice at the south end of Suðuroy. All those seen in 2007–09 appeared to be young (J.-K. Jensen pers. comm.). Their fate is unknown.

Obviously, the gene for dilution is present in Faroese ravens and probably has been for a considerable period. Returning to the observations in 1916, 1947, 1948 and 1965, all of these records were listed as 'white' ravens and not 'white-speckled'. Given that the gene for dilution is present and this aberration causes a solid grey-white plumage coloration, it is probable that these records were all diluted individuals. Only the record of 1902 mentioned white-speckling and therefore this date is considered the official date of extinction of the white-speckled variant of the Faeroes raven.

Conclusion

Despite being an icon for several centuries, the last white-speckled Faeroes raven was shot in 1902. One can assume that, along with the bird, the recessive allele for white-speckled plumage was also lost as a result of genetic drift combined with the severely depleted population. In addition to the species being hunted for pest control purposes, especially in the 19th century, white-speckled birds were consistently targeted by bird collectors.

The white-speckled plumage was caused by a recessive gene mutation known as leucism: a lack of melanin pigment due to the congenital and heritable lack of pigment cells from some or all of the skin parts where they would normally provide the growing feather

with pigment. Inheritable leucism in birds is rare, but the black-and-white pattern in ravens (lack of pigment in the face, the ‘hand’ of the wings, the feet and belly) is the commonest form and occurs in many bird species.

Although the allele for leucism is apparently lost, another inheritable, recessive colour mutation now occurs in Faeroes ravens; dilution—a quantitative reduction of melanin pigment that produces a solid silvery grey plumage. Dilution is less rare and is occasionally found in other raven populations in North America and Europe.

To date, there are no confirmed records of diluted ravens breeding in the Faeroes, or elsewhere, but there is no reason to suppose that is impossible. Therefore, given that the Faeroe ravens represent an island population, the allele for dilution may become established in the future, just as the allele for leucism was in the past. Other island species offer examples of inheritable colour aberrations in their populations, of which the best is probably the flightless Weka *Gallirallus australis* in New Zealand. Three independent inheritable colour aberrations, melanism, leucism and progressive greying, occur in the South Island population (pers. obs.), and the extinct White Gallinule *Porphyrio albus* of Lord Howe Island was the result of inherited progressive greying in the local Purple Gallinule *P. porphyrio* population (Hume & van Grouw submitted).

For at least a century, carriers of the dilution allele have been present on the Faeroes and a new icon in the island’s avifauna is likely to arise, albeit only if diluted individuals are not targeted as a collector’s item. The continued occurrence of ‘white’ ravens on the Faeroes is conditional upon naturalists of the future learning a lesson from the past.

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Breeding biology of the Grey-breasted Flycatcher *Lathrotriccus griseipectus* in south-west Ecuador

by Harold F. Greeney

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SUMMARY.—I studied two nests of Grey-breasted Flycatcher *Lathrotriccus griseipectus* in seasonally deciduous dry forest in south-west Ecuador. Nests were open cups constructed in natural depressions, one in the buttress of a large tree and one in a clump of bromeliads. Construction of one nest was completed in five days. Clutch size was two at one nest, and the eggs were pale beige with sparse, red-brown blotching. Eggs at both nests were laid 48 hours apart, and at one nest both eggs hatched 16 days after clutch completion. One nest was depredated immediately after the second egg was laid, but both nestlings fledged after 14 days at the other. Only one adult incubated, but both provisioned nestlings. The species' breeding biology is similar in all respects to that of the congeneric Euler's Flycatcher *L. euleri*, as well as to members of the closely related genus *Empidonax* of temperate and subtropical America.

Grey-breasted Flycatcher *Lathrotriccus griseipectus* is a monotypic species restricted to the Tumbesian region of western Ecuador and Peru (Fitzpatrick 2004). Within its small range, the species is generally uncommon and has apparently declined in recent years, consequently Birdlife International (2013) treat it as Vulnerable. The species' only congeneric, Euler's Flycatcher *L. euleri*, is comparatively widespread and its breeding biology well known (Allen 1893, Euler 1900, Belcher & Smooker 1937, Aguilar *et al.* 1999, Aguilar & Marini 2007, Marini *et al.* 2007). The breeding biology of *L. griseipectus*, however, is wholly unknown. Here I describe the species' nest, eggs and nestlings from south-west Ecuador.

Methods and Results

I studied two nests of *L. griseipectus* at the Jorupe Reserve (Jocotoco Foundation), near Macará, Loja province, south-west Ecuador (04°23'S, 79°57'W; 600 m). Jorupe encompasses tropical deciduous forest typical of the Tumbesian bioregion (Best & Kessler 1995) and protects several other range-restricted species that have only recently had their breeding biology described (Miller *et al.* 2007, Rheindt 2008, Gelis *et al.* 2009). I took linear measurements of eggs to the nearest 0.1 mm and weighed them periodically during incubation using an electronic balance sensitive to 0.001 g. Eggs were individually marked using a permanent marker. I equate loss of mass during incubation with loss of water from the embryo (Ar & Rahn 1980). I made nest measurements to the nearest 0.5 cm. I collected nests after fledging or abandonment and let them dry *ex-situ* for two weeks before taking them apart and weighing their components to the nearest 0.001 g.

On 10 February 2010 I discovered the first nest (Fig. 1) at 18.00 h. It was empty and no adults were nearby. When I returned next day at 14.00 h, it contained a single egg, which was dry and cool to the touch. I returned six times during the afternoon but I did not observe an adult and the egg was cold and unattended until after dark. Next morning, pre-dawn, the egg was still cold, indicating that an adult had not spent the night at the nest. During seven visits on 12 February I encountered an adult only twice, suggesting that little time

was devoted to incubation that day. The nest still held a single egg at 18.00 h and next morning at 05.00 h the egg was cold, again indicating that no adult had spent the night at the nest. When I returned that afternoon the second egg had been laid. I checked the nest contents daily until, on 1 March at 10.45 h, I discovered that the first egg to have been laid was hatching. The second hatched a few hours later. These observations indicate an incubation period of 16 days from the laying of the second egg until hatching of both eggs. Both nestlings left the nest at c.11.00 h on 15 March, giving a nestling period of 14 days.

I found the second nest on 16 February at 08.00 h, when I flushed an adult from a natural indentation at the base of a bromeliad (see below). On closer inspection I was unable to detect a nest, but 3–4 dead leaves inside the depression had possibly been brought by the adult. By the morning of 18 February, however, the nest cup was well formed and a few rootlets had been added to the lining. The first egg was laid on the morning of 20 February, giving a building period of no more than five days. The nest still contained one egg at 18.00 h on 21 February and the second egg was laid between 06.15 and 10.00 h on 22 February. On 23 February, however, the nest was empty at 16.15 h. Both adults were still present and swooped close to me while bill snapping. There were no signs of eggshells and the nest was undamaged.

Both nests were open cups composed externally of dead leaves and bark, with a relatively sparse inner lining of fungal rhizomorphs, dark rootlets and pale grass stems and fibres. Mean (\pm SD) total dry weight of both nests was 7.2 ± 1.9 g. The relative contribution of materials is presented in Table 1. The first nest (Fig. 1) was placed 1 m above ground in a shallow, upward-opening cavity in the buttress root of a canopy-emergent *Ceiba* tree. The cavity was longer than it was wide, and the nest completely filled it. The second nest (Fig.

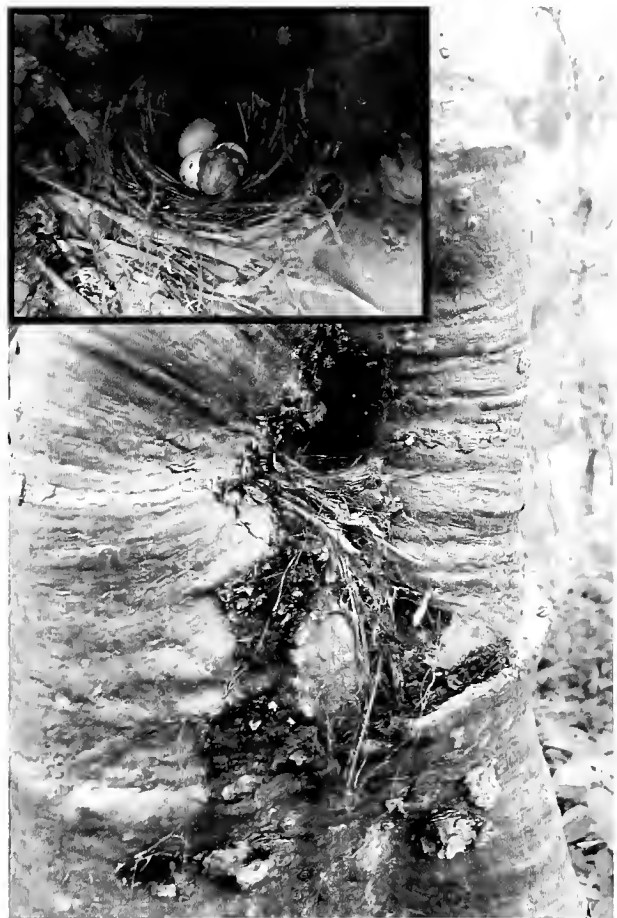


Figure 1. Position of nest 1 of Grey-breasted Flycatcher *Lathrotriccus griseipectus* in a shallow cavity on a tree root, with inset showing a detail of the nest, Jorupe Reserve, Loja province, Ecuador (Harold F. Greeney)

TABLE 1

Dry weight (g) of materials comprising the nests of two Grey-breasted Flycatchers *Lathrotriccus griseipectus* in south-west Ecuador.

| | flexible bark strips | stiff bark chips | total bark | dead leaves | fungal rhizomorphs | dark rootlets | thin stems | Total |
|------------|----------------------|------------------|------------|-------------|--------------------|---------------|------------|-------|
| Nest 1 | 0.295 | 1.752 | 2.047 | 0.549 | 1.289 | 0.527 | 0.111 | 4.523 |
| Nest 2 | 3.693 | 3.064 | 6.757 | 1.380 | 0.521 | 0.703 | 0.518 | 9.879 |
| Mean | 1.994 | 2.408 | 4.402 | 0.965 | 0.905 | 0.615 | 0.315 | 7.201 |
| SD | 1.201 | 0.464 | 3.330 | 0.294 | 0.272 | 0.062 | 0.144 | 1.894 |
| % of total | 27.7 | 33.4 | 61.1 | 13.4 | 12.6 | 8.5 | 4.4 | |



Figure 2. Position of nest 2 of Grey-breasted Flycatcher *Lathrotriccus griseipectus* in a depression amongst epiphytic bromeliads, with inset showing three eggs from two separate clutches, Jorupe Reserve, Loja province, Ecuador (Harold F. Greeney)

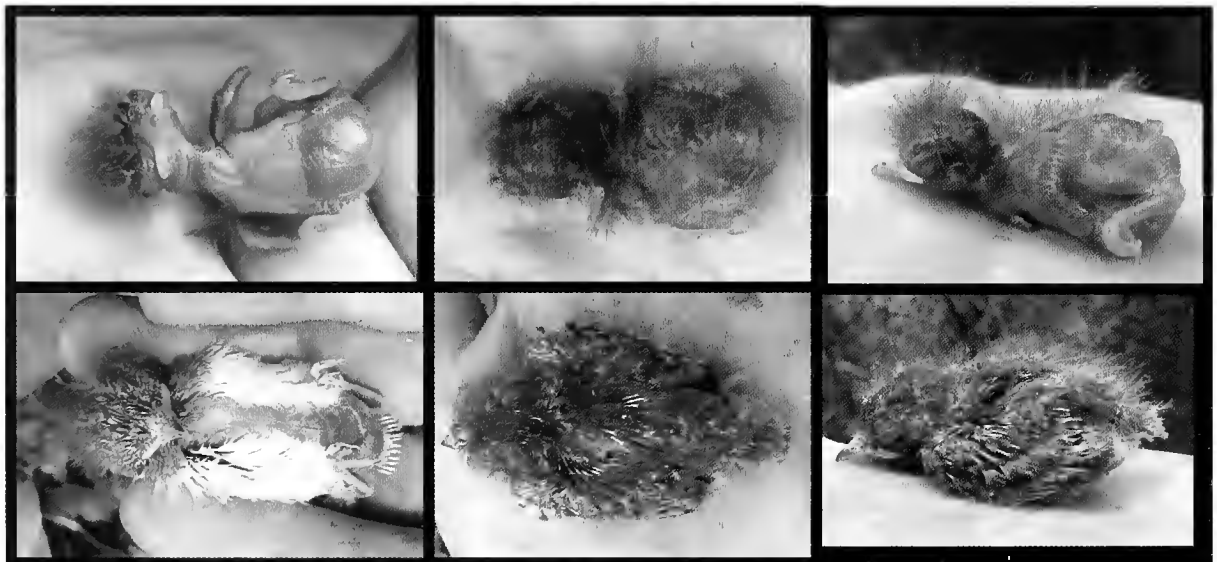


Figure 3. Nestlings of Grey-breasted Flycatcher *Lathrotriccus griseipectus*: upper row two days after hatching, and lower row nine days after hatching, Jorupe Reserve, Loja province, Ecuador (Harold F. Greeney)

2) was 4 m above ground, filling a slightly oblong hollow between the leaf bases of two bromeliads in a suspended clump of epiphytes. The external shape of the nests was oblong, fitting their respective cavities. The egg cups, however, were almost circular. Mean (cm \pm SD) measurements were: greatest external diameter, 8.3 ± 0.4 ; smallest external diameter, 5.5 ± 0.7 ; external height, 5.3 ± 0.4 ; internal diameter, 4.8 ± 0.4 ; internal depth, 3.3 ± 0.4 . Post-

fledging, the internal cup of the first nest was slightly stretched and the internal diameter (measured at perpendicular angles) was 6×5 cm.

All four eggs had a pale beige ground colour with sparse cinnamon and orange-brown spotting, heaviest near the larger end (Fig. 2). Mean (\pm SD) size of three eggs was $18.0 \pm 1.4 \times 13.5 \pm 0.5$ mm. Mean fresh weight of these eggs was 1.76 ± 0.27 g, all measured on the day they were laid. During incubation the two eggs at the first nest lost mass at a mean rate of $0.9 \pm 0.1\%$ / day of their original mass (range = 0.8–1.0% / day).

I was unable to obtain linear measurements or weights of the nestlings but here provide a qualitative description. On hatching, nestlings bore a dorsal covering of pale brown natal down, which was paler at the base of the plumes and even paler posteriorly, affording them a camouflaged, sun-dappled appearance. Their skin was dusky, pinker ventrally and their legs yellowish. Their bills were similar in coloration to their legs and bore contrasting, bright yellow-white rictal flanges. The mouth lining, throughout the nestling period, was bright yellow-orange. Two days after hatching their appearance had changed little. By nine days of age, however, the nestlings were well feathered, with only sparse tufts of natal down remaining (Fig. 3).

Adults were extremely wary around the nests, generally flushing when approached to within 10 m, disappearing silently into the nearest dense vegetation. Using a tripod-mounted video camera I was able to ascertain that only one adult (presumably the female as in other tyrannids: Fitzpatrick 2004) incubated. However, both sexes provisioned the young.

Discussion

Unsurprisingly, all aspects of the biology of *L. griseipectus* described here are similar to those of *L. euleri* (Aguilar *et al.* 1999, Aguilar & Marini 2007, Marini *et al.* 2007). In fact, the nest and eggs of *L. euleri* photographed by Buzzetti & Silva (2008) are extremely similar in colour, placement and construction to one of the two nests described here. While a sample size of two nests precludes any firm comparisons, it appears that *L. griseipectus* may lay fewer eggs than *L. euleri*, which is usually reported as having a modal clutch size of three (Aguilar *et al.* 1999, Auer *et al.* 2007). The incubation and nestling periods documented here at a single nest of *L. griseipectus* are both *c.*1 day shorter than mean durations reported for *L. euleri* (Aguilar *et al.* 1999, Auer *et al.* 2007). Both species of *Lathrotriccus* are also similar in their breeding habits to members of the closely related genus *Empidonax* of temperate regions (Lanyon 1986, Cicero & Johnson 2002), within which they have been placed in the past (Cory & Hellmayr 1927, Traylor 1979). Among other aspects, both genera share similar, cream-coloured or pale white, lightly spotted eggs, and well-constructed open-cup nests using a variety of substrates, but seemingly preferring well-supported sites such as ledges, thick branches, branch forks and even man-made structures (Russell & Woodbury 1941, King 1955, Walkinshaw & Henry 1957, Bowers & Dunning 1994, Briskie 1994, Wilson & Cooper 1998, Lowther 2000, Dobbs 2005).

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A taxonomic revision of the genus *Pitohui* Lesson, 1831 (Oriolidae), with historical notes on names

by John P. Dumbacher

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SUMMARY.—Since 1925, the genus *Pitohui* has included six species: Hooded *Pitohui dichrous*, Variable *P. kirhocephalus*, Crested *P. cristatus*, Black *P. nigrescens*, Rusty *P. ferrugineus* and White-bellied Pitohuis *P. incertus*. Recent molecular work has shown that the genus, as thus circumscribed, is polyphyletic, and includes four different lineages of disparate taxonomic affinities. Here, I review the taxonomic placement of the pitohuis and discuss appropriate names for each taxon. Each monophyletic group has an available generic name, and the true pitohuis (genus *Pitohui*) include only *P. kirhocephalus* and *P. dichrous*. A recommended genus-level taxonomy is proposed, including a new genus-species combination for the Morningbird *Pachycephala tenebrosa* of Palau.

The genus *Pitohui* currently includes six species of medium-sized (60–100 g) forest-dwelling birds restricted to New Guinea and nearby continental islands. They are: Hooded Pitohui *Pitohui dichrous*, Variable Pitohui *P. kirhocephalus*, Crested Pitohui *P. cristatus*, Black Pitohui *P. nigrescens*, Rusty Pitohui *P. ferrugineus* and White-bellied Pitohui *P. incertus* (Stresemann 1925, Mayr 1941). All have jay-like omnivorous habits, are gregarious (Diamond 1987) and recent work has demonstrated that they carry potent neurotoxins in their skin and feathers that may function in chemical defence in some species (Dumbacher *et al.* 1992, 2000, Dumbacher 1999). Because of recent interest in the evolution of toxicity, they have been the subject of phylogenetic studies (Dumbacher & Fleischer 2001, Jönsson *et al.* 2007, Dumbacher *et al.* 2008); these have suggested that the genus *Pitohui* is currently misclassified. Below, I summarise the taxonomic history of the genus and propose a classification based upon the most recent available genetic data.

Variable Pitohui *Pitohui kirhocephalus* (Lesson & Garnot, 1827) was first described in 1827 in the zoological reports of the French exploration ship, the *Coquille* (Lesson & Garnot 1827), which sailed in 1822–25. The ship's zoological findings were published in several volumes and an atlas (Lesson & Garnot 1826–30), in which the written description of this species was given under the name *Vanga kirhocephalus* in livr. 14, pp. 632–633, attributed to Lesson alone. Zimmer (1926) reported that this part was published on 9 January 1930. However, a figure of the species was published earlier under the authorship of Lesson & Garnot with the name 'Pie-grièche cap-gris *Lanius kirhocephalus*' on pl. 11 of the Atlas, released on 17 January 1827 (Zimmer 1926). Thus, this name has precedence, with Lesson & Garnot as authors (ICZN 1999: Art. 12.2.7). In his written description, Lesson recorded that 'Le vanga cap-gris habite les forêts de la Nouvelle-Guinée, aux alentours de Doréry, où les Papous le nomment *Pitohoui*.' Thereafter, Lesson (1831) recognised the distinctness of the grey-capped bird and placed it in a new genus, *Pitohui*. No explanation was given for the origin of the name, but it presumably came from the local 'pitohoui' used by New Guinean villagers near Dorey (now Manokwari), New Guinea, Indonesia (Lesson & Garnot 1827). Thus, the name is properly cited as *Pitohui kirhocephalus* (Lesson & Garnot, 1827).

In 1850, Reichenbach proposed the name *Rectes* for this genus in his *Avium systema naturale*, but proffered no explanation for the name change, just a single black-and-white

figure (no. 65) derived from Lesson & Garnot (1827), with the caption '*Reetes*'. At the time, no other species in the genus was described, so *Reetes* was proposed effectively as a replacement name for *Pitohui*, with *P. kirhocephalus* the type species by monotypy. Shortly thereafter, Bonaparte (1850) supported this, saying of *P. kirhocephalus*, 'C'est le type d'un genre distinct pour lequel nous préférons adopter le nom de *Reetes*, proposé par Reichenbach.' Bonaparte (1850) also added two other species to the genus *Reetes*, *R. diehrous* and *R. ferrugineus*, but *P. kirhocephalus* remained the type species as confirmed by multiple authors (Gray 1855, Salvadori 1881, Sharpe 1877). Although no justification was provided for their preference for *Reetes*, it was customary among taxonomists at the time to prefer scientific names with Latin roots over those without and to provide new names for those that had been 'improperly' formed. Sharpe later confirmed that '*Pitohui* is doubtless an older name than *Reetes*, but can surely be laid aside as a barbarous word' (Sharpe 1903).

The genus *Reetes* was in general usage after 1850, and two additional species were discovered and added to it, *Reetes nigrescens*, Black Pitohui (Schlegel, 1871), and *R. eristatus*, Crested Pitohui (Salvadori, 1875). When Rothschild & Hartert (1903) resurrected the name *Pitohui* for the genus, they treated all other generic names that had been proposed for its various species as synonyms. Stresemann (1925) then reduced the number of species recognised by Sharpe (1877), Salvadori (1881) and others from 16 to six, relegating many taxa to subspecies but accepting those mentioned above and *P. incertus* van Oort (1909). For the remainder of the 20th century, the genus *Pitohui* was restricted to the above six species (Mayr 1941, Rand & Gilliard 1967, Beehler & Finch 1985, Beehler *et al.* 1986).

But generic dismemberment had been foreshadowed. *Pseudoreetes* was introduced by Sharpe (1877) for Rusty Pitohui *Pitohui ferrugineus* (C. L. Bonaparte, 1850). With *Reetes ferrugineus* as its type species, *Pseudoreetes* is a valid available name for the genus now known to include the species *ferrugineus* and *incertus* (Dumbacher *et al.* 2008). In recent phylogenies, *Pseudoreetes* is strongly supported as a monophyletic genus sister to *Colluricincla* (shrike-thrushes) and distant from *Pitohui* (*P. kirhocephalus*) at family level (Jonsson *et al.* 2007, Dumbacher *et al.* 2008).

Black Pitohui *Reetes nigrescens* Schlegel, 1871, was also placed in its own genus, *Melanoreetes*, by Sharpe (1877). Recent molecular work has shown that it too is not closely related to *Pitohui* but is sister to the whistler genus *Paehyecephala* (Jonsson *et al.* 2007, Dumbacher *et al.* 2008) and should be recognised generically as well.

Crested Pitohui has also been recognised as distinct, and Iredale (1956) proposed the generic name *Ornoreetes* for it. Molecular analysis has revealed that Crested Pitohui is most closely related to Crested Bellbird *Oreoica gutturalis* of Australia and Rufous-naped Whistler *Alcedryas rufinucha* of New Guinea (Jonsson *et al.* 2007, Dumbacher *et al.* 2008). Nevertheless, it is quite distinct morphologically and behaviourally from these relatives, so recognition of *Ornoreetes* is recommended and the genus has recently been resurrected (Norman *et al.* 2009). These three taxa—*Oreoica*, *Alcedryas* and *Ornoreetes*—have historically been placed in the polyphyletic Pachycephalidae or, possibly incorrectly, in the Colluricinclidae. Recent analyses suggest that they are distantly related to other members of the basal core Corvoidea, and the family name Oreocidae has been applied to this group (Norman *et al.* 2009).

Molecular work also suggests that *P. kirhocephalus* and *P. diehrous* are indeed sister taxa (Dumbacher & Fleischer 2001, Jonsson *et al.* 2007, Dumbacher *et al.* 2008) and that this clade is probably a basal member of the Oriolidae, and perhaps sister to the figbirds, *Sphecotheres* Vieillot (Jonsson *et al.* 2010). Thus, the genus *Pitohui* contains only *P. diehrous* and *P. kirhocephalus*, and the best-available data place *Pitohui* within the Oriolidae, although more work is needed to confirm this.

I recommend that common names remain unchanged, because, although the 'pitohuis' are not monophyletic, they do form an ecological group, much like warblers around the world that are not monophyletic either. Pitohuis also resemble one another in their use of potent toxins (Dumbacher *et al.* 1992, 2000, 2008), in their participation and movements in mixed-species flocks (Diamond 1987), their geographic restriction to New Guinea, and in morphology and other behaviours (Stresemann 1925). The only proposal for an alternative common name has been 'wood-shrike' (Iredale 1956), an epithet already in use for *Teplirodornis* (Prionopidae).

The Morningbird (*Rectes tenebrosus* Hartlaub & Finsch, 1868) of Palau has been placed with the genus *Pitohui* by some authors. Although currently placed in *Colluricincla*, two independent DNA studies suggest that it is nested well within the whistler clade, *Pachycephala* (Dumbacher *et al.* 2008, Jönsson *et al.* 2008), and should be transferred to that genus.

A recommended taxonomy of pitohuis follows:

Family Oriolidae

Genus *Pitohui* Lesson, 1831

Pitohui dichrous (Bonaparte, 1850), Hooded Pitohui

Pitohui kirhocephalus (Lesson & Garnot, 1827), Variable Pitohui

Family Colluricinclidae

Genus *Pseudorectes* Sharpe, 1877

Pseudorectes ferrugineus (C. L. Bonaparte, 1850), Rusty Pitohui

Pseudorectes incertus (van Oort, 1909), White-bellied Pitohui

Family Pachycephalidae

Genus *Melanorectes* Sharpe, 1877

Melanorectes nigrescens (Schlegel, 1871), Black Pitohui

Genus *Pachycephala* Vigors, 1825

Pachycephala tenebrosa (Hartlaub & Finsch 1868), Morningbird (nov. comb.)

Family Oreoicidae

Genus *Ornorectes* Iredale, 1956

Ornorectes cristata (Salvadori, 1875), Crested Pitohui

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Notes on the birds of Parque Nacional Saslaya, Reserva de Biosfera Bosawás, Nicaragua

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SUMMARY.—We detail records of 23 rare or poorly known species from Parque Nacional Saslaya in the Reserva de Biosfera Bosawás of the Región Autónoma del Atlántico Norte in Nicaragua. These include the northernmost records of Violaceous Quail-Dove *Geotrygon violacea*, Black-headed Tody-Flycatcher *Todirostrum nigriceps* and Scarlet-thighed Dacnis *Dacnis venusta*. These findings clarify the northern range limits of several Caribbean slope species and highlight the importance of Central America's largest remaining wilderness area for biodiversity conservation.

Recent field work in eastern Honduras has documented northward range extensions for several Central American Caribbean slope species previously thought to reach only to Costa Rica or southern Nicaragua (Marcus 1983, Anderson *et al.* 2004, Vallely *et al.* 2010). Northern Nicaragua also hosts extensive Caribbean slope humid forest but remains little surveyed since the collections of W. W. Huber (1932) at El Edén on 20 March–10 April 1922. In particular, the extensive Reserva de Biosfera Bosawás (RBB), including parts of dpto. Jinotega and the Región Autónoma del Atlántico Norte (RAAN), and spanning elevations of 200–1,650 m, is poorly explored. RBB encompasses 19,922 km² including buffer zones and several core areas of 8,060 km². This protected area, with those in adjacent eastern Honduras, forms the largest remaining wilderness in Central America. Although the northern RBB is sparsely populated, Parque Nacional Saslaya (PNS) encompassing 631 km² in the south-eastern RBB is threatened by deforestation from small-landholder claims, some well inside the park boundaries (Kaimowitz *et al.* 2003, Stocks *et al.* 2007; ACV, LC-D pers. obs.). Anthropogenic landscapes now almost completely surround the eastern and southern borders of PNS (Stocks *et al.* 2007). While management challenges facing PNS are formidable, the area hosts many rare and poorly known species, and offers valuable opportunities for research, conservation and tourism. We are unaware of previously published reports on the avifauna of PNS and the larger core areas of the RBB to the north are virtually unknown to ornithologists. To date, 262 bird species have been reported in PNS (pers. obs.). Here, we detail observations of 23 rare or poorly known species in PNS, mostly in the río Labú drainage, but also at Cerro El Torito in the western PNS.

Methods

We visited the PNS on 14–20 April 2009 (LC-D), 30 April–8 May 2012 (LC-D) and 3–13 March 2013 (ACV, LC-D). We searched for birds primarily in humid lowland rainforest and along adjacent watercourses. In May 2012 and March 2013 we used a dozen 12 × 2.5 m mist-nets with 30–36 mm mesh size deployed in forest understorey. On 2–8 May 2012 we amassed 546.33 mist net hours, and on 4–12 March 2013 another 582 mist-net hours. Observations were gathered opportunistically along the limited network of existing trails and passable watercourses. Coordinates for sites within PNS are: Cerro El Torito 13°42'50"N, 85°02'50"W, río Labú drainage 13°41'20"N, 85°01'20"W, Camp La Vaquita 13°43'50"N, 85°01'49"W. The locations of these and most other localities mentioned in the text are shown in Fig. 1.

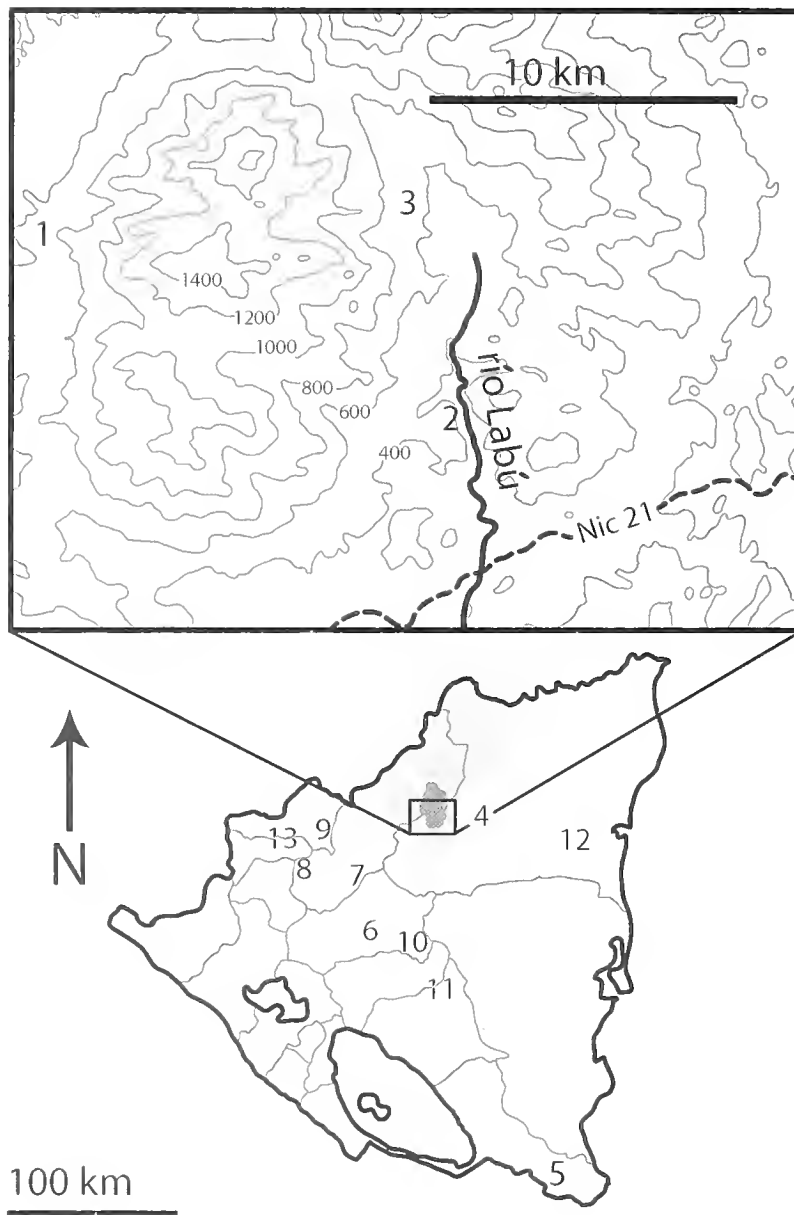


Figure 1. Map showing the location of Parque Nacional Saslaya (PNS, dark shaded area) within the Reserva de Biosfera Bosawás (pale shaded area) in Nicaragua. Inset shows topography and individual sites within PNS. Numbers refer to sites mentioned in the text: (1) Cerro El Torito, PNS; (2) río Labú drainage, PNS; (3) Camp La Vaquita, PNS; (4) El Edén, Región Autónoma del Atlántico Norte (RAAN); (5) río San Juan drainage, dpto. Río San Juan; (6) río Grande, dpto. Matagalpa; (7) Peñas Blancas, dpto. Jinotega; (8) Reserva El Jaguar, dpto. Jinotega; (9) Cerros Las Chachagüas, dpto. Jinotega; (10) Cerro Musún, dpto. Matagalpa; (11) Santo Domingo, dpto. Chontales; (12) Alamikangban / Layasiksa area, RAAN; (13) San Rafael del Norte, dpto. Jinotega.

Species accounts

SOLITARY EAGLE *Butorogallus solitarius*

Considered Near Threatened (IUCN 2013) and very rare and local throughout its range. T. R. Howell (*in* Martínez-Sánchez & Will 2010) considered *B. solitarius* hypothetical in Nicaragua and knew of no records. Martínez-Sánchez (2007) mentioned a sight record from the north-central highlands of Nicaragua (dpto. Nueva Segovia) on 18 January 2004. On 3 May and 6 May 2012, LC-D & G. Duriaux observed singles over the río Labú drainage at 425 m. On 11 March 2013 we observed a pair in courtship flight near Camp La Vaquita at c.650 m. A few minutes later a single, persistently vocalising, adult was seen at close range flying low over the canopy. On 13 March 2013 we observed an adult circling over the río Labú drainage at c.400 m. D. Hille (pers. comm.) also observed one at PNS on 15 January 2013. Given the few reports in recent years from northern Central America (outside Belize) we suspect that PNS (and perhaps the greater RBB) may represent an important regional stronghold.

BLACK-AND-WHITE HAWK-EAGLE *Spizaetus melanoleucus*

T. R. Howell (*in* Martínez-Sánchez & Will 2010) listed just two historical records from Nicaragua and the species is generally considered scarce and local over its extensive range. Three records from the río Labú drainage appear to be the first in northern Nicaragua: ACV & LC-D observed a single adult over the río Labú drainage, at 425 m, on 5, 7 and 8 March 2013.

SLATY-BACKED FOREST FALCON *Micrastur mirandollei*

Poorly known in Central America and long thought to range no further north than Costa Rica (AOU 1998). One seen by LC-D on 17 April 2009 at Cerro El Torito, PNS. It clearly showed plain white underparts and a yellow cere, eliminating Semiplumbeous Hawk *Leucopternis semiplumbeus*. ACV & LC-D also heard the distinctive song of *M. mirandollei* in the pre-dawn darkness at c.600 m on the mornings of 9–10 March 2013 at Camp La Vaquita. These are among the northernmost records, as the species has also recently been reported 140 km to the north in dpto. Gracias a Dios in eastern Honduras (Jones & Komar 2013b).

VIOLACEOUS QUAIL-DOVE *Geotrygon violacea*

Particularly rare in Central America, where unrecorded north of Nicaragua. Collected by Richardson early in the 20th century at Peñas Blancas in eastern dpto. Jinotega and in the río San Juan drainage at Los Sábalo (Martínez-Sánchez & Will 2010). More recently found in central Nicaragua at Cerro Musún by LC-D (eBird 2013). On 5 March 2013 ACV observed a single adult female for several minutes at close range in the río Labú drainage at 425 m, which is the northernmost record ever.

SCARLET MACAW *Ara macao*

Described by Huber (1932) as common around El Edén. Decades later T. R. Howell suggested that it was declining on the Caribbean slope of Nicaragua (Martínez-Sánchez & Will 2010). We encountered singles and pairs at Cerro El Torito and in the río Labú drainage, PNS. A. Farnsworth (eBird 2013) also reported it at río Labú on 27 March 1996, and D. Hille (pers. comm.) encountered two at PNS on 18 January 2013. Though the species persists at PNS, large macaws are usually easily detected and our few encounters do not suggest the presence of a large population.

RUFIOUS-VENTED GROUND CUCKOO *Neomorphus geoffroyi*

Very poorly known in Nicaragua, with historical specimens from the central foothills at Chontales (Salvin & Godman 1896), río Tuma and Peñas Blancas, and from southern Nicaragua in the río San Juan region at Savala. Unreported in northern Nicaragua since Howell (1971) listed it for the Caribbean lowlands near Waspam, RAAN. We have no conclusive evidence for its presence at río Labú, PNS, but park guards, unprompted by us, described the species in convincing detail and appeared familiar with its natural history. Pending more evidence we regard the species' occurrence as hypothetical.

CENTRAL AMERICAN PYGMY OWL *Glaucidium griseiceps*

Poorly known in northern Nicaragua. Several recent records from the río San Juan drainage on the southern Caribbean slope (Martínez-Sánchez & Will 2010). We heard and recorded this owl's distinctive song on 9 March 2013 at Camp La Vaquita, at c.600 m.

SHORT-TAILED NIGHTHAWK *Lurocalis semitorquatus*

Widespread species known from only a handful of records in Nicaragua, the earliest a specimen taken by Huber (1932) on the río Bambana, RAAN. Additional records are given by Martínez-Sánchez & Will (2010). At dusk on 6 and 12 March 2013 we observed singles in the río Labú drainage PNS. A. Farnsworth (eBird 2013) also reported it there on 27 March 1996.

TODY-MOTMOT *Hylomanes momotula*

Endemic to southern Mexico and Central America, where uncommon and local throughout. LC-D heard and saw one at 835 m at Cerro el Torito on 18 April 2009.

KEEL-BILLED MOTMOT *Electron carinatum*

Scarce, local, endemic to the Caribbean slope foothills of Central America, and treated as Vulnerable (IUCN 2013). We obtained sound-recordings at Camp La Vaquita, at c.600 m, in the río Labú PNS. A. Farnsworth (eBird 2013) also reported the species there on 27 March 1996.

GREAT JACAMAR *Jacamerops aureus*

Long thought to range no further north than Costa Rica (AOU 1998), this widespread but scarce species was first reported from adjacent eastern Honduras in 2004 (Jones 2004, Vallely *et al.* 2010). The first records for Nicaragua were in the río San Juan region (Múnera-Roldán *et al.* 2007). Given decades of habitat destruction, thought to be declining in Central America (e.g. in Costa Rica; Sigel *et al.* 2005). We heard two and observed another at close range responding to playback on 12 March 2008 in the río Labú drainage.

CINNAMON WOODPECKER *Ceelus loricatus*

Long known in Nicaragua mainly from the río San Juan region (AOU 1998). T. R. Howell (*in* Martínez-Sánchez & Will 2010) accepted its presence in northern Nicaragua based on a specimen taken at 275 m by Huber (1932) at El Edén, RAAN. Howell remarked that 'if its range is continuous it must be rare in most of eastern Nicaragua to have been missed by every other observer and collector, including Richardson'. We found it common in the río Labú with multiples heard daily and one observed at close range responding strongly to playback. A. Farnsworth (eBird 2013) also reported it on 27 March 1996. ACV & M. Tórriz detected a single by voice near Layasiksa in the eastern lowlands of RAAN on 23 August 2009. In northern Nicaragua may be confined to the interior Caribbean foothills, a little-studied region, and perhaps disjunct in relation to the southern Central American population.

WHITE-FRONTED NUNBIRD *Monasa morphoews*

This widespread species reaches its northernmost limit in eastern Honduras (AOU 1998, Rasmussen & Collar 2002). It is poorly known in Nicaragua and has perhaps declined in abundance in parts of southern Central America (Sigel *et al.* 2005). We detected the species once by voice on 4 March 2013 in the río Labú drainage. A. Farnsworth (eBird 2013) also reported *M. morphoews* there on 27 March 1996.

STRIPED WOODHAUNTER *Hyloctistes subulatus*

Reaches its northernmost limit in eastern Honduras (Vallely *et al.* 2010) and known in northern Nicaragua from specimens taken at Río Grande, dpto. Matagalpa, and Peñas Blancas, dpto. Jinotega, by W. B. Richardson in 1908–09 (Miller & Griscom 1925). LC-D

trapped two on 3–4 May 2012 in the río Labú drainage (Jones & Komar 2013a) and ACV observed a single responding to playback there on 15 March 2013.

SCALE-CRESTED PYGMY TYRANT *Lophotriccus pileatus*

Long thought to range no further north than Costa Rica (AOU 1998). Marcus (1983) first reported it from eastern Honduras but the species was unknown in Nicaragua until one was closely observed by LC-D at Cerro El Torito on 17–18 April 2009. On 14 May 2009 LC-D & G. Duriaux observed two at Reserva El Jaguar, dpto. Jinotega. On 23 February 2010 G. Duriaux & LC-D observed one at Cerros Las Chachagüas, dpto. Jinotega (Chavarría & Batchelder 2012). We located two by voice near Camp La Vaquita, c.650 m, in the río Labú drainage on 8–9 March 2013.

BLACK-HEADED TODY-FLYCATCHER *Todirostrum nigriceps*

Poorly known north of Costa Rica. On 5 March 2013 LC-D observed one in the canopy of tall, humid, broadleaf forest in the río Labú drainage, discerning the yellow underparts, long, narrow tail and spatulate bill. A. Farnsworth (eBird 2013) also reported the species in the río Labú drainage on 27 March 1996. These are the northernmost records and represent a range extension of 350 km from the río San Juan region.

GREY-HEADED PIPRITES *Piprites griseiceps*

Endemic to Central America and poorly known. T. R. Howell (*in* Martínez-Sánchez & Will, 2010) knew of just two records in Nicaragua, one collected by Richardson in the río San Juan region, and a specimen secured by Huber (1932) at El Edén. On 10 March 2013 ACV observed one for several minutes as it foraged with a large mixed-species flock in the midstorey of tall humid broadleaf forest at c.600 m at Camp La Vaquita. The bird perched upright in the open on a large branch before making an abrupt, upward sally to pursue a small lepidopteron. The same day LC-D & G. Duriaux observed a single nearby.

WING-BANDED ANTBIRD *Myrmornis torquata*

No documented records in Costa Rica (Stiles & Skutch 1989, Sandoval & Sánchez 2012) and only recently reported in eastern Honduras (Vallely *et al.* 2010), *M. torquata* is considered Near Threatened (IUCN 2013). In Nicaragua, known from specimens collected by W. B. Richardson, including several from Peñas Blancas, Jinotega. Another was collected in 1922 at El Edén (Huber 1932). Recently found to be locally common at Cerro Musún in dpto. Matagalpa (Chavarría & Duriaux 2011, 2013). LC-D trapped two in the río Labú drainage on 3 and 5 May 2012. On 5 March 2013 we captured one, and detected others by voice, in the same area. Known from five sites in northern Nicaragua: Peñas Blancas, dpto. Jinotega, El Edén, RAAN, Cerro Musún, dpto. Matagalpa, río Labú drainage, RAAN, and Santo Domingo, dpto. Chontales. Records from southern Nicaragua in the río San Juan region were presented by Cody (2000) and Múnera-Roldán *et al.* (2007). Some sites listed in the literature are now largely deforested and we assume that the species must be locally extinct, e.g. at Santo Domingo (Salvin 1872) and El Edén (Huber 1932). Our experience suggests that in northern Central America the species prefers tall, humid, broadleaf forest with sparse understorey on steep, well-drained, slopes at 200–1,200 m. Known sites for *M. torquata* in Nicaragua, as in Honduras (Vallely *et al.* 2010), feature irregular forest floors with large boulders or karstic outcrops.

LOVELY COTINGA *Cotinga amabilis*

Poorly documented in Nicaragua and probably declining in Central America (e.g. in Costa Rica; Sigel *et al.* 2005), where it is at best uncommon to rare and local throughout (Snow 2004). Kjeldsen (2005) reported it from Alamikangban in the lowlands of eastern RAAN. We did not find the species but A. Farnsworth (eBird 2013) reported it in the río Labú drainage on 27 March 1996.

THREE-WATTLED BELLBIRD *Procnias tricarunculatus*

Regarded as Vulnerable (IUCN 2013) and undertakes complex migrations (Powell & Bjork 2004), with those of northern populations incompletely understood. LC-D encountered the species at Cerro El Torito on 17 April 2009. We heard several calling in late March 2013 in the río Labú drainage, but the species was not common, with a silent female or young male on 6 March 2013 at c.400 m. Present in the north-central Nicaraguan highlands above 1,200 m in February–June (LC-D pers. obs). We consider those we encountered at 425–600 m in PNS as stragglers or late transients.

BLACK-THROATED WREN *Pheugopedius atrogularis*

Endemic to the Caribbean slope of Central America and poorly known near the northernmost limit of its range. T. R. Howell (*in* Martínez-Sánchez & Will, 2010) considered it to reach no further north than the río Escondido. However, it was recently recorded in eastern Honduras, in dpto. Gracias a Dios (Jones 2004, Vallely *et al.* 2010). LC-D observed one on 17 April 2009 at c.600 m at Cerro El Torito PNS.

AMERICAN DIPPER *Cinclus mexicanus*

Very rare and local in Central America and unreported in Nicaragua since Richardson collected it at San Rafael del Norte in 1892 (Martínez-Sánchez & Will 2010). During May 2012 and March 2013 we observed singles and pairs on most days in appropriate habitat on the río Labú and its tributaries. A Farnsworth also reported the species in this region on 27 March 1996 (eBird 2013). First records from Nicaragua in >100 years.

SCARLET-THIGHED DACNIS *Dacnis venusta*

Long thought to range no further north than Costa Rica (AOU 1998, Isler & Isler 1999), this widespread but scarce species was recently found in Nicaragua in the río San Juan basin at Bartola (Jones & Komar 2012). On 30 April 2012 LC-D observed a male near Rosa Grande in the buffer zone of PNS. In the río Labú drainage, on 5 March 2013, and at Camp La Vaquita, on 7 March 2013, we observed at least two pairs foraging on inflorescences of canopy vines together with Blue Dacnis *D. cayana*, Shining Honeycreeper *Cyanerpes lucidus* and Green Honeycreeper *Chlorophanes spiza*. These are the northernmost records and represent a range extension of 350 km from the río San Juan records.

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The avifauna of Mt. Karimui, Chimbu Province, Papua New Guinea, including evidence for long-term population dynamics in undisturbed tropical forest

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SUMMARY.—We conducted ornithological field work on Mt. Karimui and in the surrounding lowlands in 2011–12, a site first surveyed for birds by J. Diamond in 1965. We report range extensions, elevational records and notes on poorly known species observed during our work. We also present a list with elevational distributions for the 271 species recorded in the Karimui region. Finally, we detail possible changes in species abundance and distribution that have occurred between Diamond's field work and our own. Most prominently, we suggest that Bicolored Mouse-warbler *Crateroscelis nigrorufa* might recently have colonised Mt. Karimui's north-western ridge, a rare example of distributional change in an avian population inhabiting intact tropical forests.

The island of New Guinea harbours a diverse, largely endemic avifauna (Beehler *et al.* 1986). However, ornithological studies are hampered by difficulties of access, safety and cost. Consequently, many of its endemic birds remain poorly known, and field workers continue to describe new taxa (Pratt 2000, Beehler *et al.* 2007), report large range extensions (Freeman *et al.* 2013) and elucidate natural history (Dumbacher *et al.* 1992). Of necessity, avifaunal studies are usually based on short-term field work. As a result, population dynamics are poorly known and limited to comparisons of different surveys or differences noticeable over short timescales (Diamond 1971, Mack & Wright 1996).

Here, we report new distributional and ecological observations made during field work on Mt. Karimui, Chimbu Province. Mt. Karimui's avifauna was studied by Jared Diamond in 1965 (Diamond 1972) and we purposely returned to the same ridge he worked. Analysis of elevational changes in Mt. Karimui's avifauna will be presented elsewhere; here, we describe our survey results, including differences from Diamond's historical transect that may reflect avifaunal changes. Tropical bird communities in undisturbed forest are seldom subject to long-term monitoring studies, but populations are thought to be relatively stable (Munn 1985, Greenberg & Gradwohl 1997, Brooks *et al.* 2005, Martinez & Gomez 2013), albeit with local extinctions and colonisations well documented in fragmented forest (Willis 1974, Robinson 1999, Brook *et al.* 2003, Sodhi *et al.* 2004). Finally, we present a comprehensive list of Mt. Karimui's birds, including known elevational ranges and conservation status.

Methods

Study site.—The extinct volcano of Mt. Karimui lies in the southern part of New Guinea's Central Ranges, in Chimbu Province (Fig. 1). Satellite imagery and maps clearly demonstrate Mt. Karimui to be an old volcano with a blown-out caldera. However, when viewed from the Karimui Plateau it appears as a series of discrete peaks. These ridges rise steeply from the relatively level Karimui Plateau (c.1,100 m), and are tallest in the north, where they reach c.2,550 m. Whereas Mt. Karimui is covered in primary forest, a significant part of the fertile Karimui Plateau is under small-scale agriculture, particularly at Karimui Station, a government post c.6 km north-east of Mt. Karimui. For our purposes, we define

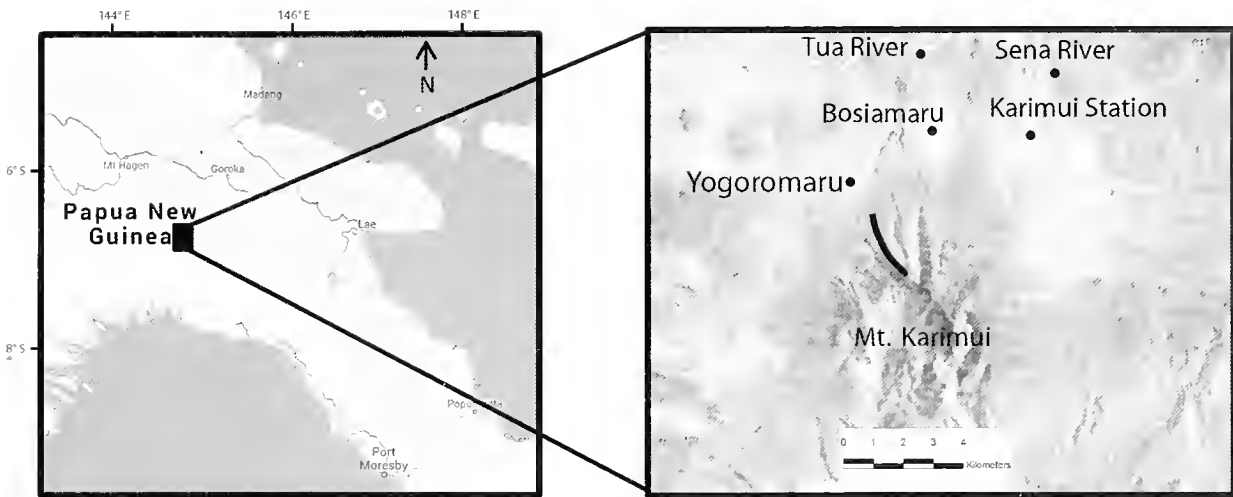


Figure 1. Map of Mt. Karimui, Chimbu Province, Papua New Guinea. The airstrip at Karimui Station, served primarily by small aircraft from Goroka, provides the principal access to the area. Our field work was concentrated on Mt. Karimui's north-west ridge above Yogoromaru village, the same ridge surveyed by Diamond (1972). The transect we surveyed is marked by the black line. See Table 1 for more information on site locations.

the Karimui area as the northern slopes of Mt. Karimui and adjacent Karimui Plateau south and east of the Tua River (see Fig. 1). All field work reported here pertains to this 'Karimui area': the southern ridges, foothills and adjacent lowlands of Mt. Karimui are ornithologically unexplored.

We first visited Mt. Karimui in 2011 during a week-long exploratory visit. We returned for two field seasons in 2012 to survey its birdlife: 13 June to 27 July (June–July) and 12 October to 14 December (October–December). Field work was concentrated on the same ridge studied by Diamond in 1965, Mt. Karimui's north-west ridge located above Yogoromaru village (Diamond 1972, see Fig. 1). In 1965, this ridge was entirely covered by primary forest. Environmental changes in the intervening years have been minor; we found it to be covered with primary forest above *c.*1,200 m, with the exception of two recently cleared small (*c.*1 ha) patches, the first a subsistence garden at 1,280 m and the second a clearing at the base of a recently constructed cellphone tower at the summit (2,520 m). To facilitate comparisons with previous data, we avoided surveying in the vicinity of non-forest habitats. We therefore conducted lower elevation field work (at 1,130–1,330 m) on an entirely forested ridge 0.5 km east of Mt. Karimui's north-west ridge (Camp 3, see Table 1), then surveyed the spine of the ridge from 1,330 m to the summit at 2,520 m (based at Camps 1–2, see Table 1). We also visited several lower elevation sites for short periods (see Table 1 for sites and survey effort).

Field work.—We censused bird communities using mist-net surveys, point counts and *ad lib* observations (Table 1). Mist-net surveys in June–July were made along the spine of Mt. Karimui's north-west ridge, with a single mist-net survey at Bosiamaru (see Table 1). Mist-nets touched the ground in order to trap terrestrial species. Along Mt. Karimui's north-west ridge, we used flagging tape to partition the ridge into sections of 25 vertical m (e.g. 1,400–1,425 m). We measured elevation using the barometric altimeter in a Garmin 62S GPS unit, calibrated at Karimui airstrip (1,112 m per Diamond 1972) and using the average of readings taken on multiple days. We mist-netted along the ridgeline in discrete 'segments' of 24–30 nets (corresponding to 100–175 m elevation), and opened nets from 06.00 h to 13.00 h for two days per segment. Mist-nets were not operated in rain. Upon finishing one segment, we moved nets to higher elevations along the same trail and repeated the

TABLE 1

Location of field sites surveyed in the Karimui area, with approximate survey effort and brief habitat description. The vast majority of field work occurred in the vicinity of our three field camps along Mt. Karimui's north-west ridge.

| | Elevation (m) | Latitude | Longitude | Survey type | Survey effort | Habitat |
|-------------------------|------------------|-----------|------------|---|-------------------|---|
| Mt. Karimui Camp 1 | 1,420 | 06°54.123 | 144°74.263 | Mist-nets; point counts | c.45 man-days | Tall primary forest near base of ridgeline |
| Mt. Karimui Camp 2 | 1,890 | 06°54.693 | 144°75.250 | Mist-net; point counts | c.45 man-days | Primary montane forest with epiphyte- laden trees, some bamboo tangles |
| Mt. Karimui Camp 3 | 1,240 | 06°52.748 | 144°74.518 | Mist-nets; point counts | 20 man-days | Tall primary forest at Mt. Karimui's base |
| Yogoromaru | c.1,100 | 06°50.672 | 144°74.178 | Qualitative observations | four man-days | Mostly agricultural landscape |
| Karimui Station area | c.1,100 | 06°49.254 | 144°82.473 | Qualitative observations | c.20 man-days | Mostly agricultural landscape |
| Bosiamaru | 1,100–1,150 | 06°50.689 | 144°80.149 | Mist-nets | six man-days | Second growth, heavily hunted |
| Sena River | 750 | 06°47.735 | 144°83.475 | Qualitative observations of 'salt lick' site | three man-days | Second growth, heavily hunted |
| Tua River | 570 | 06°45.176 | 144°78.164 | Qualitative observations | two man-days | Mix of second growth and primary forest |

process. Our net-line stretched unbroken from 1,330 m to 2,200 m in this fashion. Difficult terrain in the high-elevation elfin forest permitted only scattered mist-netting above 2,200 m and entirely prevented it above 2,400 m. Finally, we mist-netted in lower elevation forest (1,130–1,330 m) along a parallel ridge (described above, Camp 3, see Table 1). Importantly, this mist-net effort closely matches that of Diamond (1972), who likewise ran a nearly continuous mist-net lane along Mt. Karimui's north-west ridge. Unlike Diamond, we did not collect specimens. Instead, individuals trapped were weighed, measured (wing, tail, culmen, tarsus), scored for moult and photographed. We also took blood samples from the brachial vein of the majority of captured individuals. Finally, we clipped the distal portion of the right three outer rectrices, permitting easy diagnosis of recaptures.

One observer (BGF) completed point counts in both 2012 field seasons on Mt. Karimui's north-west ridge. Point counts in June–July were at 1,130–2,520 m ($n = 40$); in October–December at 1,330–2,520 m ($n = 30$). Each point count location was at least 150 m distant from neighbouring point count sites. We conducted five-minute audiovisual point counts, repeating counts on each of three separate mornings (06.00–12.00 h, mostly 06.30–09.00 h). We augmented our quantitative surveys with qualitative observations lacking effort information during the course of field work. Survey effort on Mt. Karimui's ridge was approximately equal between Diamond's July–August transect (33 days) and our June–July (38 days) and October–December (34 days) field seasons, facilitating comparisons. Audio-recordings will be archived at the Macaulay Library of Natural Sounds at the Cornell Lab of Ornithology, Ithaca, NY, while observational data are archived in the Avian Knowledge Network via eBird.

Results

Some 271 bird species occur in the Karimui area, with a further four species reported by local informants (Appendix 1). This total sums extensive field work by ourselves and Diamond, and is probably near-complete. Nevertheless, species richness estimated by Diamond's survey and our own differed: we documented 245 species, Diamond 234. These different totals largely reflect geographic differences in survey effort. Diamond (1972) spent more time at low elevations on the Karimui Plateau and employed native hunters to collect specimens, while our field work was concentrated on Mt. Karimui's slopes. However, research effort on Mt. Karimui's north-west ridge was qualitatively similar between historical and modern transects, suggesting that some of the observed differences may reflect changes in species' populations. Diamond's extensive surveys on Mt. Karimui lack quantitative effort data: our mist-net effort summed 3,665 net-hours, during which time we captured 977 individuals of 91 species. Point counts detected 130 species in 2,082 species / point count combinations. We describe our observations of population dynamics, elevational range extensions and ecological notes for 21 species below.

DWARF CASSOWARY *Casuarius bennetti* / **SOUTHERN CASSOWARY** *C. casuarius*
Cassowaries are New Guinea's largest terrestrial animals and highly valued for their meat (Beehler *et al.* 1986). Informants consistently described them as largely extirpated from the Karimui region, correlating their disappearance to a period of intense hunting in the 1960s and 1970s when metal snares were first used. We never encountered cassowary droppings in the forest—which are frequently encountered where cassowaries are present (BGF pers. obs.)—and saw just one captive bird, a Dwarf Cassowary chick acquired by a Yogoromaru hunter from a remote and seldom-hunted location near the Tua River. The species resident in the Karimui area is Dwarf Cassowary. However, informants described Southern Cassowary as resident in the lowlands south of Mt. Karimui, and reported it to occasionally venture to the Karimui area treated by this manuscript.

COLLARED BRUSHTURKEY *Talegalla jobiensis* /
BLACK-BILLED BRUSHTURKEY *T. fuscirostris*

Talegalla are shy forest-dwellers with braying vocalisations. Due to the difficulty in identifying *Talegalla* vocalisations to species, distributional knowledge is poor. For example, Diamond was unable to identify which *Talegalla* inhabits Mt. Karimui (Diamond 1972) and it was only recently that Collared Brushturkey was documented south of New Guinea's Central Ranges (Mack & Wright 1996). We frequently heard *Talegalla* vocalisations below 1,890 m, eventually photographing a Collared Brushturkey at its mound nest at 1,390 m. We suspect Black-billed Brushturkey also occurs at Karimui and replaces Collared Brushturkey at lower elevations: our best local informant described the green-legged Black-billed Brushturkey as a common resident near the Tua River. We consider this informant credible, as he accurately described the leg colours and preferred elevations of the three megapodes we encountered, the montane Collared and Wattled Brushturkeys *Aepygodius arfakianus* and widespread Orange-footed Scrubfowl *Megapodius reinwardt*.

PAPUAN EAGLE *Harpyopsis novaeguineae*

We recorded this raptor only a few times: one was observed perched in the canopy at 1,300 m in 2011, and vocalising birds were heard *c.*3 times in 2012 at our 1,420 and 1,890 m camps. While never abundant throughout its range, this eagle is usually easily detected by voice in forested montane environments (Beehler *et al.* 1986; BGF pers. obs.). Diamond (1972)

noted the species on Mt. Karimui, but did not assess its relative abundance, which often correlates with hunting levels (K. D. Bishop pers. comm.), and we consider it probable that this species is impacted by hunting at Karimui. For example, one local informant showed us a full set of talons from a bird hunted in early 2012 and several informants told us that hunters frequently target Papuan Eagles.

BUFF-BANDED RAIL *Gallirallus philippensis*

Widespread throughout Melanesia, colonising even remote Pacific islands (Beehler *et al.* 1986). We found it relatively common in agricultural areas at Karimui Station. Diamond did not record it. It is unlikely that Diamond overlooked this rail: he surveyed appropriate habitats near Karimui airstrip and collected five Rufous-tailed Bush-hens *Amaurornis moluccana* (Diamond 1972), a more secretive species (BGF pers. obs.). It is therefore probable that Buff-banded Rail—an excellent coloniser (Diamond & LeCroy 1979)—has recently colonised the area, presumably in response to the large increase in agricultural land since 1965.

RUFESCENT IMPERIAL PIGEON *Ducula chalconota*

We regularly heard this montane pigeon on Mt. Karimui. Diamond (1972) was familiar with its distinctive vocalisations, but did not find it on Mt. Karimui. Because columbids regularly undertake seasonal movements and are difficult to detect when not vocal (Diamond 1972), this species may have been overlooked by Diamond or was rare or absent at the time of his survey.

ZOE'S IMPERIAL PIGEON *Ducula zoeae*

We found this lowland species well above its published elevation limit of 1,500 m (Baptista *et al.* 1997). In June–July, it was one of the most commonly detected species on point counts, vocally abundant to c.1,900 m with some heard up to 2,080 m. It probably undertakes seasonal elevational movements: in October–November, we recorded this species infrequently and only below 1,620 m.

STRIATED LORIKEET *Charmosyna multistriata*

Formerly considered absent from Papua New Guinea's southern watershed (Beehler *et al.* 1986). We identified the species on three occasions in November 2012 at our 1,420 m camp. All observations were of small flocks (2–4 birds) in flight, identified by their all-green coloration with yellowish-streaked underparts, distinct from the similar Goldie's Lorikeet *Psitteuteles goldiei*, also present. Lorikeets are difficult to positively identify in flight and our records should be considered provisional. *C. multistriata* is nomadic, often present at a site for several years before disappearing (K. D. Bishop pers. comm.). Our probable records and recent observations from the Crater Mountain area immediately east of the Karimui Plateau (Mack & Wright 1996) suggest this species' wanderings include much of Papua New Guinea's southern watershed.

LORIKEET SP. *Charmosyna* sp.

We observed a vocalising *Charmosyna* in August 2011, when an adult flew by at eye level on the rim of the Karimui Plateau. We judged it to be smaller than Coconut Lorikeet *Trichoglossus haematodus*, the commonest lorikeet at the site, and provisionally identified it as Josephine's Lorikeet *Charmosyna josefinae* based on its relatively large size, very long yellow-tipped tail and red rump. However, we could not conclusively eliminate other *Charmosyna* species (e.g. Papuan Lorikeet *C. papou*) and Josephine's Lorikeet has not been

documented east of Mt. Bosavi (Collar 1997), c.175 km west of Mt. Karimui. This was our sole, possible, observation suggesting it may be an occasional visitor to the region and that future field workers should remain alert for Josephine's Lorikeet.

PESQUET'S PARROT *Psittichas fulgidus*

Prized for its vermilion and black flight feathers, hunting has extirpated this species in many locations (Beehler *et al.* 1986, Mack & Wright 1998). We did not record it on the Karimui Plateau, where hunting pressure has been intense for at least 50 years (Wagner 1967). In fact, hunting may have formerly almost extirpated the species from the entire Karimui area: Diamond observed the species just once during several months of field work on the Karimui Plateau and on Mt. Karimui. However, we regularly observed pairs or small groups roosting around our 1,420 m and 1,890 m camps, suggesting that it is currently uncommon on the slopes of Mt. Karimui. Local informants reported the species to be fairly common in parts of the Tua River Valley far from human settlements.

PACIFIC KOEL *Eudynamys orientalis*

Regularly heard up to 2,120 m, well above its previously known elevational ceiling of 1,500 m (Beehler *et al.* 1986).

WHITE-CROWNED CUCKOO *Cacomantis leucolophus*

This lowland species generally occurs below 1,740 m (Coates 1985). We frequently heard it during both 2012 field seasons up to c.2,200 m, with one record from 2,520 m in July 2012. We have also heard the species at 2,200–2,300 at Hogave, Mt. Michael, Eastern Highlands, and it is regularly encountered at other highland locations (e.g. Ambua Lodge near Tari, Papua New Guinea; K. D. Bishop pers. comm.): It is probably widespread in montane forest.

HOOK-BILLED KINGFISHER *Melidora macrorrhina*

Commonly heard pre-dawn up to 1,870 m. This is a new high-elevation record for this lowland species, which was previously known only to 1,280 m (Woodall 2001).

YELLOWISH-STREAKED HONEYEATER *Ptiloprora meekiana*

This rare and unobtrusive montane species is probably nomadic (K. D. Bishop pers. comm.), and has been recorded only a few times in the Central and Eastern Highlands of Papua New Guinea (Higgins *et al.* 2008). We did not find it in June–July 2012, nor did Diamond record this species in 1965. However, we observed one in a flowering tree at 1,880 m on three consecutive days in October 2012.

BICOLORED MOUSE-WARBLER *Crateroscelis nigrorufa*

Patchily distributed throughout montane New Guinea. When present, it occupies a narrow elevational band between the closely related lowland Rusty Mouse-warbler *C. murina* and montane Mountain Mouse-warbler *C. robusta*. Despite extensive mist-netting effort and numerous mist-netted Rusty and Mountain Mouse-warblers, Diamond did not record Bicolored Mouse-warbler on Mt. Karimui in 1965. In contrast, we mist-netted 16 *C. nigrorufa* in June–July 2012 (1,620–1,940 m) and regularly observed small parties during both field seasons. Given that Diamond operated a series of mist-nets across the entire elevational zone (J. Diamond pers. comm.), we consider it highly unlikely that this species was overlooked by him. Instead, we suggest that this species was very rare or truly absent on Mt. Karimui's north-west ridge in 1965 and has since become relatively common.

SCRUBWREN SP. *Sericornis* sp.

We observed small flocks of an unidentified scrubwren (*Sericornis* sp.) on six occasions at 1,280–1,355 m. Flocks comprised 3–8 individuals that foraged 1–12 m above ground. Three were mist-netted at 1,310 m and blood samples taken. They were morphologically similar (if not identical) to Large Scrubwren *S. nouhuysi*, which was commonly seen and mist-netted above 1,470 (AMCF photographs). However, the only *Sericornis* we observed at 1,355–1,470 m was the much smaller Grey-green Scrubwren *S. arfakianus*. Although speculative, these unidentified lower elevation *Sericornis* could represent a new population of Perplexing Scrubwren *S. virgatus*, a phenotypically variable low-elevation species confusingly similar to Large Scrubwren. This possibility is bolstered by recent records of Perplexing Scrubwren in southern Papua New Guinea (J. Diamond pers. comm.). Genetic studies are necessary to evaluate the taxonomic status of these unidentified scrubwrens.

CHESTNUT-BACKED JEWEL-BABBLER *Ptilorrhoa castanonota* /**SPOTTED JEWEL-BABBLER** *P. leucosticta*

Many species in tropical mountains are elevational replacements (closely related species with parapatric elevational distributions: Diamond 1973, Terborgh & Weske 1975, Jankowski *et al.* 2012, Freeman *et al.* 2013). Range borders are often very abrupt, but elevational gaps sometimes exist between two replacements (Terborgh & Weske 1975). For example, Diamond noted a substantial gap between the foothill Chestnut-backed Jewel-babbler and montane Spotted Jewel-babbler on Mt. Karimui (Diamond 1972). This gap appears to have been maintained. We expended significant effort determining *Ptilorrhoa* elevational distributions, and found a gap between the highest Chestnut-backed Jewel-babbler territory at 1,460 m and the lowest Spotted Jewel-babbler territory at 1,510 m.

RUFOUS-NAPED WHISTLER *Aleadryas rufinucha*

Regularly recorded above 1,920 m. Our only record below this was a juvenile mist-netted at 1,300 m, which echoes records of juveniles of other species found well outside their typical elevational distributions in New Guinea, supporting the hypothesis that juveniles disperse beyond regular altitudinal limits (Diamond 1972, Freeman *et al.* 2013).

SINGING STARLING *Aplonis cantoroides*

This urban / agricultural species has greatly expanded its distribution in response to urbanisation of New Guinea's landscape. It was not recorded by Diamond at Karimui in 1965. However, we observed a small flock on four occasions in 2012, in a small grove of fig trees adjacent to Karimui airstrip. Local informants declared that the species had arrived within the past decade, but is only seen in the vicinity of the airstrip.

LAWES'S PAROTIA *Parotia lawesii*

Regularly observed by Diamond (1972), who collected six specimens on Mt. Karimui's north-west ridge. In contrast, despite many weeks of field work at appropriate elevations, our sole observation was a pair at 1,640 m in November 2012. Parotias are vocal and easily detected (BGF pers. obs.) suggesting that the species has declined in abundance along Mt. Karimui's north-west ridge since 1965.

BANDED YELLOW ROBIN *Poecilodryas placens*

Diamond (1972) found this species near Karimui Station, where he collected two specimens and repeatedly observed lone individuals foraging in the understorey. We did not encounter this easily mist-netted and vocally distinctive understorey species in primary

forest at Karimui Station, nor did we detect it during opportunistic field work at lower elevations. However, we were unable to mist-net in lower elevation (<1,000 m) forest on the Karimui Plateau. Thus, it is unclear if the species persists, even patchily, in the region or is truly absent.

We also documented minor elevational records (<250 m above previously reported limits) for 12 additional species. **STEPHAN'S EMERALD DOVE** *Chalcophaps stephani*: mist-netted at 1,390 m, observed at 1,420 m camp, vs. below 1,200 m (Baptista *et al.* 1997). **RED-CHEEKED PARROT** *Geoffroyus geoffroyi*: to 1,240 m, vs. below 1,113 m (Diamond 1972). **VARIABLE DWARF KINGFISHER** *Ceyx lepidus*: mist-netted to 1,385 m, vs. below 1,300 m (Woodall 2001). **WHITE-EARED CATBIRD** *Ailuroedus buccoides*: mist-netted to 1,300 m, vs. below 1,200 m (Mack & Wright 1996). **TAWNY-BREASTED HONEYEATER** *Xanthotis flaviventer*: to 1,660 m, vs. below 1,500 m (Higgins *et al.* 2008). **RUBY-THROATED MYZOMELA** *Myzomela eques*: to 1,310 m, vs. below 1,200 m (Higgins *et al.* 2008). **GREY-GREEN SCRUBWREN** *Sericornis arfakianus*: to 1,780 m, vs. below 1,700 m (Gregory 2007). **YELLOW-BELLIED GERYGONE** *Gerygone chrysogaster*: to 1,030 m, vs. below 800 m (Beehler *et al.* 1986). **GOLDENFACE** *Pachycare flavogriseum*: to 1,920 m, vs. below 1,800 m (Boles 2007). **GOLDEN CUCKOOSHRIKE** *Campochaera sloetii*: to 1,240 m, vs. below 1,100 m (Taylor 2005). **SOOTY THICKET FANTAIL** *Rhipidura threnothorax*: to 1,240 m, vs. to 1,100 m (Boles 2006). **BLACK-FRONTED WHITE-EYE** *Zosterops atrifrons*: to 1,700 m, vs. below 1,460 m (van Balen 2008).

Discussion

Our studies confirm the high avian diversity of Mt. Karimui and the Karimui Plateau: 271 species are documented to occur, a total comparable to other extensively surveyed New Guinean elevational gradients (Freeman *et al.* 2013), and remarkably high given the absence of lakes, marshes and both low-elevation (<500 m) and upper montane forests (>2,500 m) in the Karimui area. Mt. Karimui's avian diversity includes many species detected during our field work but not by Diamond (1972) in 1965. Conversely, we failed to detect several species reported by Diamond (1972).

Avian community dynamics in the tropics have been seldom studied in undisturbed forests. The sparse data that exist support the hypothesis that tropical bird populations are relatively stable through time, especially among forest-dwelling insectivores (Munn 1985, Brooks 2005, Martinez & Gomez 2013). We lack quantitative data to statistically assess population changes in Mt. Karimui's avifauna. Nevertheless, several species may have undergone substantial population changes during this interval. Most obviously, Bicolored Mouse-warbler was apparently absent on Mt. Karimui's north-west ridge in 1965 but relatively common in 2012. We believe this is the most extreme example of population changes in a resident understorey tropical bird in undisturbed forest. Bicolored Mouse-warbler is patchily distributed across New Guinea and inhabits a narrow elevational zone between two more widespread congeners (Beehler *et al.* 1986, Freeman *et al.* 2013), distributional attributes that may predispose this species to local colonisations and extinctions at individual sites (Diamond 1973). Conversely, it seems that the Lawes's Parotia has almost disappeared from Mt. Karimui's north-west ridge since 1965. Examples of local colonisations and extinctions in disturbed tropical habitats are much more common (Diamond 1971), and we documented the probable recent colonisation of agricultural habitats on the Karimui Plateau by Buff-banded Rail and Singing Starling.

Distributional ecology.—Distributional data describing range limits of New Guinean birds have been previously used to test hypotheses of community assembly and

diversification (Diamond 1973, Diamond 1986, Mack & Dumbacher 2007). We briefly comment on one well-known pattern—the tendency for closely related species to replace one another parapatrically along elevational gradients (Diamond 1986, Freeman *et al.* 2013). Elevational replacements occur in tropical mountains worldwide in many taxa. Understanding the ecological factors that maintain their parapatric distributions is an active arena of ecological research, focused on answering the question of why elevational gradients contain multiple closely related species that partition elevational space, instead of just one widespread species (Jankowski *et al.* 2012).

However, the contribution of elevational replacements to tropical montane biodiversity is seldom quantified. We updated Diamond's (1972) list of elevational replacements on Mt. Karimui. Nearly all elevational replacements are congeners with similar body sizes and diets. In total, we identified 24 pairs, five trios and two quartets of elevational replacements on Mt. Karimui (71 species; Appendix 1). Why do 71 species with narrow elevational distributions exist instead of 31 more widespread species? Providing a satisfactory answer to this question is beyond our scope, but these statistics demonstrate that elevational replacements comprise a significant portion of Mt. Karimui's avian diversity. Mt. Karimui contains 238 species of forest-dwelling birds (Appendix 1), a total 20.2% higher than it would be if all 40 'ecologically redundant' elevational replacements were excluded. This coarse analysis is one of the first to explicitly quantify the contribution of elevational replacements to montane biodiversity for a taxonomic group (Terborgh & Weske 1975), strengthening the hypothesis that elucidating the evolution of elevational distributions is a key component of understanding montane biodiversity in New Guinea (Diamond 1973, 1986).

Conservation.—Conserving Mt. Karimui's diverse avifauna is a significant challenge. The principal negative impacts on bird populations result from hunting and, increasingly, forest clearance. The latter will almost certainly be the main cause of avifaunal declines in the Karimui area in the near future. Human population on the Karimui Plateau has quintupled since the early 1960s (Wagner 1967; J. Anuabo pers. comm.), with concomitant habitat loss due to both subsistence and cash-crop (e.g. coffee) agriculture, with forest clearance likely to accelerate via current plans to construct a road to Karimui. Conserving entire elevational gradients of primary forest provides watershed benefits to local communities while conserving the vast majority of montane biodiversity and providing space to accommodate climate change-driven range shifts (Laurance *et al.* 2011).

Bird populations may also be impacted by hunting. We did not attempt to document the impact of hunting on Mt. Karimui, but did collect several observations consistent with the hypothesis that it affects populations of several species. Subsistence hunting remains common in New Guinean cultures (Wagner 1967). We frequently encountered boys and men hunting birds with slingshots and / or bow-and-arrows, and observed numerous hunting blinds. The latter are used especially frequently (daily or near-daily) during droughts or if located near 'salt licks' where birds, especially columbids, gather to drink water and / or ingest grit or minerals (Diamond *et al.* 1999, Symes *et al.* 2006). Informants reported regularly taking large numbers (>10) of birds, principally columbids, on single visits to such sites. Lastly, it is common practice to consume eggs or nestlings on encountering an active nest, even of small (<15 g) passerines. It is probable that hunting has significantly impacted populations of certain species. For example, Dwarf Cassowary is extirpated from accessible parts of the Karimui Plateau and Mt. Karimui. Likewise, *Talegalla* brushturkeys are absent from forests around Karimui Station, even in large tracts of primary forest. Additionally, Papuan Eagle and Pesquet's Parrot appear to be largely absent from the Karimui Plateau, although the parrot persists on the lower slopes of Mt. Karimui, in rugged terrain near the

Tua River, and may be increasing. These species are regularly targeted by hunters, and it is probable that their distributions are currently limited by hunting pressure.

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Appendix 1: Complete list of the Karimui area avifauna

Nomenclature follows IOC classification (Gill & Donsker 2013). Conservation status reflects IUCN classification (IUCN 2013), while habitat classifications are based on Beehler *et al.* (1986) and pers. obs. Elevational replacements (pairs, trios and quartets) are based on references (Diamond 1972, Beehler *et al.* 1986) and pers. obs. We note those bird species documented by our recent field work and those by Diamond (1972). We also report elevational distributions at Mt. Karimui of most forest-dwelling species. We describe high elevation limits for many species, and low elevation limits for those species whose lower limit lies above c.1,100 m. Finally, we summarise additional information pertaining to our observations as brief notes. Habitats: F = Forest, Ag = Agricultural, Aq = Aquatic. Conservation status: VU = Vulnerable, NT = Near Threatened, DD = Data Deficient.

| English name | Scientific name | Habitat | Conservation status | Elevational replacement | BGE/AMCF Diamond Lower limit (m) | Upper limit (m) | Notes |
|--------------------|------------------------------|---------|---------------------|-------------------------|----------------------------------|-----------------|---|
| Southern Cassowary | <i>Casuarinus casuarinus</i> | F | VU | pair, low | | | Reported by informants to occur near border of Chimbu and Gulf provinces |
| Dwarf Cassowary | <i>Casuarinus bennetti</i> | F | NT | pair, high | | | Reported by informants to persist in remote forests, one captive bird in Yogoromaru village |

| English name | Scientific name | Habitat | Conservation status | Elevational replacement | BGF/AMCF | Diamond | Lower limit (m) | Upper limit (m) | Notes |
|-----------------------------|-----------------------------------|---------|---------------------|-------------------------|----------|---------|-----------------|-----------------|--|
| Wattled Brushturkey | <i>Aepyodius arfakianus</i> | F | | | X | X | | | Heard several times around 1,890 m camp |
| Black-billed Brushturkey | <i>Talegalla fuscirostris</i> | F | | pair, low | | | | | Reported by informants to occur below c.800 m |
| Collared Brushturkey | <i>Talegalla jobiensis</i> | F | | pair, high | X | | | 1,893 | |
| Orange-footed Scrubfowl | <i>Megapodius reinwardt</i> | F | | | X | X | | 1,923 | |
| Brown Quail | <i>Coturnix ypsiloptera</i> | Ag | | | | | | | Reported by informants to occur in agricultural land |
| Salvadori's Teal | <i>Salvadorina waigiutensis</i> | Aq | VU | | X | X | | | Seen at Sena River (730 m) and Tua River (550 m) |
| Great Egret | <i>Ardea alba</i> | Aq | | | X | | | | Seen once at Tua River (550 m) |
| Pied Heron | <i>Egretta picata</i> | Aq | | | | X | | | |
| Little Black Cormorant | <i>Phalacrocorax sulcirostris</i> | Aq | | | X | | | | Seen once at Sena River (730 m) |
| Pacific Baza | <i>Aviceda subcristata</i> | Ag | | | X | X | | 1,203 | |
| Long-tailed Honey Buzzard | <i>Henicopernis longicauda</i> | F | | | X | X | | 2,263 | |
| Papuan Eagle | <i>Harpyopsis novaeguineae</i> | F | VU | | X | X | | 1,888 | Scarce |
| Pygmy Eagle | <i>Hieraetus weiskei</i> | F | | | X | | | | Seen once at 1,300 m |
| Chestnut-shouldered Goshawk | <i>Erythrotriorchis buergersi</i> | F | DD | | | X | | | |
| Doria's Goshawk | <i>Megatriorchis doriae</i> | F | | | | X | | | |
| Variable Goshawk | <i>Accipiter hiogaster</i> | Ag | | | X | X | | | Seen 3–4 times around Karimui Station |
| Brown Goshawk | <i>Accipiter fasciatus</i> | Ag | | | | X | | | |
| Black-mantled Goshawk | <i>Accipiter melanoculamyx</i> | F | | pair, high | X | X | 1,423 | 2,143 | |
| Grey-headed Goshawk | <i>Accipiter poliocephalus</i> | F | | pair, low | X | X | | 1,215 | |
| Collared Sparrowhawk | <i>Accipiter cirrocephalus</i> | Ag | | | X | | | | Seen once near Karimui Station |
| Swamp Harrier | <i>Circus approximans</i> | Ag | | | X | X | | | Seen once at Karimui airstrip |
| Brahminy Kite | <i>Haliastur indus</i> | F | | | X | X | | 2,383 | |
| Nankeen Kestrel | <i>Falco ceucrooides</i> | Ag | | | X | X | | | Seen twice around Karimui Station |
| Oriental Hobby | <i>Falco severus</i> | F | | | | X | | | |
| Brown Falcon | <i>Falco berigora</i> | Ag | | | X | X | | | Seen regularly around Karimui Station |

| English name | Scientific name | Habitat | Conservation status | Elevational replacement | BGF/AMCF | Diamond | Lower limit (m) | Upper limit (m) | Notes |
|----------------------------|---------------------------------|---------|---------------------|--|----------|---------|-----------------|-----------------|--|
| Forbes's Forest Rail | <i>Rallidula forbesi</i> | F | | pair, high | X | | 1,343 | 1,763 | |
| Red-necked Crake | <i>Rallina tricolor</i> | F | | pair, low | | X | | | |
| Buff-banded Rail | <i>Gallirallus philippensis</i> | Ag | | | X | | | | Common around Karimui Station |
| Lewin's Rail | <i>Lewinia pectoralis</i> | Ag | | | X | | | | Heard once near Karimui Station |
| Pale-vented Bush-hen | <i>Amaurornis moluccana</i> | Ag | | | X | X | | | Common around Karimui Station |
| Common Sandpiper | <i>Actitis hypoleucos</i> | Aq | | | X | | | | Seen along Tua River (550 m) |
| Australian Pratincole | <i>Stiltia isabella</i> | Ag | | | X | X | | | Seen once at Karimui airstrip |
| Slender-billed Cuckoo-Dove | <i>Macropygia amboinensis</i> | F | | | X | X | | 1,903 | Very common at lower elevations (below c.1,500 m) and in anthropogenic landscapes |
| Bar-tailed Cuckoo-Dove | <i>Macropygia nigrirostris</i> | F | | largely replaces <i>M. amboinensis</i> at high elevations, but significant overlap | X | X | | 2,520 | Very common at higher elevations (above c.1,300 m), not recorded in anthropogenic areas |
| Great Cuckoo-Dove | <i>Reinwardtoena reinwardti</i> | F | | | X | X | | 2,233 | |
| Stephan's Emerald Dove | <i>Chalcophaps stephani</i> | F | | | X | X | | 1,423 | |
| New Guinea Bronzewing | <i>Henicophaps albifrons</i> | F | | | | X | | | |
| Cinnamon Ground Dove | <i>Gallicolumba rufigula</i> | F | | pair, low | X | X | | 1,288 | |
| White-breasted Ground Dove | <i>Gallicolumba jobiensis</i> | F | | | | X | | | |
| Bronze Ground Dove | <i>Gallicolumba beccarii</i> | F | | pair, high | X | X | 1,363 | 2,068 | |
| Pheasant Pigeon | <i>Otidiphaps nobilis</i> | F | | | X | X | | 1,693 | |
| Southern Crowned Pigeon | <i>Goura scheepmakeri</i> | F | VU | | | | | | Reported by elderly local informants to occur near Tua River, but unclear if still present in the Karimui area |
| Wompoo Fruit Dove | <i>Ptilinopus magnificus</i> | F | | | X | X | | 1,033 | |
| Pink-spotted Fruit Dove | <i>Ptilinopus perlatus</i> | F | | | X | X | | | Regular at Sena River salt lick (750 m) |
| Ornate Fruit Dove | <i>Ptilinopus ornatus</i> | F | | | X | X | | 2,520 | |
| Superb Fruit Dove | <i>Ptilinopus superbus</i> | F | | | X | X | | 1,273 | |
| Beautiful Fruit Dove | <i>Ptilinopus pulchellus</i> | F | | | X | X | | 1,243 | |

| English name | Scientific name | Habitat | Conservation status | Elevational replacement | BGF/AMCF | Diamond | Lower limit (m) | Upper limit (m) | Notes |
|-------------------------------|-------------------------------------|---------|---------------------|---|----------|---------|-----------------|-----------------|---|
| White-bibbed Fruit Dove | <i>Ptilinopus rivoli</i> | F | | | X | X | 1,243 | 2,105 | |
| Dwarf Fruit Dove | <i>Ptilinopus nainus</i> | F | | | X | X | | | Regular at Sena River salt lick (750 m) |
| Purple-tailed Imperial Pigeon | <i>Ducula rufigaster</i> | F | | pair, low | X | X | | 1,283 | |
| Rufescent Imperial Pigeon | <i>Ducula chalconota</i> | F | | pair, high | X | | 1,793 | 2,272 | |
| Zoe's Imperial Pigeon | <i>Ducula zoeae</i> | F | | | X | X | | 2,083 | |
| Papuan Mountain Pigeon | <i>Gymnophaps albertisii</i> | F | | | X | X | | 2,333 | |
| Palm Cockatoo | <i>Probosciger aterrimus</i> | F | | | X | X | | 1,283 | Scarce |
| Sulphur-crested Cockatoo | <i>Cacatua galerita</i> | F | | | X | X | | 2,373 | |
| Pesquet's Parrot | <i>Psittichas fulgidus</i> | F | VU | | X | X | | 1,903 | |
| Red-breasted Pygmy Parrot | <i>Micropsitta bruijnii</i> | F | | | X | | 1,453 | 2,133 | |
| Yellowish-streaked Lory | <i>Chalcopsitta scintillata</i> | F | | | | X | | | |
| Dusky Lory | <i>Pseudeos fuscata</i> | F | | | X | X | | 1,653 | |
| Coconut Lorikeet | <i>Trichoglossus haematodus</i> | F | | | X | X | | 1,423 | |
| Goldie's Lorikeet | <i>Psitteuteles goldiei</i> | F | | | X | | | 1,933 | |
| Black-capped Lory | <i>Lorius lory</i> | F | | | X | X | | 1,508 | |
| Striated Lorikeet | <i>Charmosyna multistriata</i> | F | | | X | | | | Seen at 1,420 m camp only |
| Pygmy Lorikeet | <i>Charmosyna wilhelminae</i> | F | | | X | | | 1,933 | |
| Red-flanked Lorikeet | <i>Charmosyna placentis</i> | F | | | X | X | | 1,323 | |
| Fairy Lorikeet | <i>Charmosyna pulchella</i> | F | | | X | X | 1,323 | 1,961 | |
| Josephine's Lorikeet | <i>Charmosyna josefinae</i> | F | | | X | | | | Possibly seen once at 990 m, but requires confirmation. |
| Papuan Lorikeet | <i>Charmosyna papou</i> | F | | replaces other <i>Charmosyna</i> at high elevations | X | X | | | Seen twice, at 1,735 and 1,910 m |
| Plum-faced Lorikeet | <i>Oreopsittacus arfaki</i> | F | | | X | X | 1,943 | 2,520 | |
| Yellow-billed Lorikeet | <i>Neopsittacus musschenbroekii</i> | F | | | | X | | | |
| Brehm's Tiger Parrot | <i>Psittacella brehmii</i> | F | | | X | X | 1,765 | 2,235 | |
| Madarasz's Tiger Parrot | <i>Psittacella madaraszii</i> | F | | | X | X | | | Seen twice, at 1,820 and 1,910 m |

| English name | Scientific name | Habitat | Conservation status | Elevational replacement | BGF/AMCF | Diamond | Lower limit (m) | Upper limit (m) | Notes |
|-------------------------------|--------------------------------------|---------|---------------------|-------------------------|----------|---------|-----------------|-----------------|--|
| Red-cheeked Parrot | <i>Geoffroyus geoffroyi</i> | F | | pair, low | X | X | | 1,243 | |
| Blue-collared Parrot | <i>Geoffroyus simplex</i> | F | | pair, high | X | X | 1,033 | 1,953 | |
| Eclectus Parrot | <i>Eclectus roratus</i> | F | | | X | X | | 1,393 | |
| Papuan King Parrot | <i>Alisterus chloropterus</i> | F | | | X | X | | 1,593 | |
| Orange-breasted Fig Parrot | <i>Cyclopsitta guillemittii</i> | F | | pair, low | X | X | | 1,108 | |
| Double-eyed Fig Parrot | <i>Cyclopsitta diophthalma</i> | F | | pair, high | X | | 1,163 | 1,243 | |
| Large Fig Parrot | <i>Psittaculirostris desmarestii</i> | F | | | X | X | | 1,243 | |
| Ivory-billed Coucal | <i>Centropus menbeki</i> | F | | | X | X | | 1,383 | |
| Pheasant Coucal | <i>Centropus phasianinus</i> | Ag | | | X | | | | One record from near Karimui Station |
| Dwarf Koel | <i>Microdynamis parva</i> | F | | | X | X | | 1,321 | |
| Pacific Koel | <i>Eudynamis orientalis</i> | F | | | X | X | | 2,123 | |
| Rufous-throated Bronze Cuckoo | <i>Chrysococcyx ruficollis</i> | F | | pair, high | X | | 1,793 | 2,520 | |
| White-eared Bronze Cuckoo | <i>Chrysococcyx meyerii</i> | F | | pair, low | X | X | | 1,813 | |
| White-crowned Cuckoo | <i>Cacomantis leucolophus</i> | F | | | X | X | | 2,520 | |
| Chestnut-breasted Cuckoo | <i>Cacomantis castaneiventris</i> | F | | pair, low | X | X | | 1,658 | Possibly to higher elevations (overlap unclear, Fan-tailed Cuckoo vocally similar) |
| Fan-tailed Cuckoo | <i>Cacomantis flabelliformis</i> | F | | pair, high | X | | 1,763 | 2,520 | Possibly to lower elevations (overlap unclear, Chestnut-breasted Cuckoo vocally similar) |
| Brush Cuckoo | <i>Cacomantis variolosus</i> | Ag | | | X | X | | | Common in gardens |
| Oriental Cuckoo | <i>Cuculus optatus</i> | F | | | X | | | | Seen at Tua River (550 m) |
| Greater Sooty Owl | <i>Tyto tenebricosa</i> | F | | | X | | | | Heard regularly at 1,420 m camp |
| Papuan Boobook | <i>Ninox theomacha</i> | F | | | X | X | | 2,520 | |
| Marbled Frogmouth | <i>Podargus ocellatus</i> | F | | | X | X | | 1,233 | |
| Papuan Frogmouth | <i>Podargus papuensis</i> | F | | | X | X | | 1,233 | |
| White-throated Nightjar | <i>Eurostopodus mystacalis</i> | Ag | | | | X | | | |
| Papuan Nightjar | <i>Eurostopodus papuensis</i> | F | | | X | | | | Seen at Sena River (730 m) |

| English name | Scientific name | Habitat | Conservation status | Elevational replacement | BGF/AMCF | Diamond | Lower limit (m) | Upper limit (m) | Notes |
|---------------------------|-----------------------------------|---------|---------------------|--|----------|---------|-----------------|-----------------|---|
| Feline Owllet-nightjar | <i>Aegotheles insignis</i> | F | | | X | X | | 1,893 | Vocalisations attributed to this species heard at 1,420 and 1,910 m camps |
| Wallace's Owllet-nightjar | <i>Aegotheles wallacii</i> | F | DD | | | X | | | <i>Aegotheles</i> sp. heard below 1,500 m could not be identified to species |
| Mountain Owllet-nightjar | <i>Aegotheles albertisi</i> | F | | replaces <i>A. wallacii</i> and <i>A. bennettii</i> at high elevations | X | | | 2,520 | <i>Aegotheles</i> sp. heard at 2,520 m presumed to be this species based on elevation |
| Barred Owllet-nightjar | <i>Aegotheles bennettii</i> | F | | | | X | | | <i>Aegotheles</i> sp. heard below 1,500 m not identified |
| Moustached Treeswift | <i>Hemiprocne mystacea</i> | F | | | X | X | | 1,253 | |
| Glossy Swiftlet | <i>Collocalia esculenta</i> | F | | | X | X | | 2,520 | |
| Mountain Swiftlet | <i>Aerodramus hirundinacens</i> | F | | | X | X | | | Commonly seen around Karimui Station |
| Oriental Dollarbird | <i>Eurystomus orientalis</i> | Ag | | | X | X | | 1,243 | |
| Hook-billed Kingfisher | <i>Melidora macrorrhina</i> | F | | | X | X | | 1,873 | |
| Shovel-billed Kookaburra | <i>Clytoceyx rex</i> | F | | | | X | | | |
| Rufous-bellied Kookaburra | <i>Dacelo gaudichaud</i> | F | | | X | X | | 1,283 | |
| Forest Kingfisher | <i>Todiramphus macleayi</i> | Ag | | | | X | | | |
| Sacred Kingfisher | <i>Todiramphus sanctus</i> | Ag | | | X | X | | | Commonly seen around Karimui Station |
| Yellow-billed Kingfisher | <i>Syma torotoro</i> | F | | pair, low | X | X | | 1,233 | |
| Mountain Kingfisher | <i>Syma megarlyyncha</i> | F | | pair, high | X | X | 1,493 | 2,158 | |
| Variable Dwarf Kingfisher | <i>Ceyx lepidus</i> | F | | | X | X | | 1,388 | |
| Azure Kingfisher | <i>Ceyx azureus</i> | Aq | | | X | X | | | Seen once at Tua River (550 m) |
| Rainbow Bee-eater | <i>Merops ornatus</i> | Ag | | | X | X | | | Seen twice near Karimui Station |
| Blyth's Hornbill | <i>Rhyticeros plicatus</i> | F | | | X | X | | | Seen on 3–4 occasions |
| Red-bellied Pitta | <i>Erythropitta erythrogaster</i> | F | | | X | X | | 1,198 | |
| White-eared Catbird | <i>Ailuroedus buccoides</i> | F | | pair, low | X | X | | 1,303 | |
| Spotted Catbird | <i>Ailuroedus melanotis</i> | F | | pair, high | X | X | 1,363 | 1,703 | |

| English name | Scientific name | Habitat | Conservation status | Elevational replacement | BGF/AMCF | Diamond | Lower limit (m) | Upper limit (m) | Notes |
|-------------------------------|---------------------------------|---------|---------------------|-------------------------|----------|---------|-----------------|-----------------|--|
| MacGregor's Bowerbird | <i>Amblyornis macgregoriae</i> | F | | | X | X | 1,693 | 2,243 | |
| White-shouldered Fairywren | <i>Malurus alboscapulatus</i> | Ag | | | X | X | | 1,253 | |
| Orange-crowned Fairywren | <i>Clytomyias insignis</i> | F | | | X | X | | | Family groups seen at 2,160 m and 2,350 m |
| Ruby-throated Myzomela | <i>Myzomela eques</i> | F | | | X | X | | 1,313 | |
| Red Myzomela | <i>Myzomela cruentata</i> | F | | trio, middle | X | X | | 1,423 | Lower elevation limit unclear (not observed below 1,300 m) |
| Papuan Black Myzomela | <i>Myzomela nigrita</i> | F | | trio, low | X | X | | 1,243 | |
| Red-collared Myzomela | <i>Myzomela rosenbergii</i> | F | | trio, high | X | X | 1,273 | 2,520 | |
| Green-backed Honeyeater | <i>Glycichaera fallax</i> | F | | | X | | | 1,198 | |
| Yellowish-streaked Honeyeater | <i>Ptiloprora weckiana</i> | F | | | X | | | | Seen twice at flowering tree at 1,880 m |
| Rufous-backed Honeyeater | <i>Ptiloprora guisei</i> | F | | | X | X | 1,783 | 2,520 | |
| Plain Honeyeater | <i>Pycuopygius ixoides</i> | F | | pair, low | X | X | | | Seen once at 1,010 m near Karimui Station |
| Marbled Honeyeater | <i>Pycuopygius cinereus</i> | F | | pair, high | X | X | | | Seen once at 1,420 m camp |
| Spotted Honeyeater | <i>Xanthotis polygrammus</i> | F | | | X | X | | 1,363 | |
| Tawny-breasted Honeyeater | <i>Xanthotis flaviventer</i> | F | | | X | X | | 1,663 | |
| Meyer's Friarbird | <i>Philemon meyeri</i> | F | | | | X | | | |
| New Guinea Friarbird | <i>Philemon novaeguineae</i> | F | | | X | X | | 1,243 | |
| Long-billed Honeyeater | <i>Melilestes megarhynchus</i> | F | | | X | X | | 1,633 | |
| Common Smoky Honeyeater | <i>Melipotes fumigatus</i> | F | | | X | X | 1,338 | 2,520 | |
| Olive Straightbill | <i>Timeliopsis fulvigula</i> | F | | | X | X | 1,633 | 2,063 | |
| Black-throated Honeyeater | <i>Caligavis subfrenata</i> | F | | pair, high | X | X | 1,423 | 2,520 | |
| Obscure Honeyeater | <i>Caligavis obscura</i> | F | | pair, low | X | X | | 1,243 | |
| Yellow-browed Melidectes | <i>Melidectes rufocrissalis</i> | F | | pair, high | X | X | 1,338 | 2,520 | |
| Ornate Melidectes | <i>Melidectes torquatus</i> | F | | pair, low | X | X | 1,333 | 1,888 | |
| Mottle-breasted Honeyeater | <i>Meliplaga mimikae</i> | F | | pair, low | X | X | | 1,313 | |
| Mountain Honeyeater | <i>Meliplaga orientalis</i> | F | | pair, high | X | X | 1,423 | 1,883 | |

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|---------------------------|------------------------------------|---------|---------------------|-------------------------|----------|---------|-----------------|-----------------|---|
| Scrub Honeyeater | <i>Meliphaga albonotata</i> | Ag | | | X | X | | | Common around Karimui Station |
| Mimic Honeyeater | <i>Meliphaga analoga</i> | F | | | X | X | | 1,163 | |
| Yellow-gaped Honeyeater | <i>Meliphaga flavirictus</i> | F | | | | X | | | |
| Puff-backed Honeyeater | <i>Meliphaga aruensis</i> | F | | | X | X | | 1,158 | |
| Rusty Mouse-warbler | <i>Crateroscelis murina</i> | F | | trio, low | X | X | | 1,773 | |
| Bicolored Mouse-warbler | <i>Crateroscelis nigrorufa</i> | F | | trio, middle | X | | 1,623 | 1,943 | |
| Mountain Mouse-warbler | <i>Crateroscelis robusta</i> | F | | trio, high | X | X | 1,873 | 2,520 | |
| Pale-billed Scrubwren | <i>Sericornis spilodera</i> | F | | quartet, lowest | X | X | | 1,513 | |
| Papuan Scrubwren | <i>Sericornis papuensis</i> | F | | quartet, highest | X | X | 1,943 | 2,520 | |
| scrubwren sp. | <i>Sericornis</i> sp. | F | | | X | | | | See species account |
| Large Scrubwren | <i>Sericornis nouhuysi</i> | F | | | X | X | 1,473 | 2,426 | |
| Buff-faced Scrubwren | <i>Sericornis perspicillatus</i> | F | | quartet, high middle | X | X | 1,703 | 2,013 | |
| Grey-green Scrubwren | <i>Sericornis arfakianus</i> | F | | quartet, low middle | X | X | 1,378 | 1,783 | One possible record from 1,200 m near Bosiamaru |
| Brown-breasted Gerygone | <i>Gerygone ruficollis</i> | F | | | X | X | 1,447 | 2,380 | |
| Large-billed Gerygone | <i>Gerygone magnirostris</i> | F | | | X | | | | Seen/heard at Sena River (730 m) |
| Yellow-bellied Gerygone | <i>Gerygone chrysogaster</i> | F | | | X | X | | 1,033 | |
| Ashy Gerygone | <i>Gerygone cinerea</i> | F | | | X | X | 2,515 | 2,520 | |
| Green-backed Gerygone | <i>Gerygone chloronota</i> | F | | | X | X | | 1,383 | |
| Fairy Gerygone | <i>Gerygone palpebrosa</i> | F | | | X | X | | 1,243 | |
| Goldenface | <i>Pachycare flavogriseum</i> | F | | | X | X | | 1,923 | |
| Loria's Satinbird | <i>Cnemophilus loriae</i> | F | | pair, low | X | X | 1,423 | 2,428 | |
| Crested Satinbird | <i>Cnemophilus macgregorii</i> | F | | pair, high | X | X | | | One male seen at ridge summit (2,520 m) |
| Yellow-breasted Satinbird | <i>Loboparadisea sericea</i> | F | NT | | X | X | 1,433 | 1,933 | |
| Black Berrypecker | <i>Melanocharis nigra</i> | F | | pair, low | X | X | | 1,463 | |
| Fan-tailed Berrypecker | <i>Melanocharis versteri</i> | F | | pair, high | X | X | 1,388 | 2,520 | |
| Streaked Berrypecker | <i>Melanocharis striativentris</i> | F | | | X | X | 1,453 | 1,873 | |

| English name | Scientific name | Habitat | Conservation status | Elevational replacement | BGF/AMCF | Diamond | Lower limit (m) | Upper limit (m) | Notes |
|-------------------------------|-------------------------------------|---------|---------------------|-------------------------|----------|---------|-----------------|-----------------|---|
| Spotted Berrypecker | <i>Rhamphocharis crassirostris</i> | F | | | X | X | 2,103 | 2,323 | |
| Dwarf Longbill | <i>Oedistoma iliolophus</i> | F | | | X | X | | 1,653 | |
| Pygmy Longbill | <i>Oedistoma pygmaeum</i> | F | | | X | X | | 1,288 | |
| Slaty-headed Longbill | <i>Toxorhamphus poliopterus</i> | F | | | X | X | | 1,993 | |
| Tit Berrypecker | <i>Oreocharis arfaki</i> | F | | | X | X | 1,338 | 2,520 | |
| Crested Berrypecker | <i>Paramythia montium</i> | F | | | X | X | | | Flock seen just below summit of ridge (2,490 m) |
| Spotted Jewel-babbler | <i>Ptilorrhoa leucosticta</i> | F | | trio, high | X | X | 1,508 | 2,142 | |
| Blue Jewel-babbler | <i>Ptilorrhoa caerulescens</i> | F | | trio, middle | X | | | | Heard at Tua River (550 m) |
| Chestnut-backed Jewel-babbler | <i>Ptilorrhoa castanonota</i> | F | | trio, low | X | X | | 1,458 | Lower elevation limit not determined |
| Yellow-breasted Boatbill | <i>Machaerirhynchus flaviventer</i> | F | | pair, low | X | X | | 1,308 | |
| Black-breasted Boatbill | <i>Machaerirhynchus nigripectus</i> | F | | pair, high | X | X | 1,243 | 2,393 | |
| Lowland Peltops | <i>Peltops blainvillii</i> | F | | pair, low | | X | | | |
| Mountain Peltops | <i>Peltops montanus</i> | F | | pair, high | X | X | | 2,105 | |
| Black Butcherbird | <i>Cracticus quoyi</i> | F | | | X | X | | 1,508 | |
| Hooded Butcherbird | <i>Cracticus cassicus</i> | F | | | X | X | | 1,333 | |
| Great Woodswallow | <i>Artamus maximus</i> | F | | | X | X | | | Common around Karimui Station |
| Black-faced Cuckooshrike | <i>Coracina novaehollandiae</i> | Ag | | | | X | | | |
| Stout-billed Cuckooshrike | <i>Coracina caeruleogrisea</i> | F | | | X | X | | 1,593 | |
| Boyer's Cuckooshrike | <i>Coracina boyeri</i> | F | | | | X | | | |
| Common Cicadabird | <i>Coracina tenuirostris</i> | Ag | | | X | | | | Vocalising bird seen near Karimui Station |
| Black-shouldered Cicadabird | <i>Coracina incerta</i> | F | | | X | | | | Single seen on north slope of Mt. Karimui (1,250 m) |
| Grey-headed Cuckooshrike | <i>Coracina schisticeps</i> | F | | pair, low | X | X | | 1,363 | |
| Black Cicadabird | <i>Coracina melas</i> | F | | | X | X | | | Pair seen at Tua River (550 m) |
| Black-bellied Cuckooshrike | <i>Coracina montana</i> | F | | pair, high | X | X | 1,338 | 2,303 | |
| Golden Cuckooshrike | <i>Campochaera sloetii</i> | F | | | X | X | | 1,243 | |
| Varied Triller | <i>Lalage leucomela</i> | F | | | X | X | | 1,423 | |

| English name | Scientific name | Habitat | Conservation status | Elevational replacement | BGF/AMCF | Diamond | Lower limit (m) | Upper limit (m) | Notes |
|-------------------------------|----------------------------------|---------|---------------------|---------------------------------------|----------|---------|-----------------|-----------------|--------------------------------------|
| Varied Sittella | <i>Daphoenositta chrysoptera</i> | F | | | | X | | | |
| Mottled Whistler | <i>Rhagologus leucostigma</i> | F | | | X | X | 1,323 | 2,520 | |
| Wattled Ploughbill | <i>Eulacestoma nigropectus</i> | F | | | X | X | 1,913 | 2,263 | |
| Rufous-naped Whistler | <i>Alcedryas rufinucha</i> | F | | | X | X | 1,303 | 2,398 | |
| Crested Pitohui | <i>Ornorectes cristatus</i> | F | | | X | X | | 1,353 | |
| Black Pitohui | <i>Melanorectes nigrescens</i> | F | | pair, high (with Little Shrikethrush) | X | X | 1,573 | 2,453 | |
| Rusty Whistler | <i>Pachycephala hyperythra</i> | F | | trio, low | X | X | | 1,353 | |
| Brown-backed Whistler | <i>Pachycephala modesta</i> | F | | | X | X | 1,810 | 2,220 | |
| Grey Whistler | <i>Pachycephala simplex</i> | F | | | X | X | | 1,463 | |
| Slater's Whistler | <i>Pachycephala soror</i> | F | | trio, middle | X | X | 1,243 | 1,913 | |
| Regent Whistler | <i>Pachycephala schlegelii</i> | F | | trio, high | X | X | 1,753 | 2,520 | |
| Black-headed Whistler | <i>Pachycephala monacha</i> | Ag | | | X | X | | | Common around Karimui Station |
| Rusty Pitohui | <i>Pseudorectes ferrugineus</i> | F | | | X | X | | 1,143 | |
| Little Shrikethrush | <i>Colluricincla megarhyncha</i> | F | | pair, low (with Black Pitohui) | X | X | | 1,753 | |
| Long-tailed Shrike | <i>Lanius schach</i> | Ag | | | X | | | | Regular at Karimui airstrip |
| Southern Variable Pitohui | <i>Pitohui uropygialis</i> | F | | pair, low | X | X | | 1,231 | |
| Hooded Pitohui | <i>Pitohui dichrous</i> | F | | pair, high | X | X | | 1,658 | Lower elevation limit not determined |
| Brown Oriole | <i>Oriolus szalayi</i> | F | | | X | X | | 1,443 | |
| Pygmy Drongo | <i>Chaetorhynchus papuensis</i> | F | | | X | X | | 1,713 | |
| Spangled Drongo | <i>Dicrurus bracteatus</i> | F | | | X | X | | 1,273 | |
| Willie Wagtail | <i>Rhipidura leucophrys</i> | Ag | | | X | X | | | Common around Karimui Station |
| Northern Fantail | <i>Rhipidura rufiventris</i> | F | | | X | X | | 1,423 | |
| Sooty Thicket Fantail | <i>Rhipidura threothorax</i> | F | | | X | X | | 1,243 | |
| White-bellied Thicket Fantail | <i>Rhipidura leucothorax</i> | F | | | X | X | | | Seen once near Karimui Station |
| Black Fantail | <i>Rhipidura atra</i> | F | | | X | X | 1,241 | 2,520 | |
| Chestnut-bellied Fantail | <i>Rhipidura hyperythra</i> | F | | pair, low | X | X | | 1,658 | |

| English name | Scientific name | Habitat | Conservation status | Elevational replacement | BGF/AMCF | Diamond | Lower limit (m) | Upper limit (m) | Notes |
|---------------------------------|--------------------------------|---------|---------------------|-------------------------|----------|---------|-----------------|-----------------|--|
| Friendly Fantail | <i>Rhipidura albolimbata</i> | F | | pair, high | X | X | 1,633 | 2,520 | |
| Dimorphic Fantail | <i>Rhipidura brachyrhyncha</i> | F | | | X | X | 1,573 | 2,520 | |
| Rufous-backed Fantail | <i>Rhipidura rufidorsa</i> | F | | | | X | | | |
| Black Monarch | <i>Symposiachrus axillaris</i> | F | | | X | X | 1,188 | 1,913 | |
| Spot-winged Monarch | <i>Symposiachrus guttula</i> | F | | | X | X | | 1,183 | |
| Black-winged Monarch | <i>Monarcha frater</i> | F | | | X | X | | 1,623 | |
| Golden Monarch | <i>Carterornis chrysomela</i> | F | | | X | X | | 1,193 | |
| Frilled Monarch | <i>Arses telescopthalmus</i> | F | | | X | X | | 1,273 | |
| Torrent-lark | <i>Grallina bruijnii</i> | Aq | | | X | X | | 1,213 | |
| Grey Crow | <i>Corvus tristis</i> | F | | | X | X | | 1,233 | |
| Lesser Melampitta | <i>Melampitta lugubris</i> | F | | | X | | 1,943 | 2,520 | |
| Blue-capped Ifrit | <i>Ifrita kowaldi</i> | F | | | X | X | 1,793 | 2,356 | |
| Crinkle-collared Manucode | <i>Mamcodia chalybatius</i> | F | | | X | X | | 1,433 | |
| Trumpet Manucode | <i>Phomygammus keraudrenii</i> | F | | | X | X | | 1,423 | |
| Short-tailed Paradigalla | <i>Paradigalla brevicauda</i> | F | | | X | X | | | Seen once at 1,820 m |
| Princess Stephanie's Astrapia | <i>Astrapia stephaniae</i> | F | | | X | X | 1,713 | 2,520 | |
| Lawes's Parotia | <i>Parotia lawesii</i> | F | | | X | X | | | Pair seen once at 1,640 m |
| King of Saxony Bird-of-paradise | <i>Pteridophora alberti</i> | F | | | X | X | 1,893 | 2,520 | |
| Superb Bird-of-paradise | <i>Lophorina superba</i> | F | | | X | X | 1,283 | 1,982 | |
| Magnificent Riflebird | <i>Ptiloris magnificus</i> | F | | | X | X | | 1,473 | |
| Black Sicklebill | <i>Epimachus fastosus</i> | F | VU | | X | X | 1,683 | 2,520 | |
| Black-billed Sicklebill | <i>Drepanornis albertisi</i> | F | | | X | X | | | One mist-netted at 1,710 m |
| Magnificent Bird-of-paradise | <i>Diphyllodes magnificus</i> | F | | | X | X | | 1,709 | |
| King Bird-of-paradise | <i>Cicinnurus regius</i> | F | | | X | X | | | Singles at Sena (730 m) and Tua (550 m) Rivers |
| Raggiana Bird-of-paradise | <i>Paradisaea raggiana</i> | F | | | X | X | | 1,623 | |
| Blue Bird-of-paradise | <i>Paradisaea rudolphi</i> | F | VU | | | X | | | |

| English name | Scientific name | Habitat | Conservation status | Elevational replacement | BGF/AMCF | Diamond | Lower limit (m) | Upper limit (m) | Notes |
|-------------------------|-----------------------------------|---------|---------------------|-------------------------|----------|---------|-----------------|-----------------|---|
| Banded Yellow Robin | <i>Poecilodryas placens</i> | F | NT | | | X | | | |
| Black-throated Robin | <i>Poecilodryas albonotata</i> | F | | | X | X | 1,703 | 2,520 | |
| White-winged Robin | <i>Peneothello sigillata</i> | F | | quartet, highest | X | X | 2,333 | 2,520 | |
| Slaty Robin | <i>Peneothello cyauus</i> | F | | quartet, high middle | X | X | 1,673 | 2,398 | |
| White-rumped Robin | <i>Peneothello bimaculata</i> | F | | quartet, lowest | X | X | | 1,283 | |
| White-faced Robin | <i>Tregellasia leucops</i> | F | | | X | X | 1,198 | 1,718 | |
| White-eyed Robin | <i>Pachycephalopsis poliosoma</i> | F | | quartet, low middle | X | X | 1,218 | 1,698 | |
| Torrent Flyrobin | <i>Monachella muelleriana</i> | F | | | X | X | | | Seen at Sena (730 m) and Tua (550 m) Rivers |
| Canary Flyrobin | <i>Microeca papuana</i> | F | | trio, high | X | X | 1,763 | 2,520 | |
| Yellow-legged Flyrobin | <i>Microeca griseiceps</i> | F | | trio, middle | X | | 1,093 | 1,423 | |
| Olive Flyrobin | <i>Microeca flavovirescens</i> | F | | trio, low | X | X | | 1,313 | |
| Garnet Robin | <i>Engerygone rubra</i> | F | | | X | X | 1,753 | 2,333 | |
| Northern Scrub Robin | <i>Drymodes superciliaris</i> | F | | | X | X | | 1,393 | |
| Lesser Ground Robin | <i>Amalocichla incerta</i> | F | | | X | X | 1,794 | 2,105 | |
| Island Leaf Warbler | <i>Phylloscopus maforensis</i> | F | | | X | X | 1,321 | 1,961 | |
| Australian Reed Warbler | <i>Acrocephalus australis</i> | Ag | | | X | | | | Present around Karimui airstrip |
| Papuan Grassbird | <i>Megalurus macrurus</i> | Ag | | | X | X | | | Common around Karimui Station |
| Black-fronted White-eye | <i>Zosterops minor</i> | F | | | X | X | | 1,703 | |
| Singing Starling | <i>Aplonis cantoroides</i> | Ag | | | X | | | | Flock regular at Karimui airstrip |
| Yellow-faced Myna | <i>Mino dumontii</i> | F | | | X | X | | 1,353 | |
| Russet-tailed Thrush | <i>Zootlera heinei</i> | F | | | X | X | 1,473 | 1,643 | |
| Pied Bush Chat | <i>Saxicola caprata</i> | Ag | | | | X | | | |
| Red-capped Flowerpecker | <i>Dicaeum geelvinkianum</i> | F | | | X | X | | 1,723 | |
| Black Sunbird | <i>Leptocoma sericea</i> | Ag | | | | X | | | |
| Blue-faced Parrotfinch | <i>Erythrura trichroa</i> | F | | | X | X | 1,493 | 2,313 | |
| Streak-headed Mannikin | <i>Lonchura tristissima</i> | F | | | X | | | | Seen twice around Karimui Station |
| Hooded Mannikin | <i>Lonchura spectabilis</i> | Ag | | | X | X | | | Common around Karimui Station |

On the identification and provenance of some early specimens of grasswrens (Maluridae: *Amytornis*) and their significance for taxonomy and nomenclature

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SUMMARY.—The identity and provenance of four 19th-century *Amytornis* grasswren specimens in the Naturalis Biodiversity Center (Leiden) collection are reviewed. Three identified as Thick-billed Grasswren *Amytornis modestus inexpectatus* enable a revised diagnosis for the extinct subspecies from New South Wales. One of these and one Striated Grasswren *A. striatus* were acquired from John Gould in, or soon after, December 1840. The other two came via the Frank dealership in 1858 and 1873, but are probably also from Gould's collections. Leiden's *A. striatus* specimen and another in Philadelphia are identified here as paralectotypes of *Dasyornis* [= *Amytornis*] *striatus* Gould, 1840. Evidence is presented that Gould's brother-in-law, Charles Coxen, collected both *A. modestus* and *A. striatus*, including type material of the latter, before Gould visited Australia in 1838.

While investigating morphological and genetic diversity within Western *Amytornis textilis* (Quoy & Gaimard, 1824) and Thick-billed Grasswrens *A. modestus* (North, 1902) (Black *et al.* 2010, Black 2011a, Austin *et al.* 2013) just one specimen of the extinct far eastern (New South Wales) subspecies *A. m. inexpectatus* (Mathews, 1912) was found in an Australian museum collection and it proved uninformative genetically. Following an enquiry concerning early grasswren specimens in collections outside Australia, it became apparent that four mounted 19th-century specimens were housed in the Naturalis Biodiversity Center (hereafter NBC, formerly Rijksmuseum voor Natuurlijke Historie, RMNH), Leiden, the Netherlands. Three were listed as *A. textilis* (i.e. either *A. textilis* or *A. modestus*, see below) and one as Striated Grasswren *A. striatus*. Documentation at NBC suggested that at least two of the '*A. textilis*' specimens were from New South Wales and might be *A. m. inexpectatus*. It was also evident that a specimen of each species ('*textilis*' and *striatus*) had been sent to RMNH by John Gould, presumably from his own collection. Gould (1840) was the author of *A. striatus* but, while he collected just one specimen himself, he referred to other specimens from New South Wales (Gould 1848) and claimed to have collected both species on the lower Namoi River, although Schodde (1982) doubted that *A. striatus* could have been taken there, citing a lack of suitable habitat. The NBC specimens have the potential to contribute to unresolved questions of grasswren taxonomy and nomenclature, including a reappraisal of the phenotype of *A. m. inexpectatus* and of the type material and type locality of *A. striatus*.

Methods

Known specimens of *A. m. inexpectatus* were examined by ABB at the Academy of Natural Sciences, Philadelphia (ANSP) (Gould's collection) on 8 April 2013 and at the American Museum of Natural History, New York (AMNH) (Mathews' collection) on 10 April 2013. Gould's two *A. striatus* specimens were also examined at ANSP and the four

NBC specimens were examined at NBC, Leiden, on 16 April 2013. Measurements taken were: bill = length (total culmen to skull insertion) × depth (at level of frontal feathering), wing = flattened chord and tail = central rectrices from tip to base.

Results

NBC specimens.—RMNH.AVES.172018. Label: '*Amytis striatus* [crossed out] *Malurus* [crossed out] *textilis* Gould auct pl Uranie Zool. pl 67 f 2. Australie.' Under the socle (base of stand): '*Amytis textilis* Gould auct *Malurus textilis* Uranie Zool. Pl 67 f 2 Australie.' On examination, an *A. modestus* mount in good condition, female with bright flank patches; slightly convex lower mandible, rather dark and heavily streaked on throat and upper breast for *modestus*. Bill 12.5 × 5.1 mm, wing 57 mm, tail 80.2 mm (Fig. 1). **RMNH.AVES.172019.** Label: '*Amytis textilis* ♂ (Quoy & Gaim) Frank 1873 N. S. Wales.' Under the socle: 'mas Frank 1873 N. S. Wales.' On examination, a male *A. modestus* mount showing moderate disturbance to plumage, similarly dark and relatively streaked below for *modestus*, biconvex bill profile. Bill 12.4 × 5.9 mm, wing 64 mm, tail 84.8 mm (Fig. 2). **RMNH.AVES.172020.** No label. Under the socle 'Frank 1858.' On examination, a male *A. modestus* mount showing slight disturbance to plumage; similar to RMNH.AVES.172018 and 172019, moderately convex lower mandible. Bill 12.3 × 5.4 mm, wing 58 mm, tail 80.2 mm (Fig. 3). **RMNH.AVES.172021.** Label: '*Amytis striata* (Gould) Avant 1850 Australie.' Under socle: '*Amytis striatus* Gould auct pl *textilis* pl 67 f 2 Lesson. Australie.' On examination, an *A. striatus* mount in good condition with rufous underparts merging laterally into brighter flanks, and thus female. Bill 12.8 × 4.2 mm, wing 63 mm, tail 89.4 mm (Fig. 4).

ANSP and AMNH specimens of *A. m. inexpectatus*.—ANSP 16887. Label: 'Gould Coll ♂ *Amytis textilis* (Quoy et Gaim.) New South Wales T. B. Wilson.' Male, bill 13.6 × 5.4 mm, wing 62 mm, tail 82.5 mm. **ANSP 16888.** Label: 'Gould Coll ♀ *Amytornis textilis* (macrourus [sic]) New South Wales Thos. B. Wilson.' Female, bill 12.2 × 5.4 mm, wing 61 mm, tail 87.2 mm. **ANSP 16889.** Label: 'Rivoli [sic] Gould Coll Thos. B. Wilson.' Male, bill 13.6 × 5.6 mm, wing 62 mm, tail 79.5 mm. **AMNH 598073.** Labels: '*Diaphorillas textilis inexpectatus* ♂ New South Wales TYPE Mathews 1912 etc.' Male, bill 12.6 × 5.0 mm, wing 63 mm, tail 80.3 mm. **AMNH 598072.** Labels: '*Diaphorillas* — ROTH Exc GMM juvenile ♂ New South Wales.' Male, bill 13.5 × 5.4 mm, wing 63 mm, tail 91.2 mm. All the specimens above are relatively dark for the species and possess moderate to heavy underparts streaking.

ANSP specimens of *A. striatus*.—ANSP 16890. Labels: 'Gould Coll TYPE ♂ *Amytis striatus* (Gould) New South Wales T. B. Wilson. 379 ♂ N S Wales 16890 *Dasyornis striatus* Gld. PZS. 1839. P 143 etc.' Male, bill 12.3 × 4.9 mm, wing 60 mm, tail missing. **ANSP 16891.** Labels: 'Gould Coll TYPE ♀ *Amytis striatus* (Gould) New South Wales T. B. Wilson. This has no type sig.' Female, bill 13.0 × 4.9 mm, wing 63 mm, tail 88.4 mm.

Discussion

Identification and provenance of the '*A. textilis*' specimens.—RMNH.AVES.172018 appears to have first been identified as *Amytis striatus* and later as *A. textilis*. While these two species are very distinct, their identification was not made consistently by all early workers (see below). RMNH.AVES.172018–020 are all identified here as *Amytornis modestus*. Until the latter was described (North 1902), all such specimens were generally included under *A. textilis*. Failure to recognise *A. textilis* and *A. modestus* as separate (but sister) species commenced with Gould himself (1848, 1865) who believed that grasswrens he collected in north-eastern New South Wales were the same species, *A. textilis*, as described by Quoy and Gaimard (1824) from Shark Bay, Western Australia, on the opposite side of the



Figure 1. RMNH Aves 172018: female *Amytornis modestus inexpectatus*, from the collection of John Gould 1840–41, the plains bordering the lower Namoi, northern New South Wales (Justin J. F. J. Jansen)

Figure 2. RMNH Aves 172019: male *Amytornis modestus inexpectatus*, from Frank, dealers, 1873, New South Wales (Justin J. F. J. Jansen)

Figure 3. RMNH Aves 172020: male, probable *Amytornis modestus inexpectatus*, from Frank, dealers, 1858, provenance uncertain (Justin J. F. J. Jansen)

Figure 4. RMNH Aves 172021: female *Amytornis striatus striatus*, from the collection of John Gould 1840–41, probably collected by Charles Coxen; paralectotype of *Dasyornis striatus* Gould, 1840, Liverpool Plains, northern New South Wales (Justin J. F. J. Jansen)

continent. North (1902) subsequently described *Amytis modesta* from central Australia and included Gould's New South Wales birds in his new species (see Fig. 5).

Despite much instability in the taxonomy of this genus in ensuing years, our present understanding (Black *et al.* 2010) is as follows. Briefly, *A. textilis* is darker, more heavily streaked and has a longer tail and more slender bill profile than *A. modestus* but there is variation in all of these characters among populations of both species (Black 2011a,b).

As noted above, the three NBC specimens are relatively dark and heavily streaked for *A. modestus* and closely resemble the ANSP and AMNH specimens of the New South Wales subspecies *A. m. inexpectatus*. Mathews (1912) first listed New South Wales birds, including Gould's specimens, as *Diaphorillas textilis inexpectatus*, but subsequently (Mathews 1922–

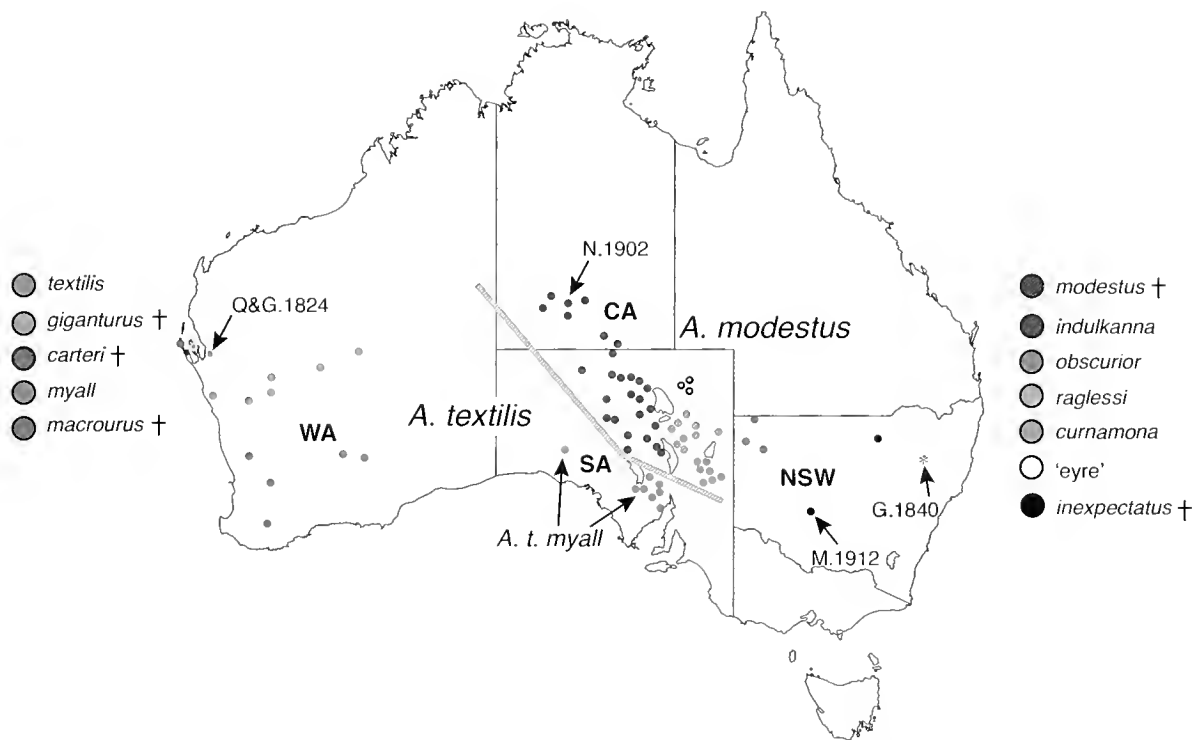


Figure 5. Map showing distributional records of Western Grasswren *Amytorus textilis* and Thick-billed Grasswren *A. modestus*. Subspecies are indicated by individual colours; † signifies extinct subspecies. 'Q&G 1824' represents the type locality of *Malurus textilis*, Shark Bay, Western Australia (WA); 'G 1840 *' shows an approximate type locality of *Dasyorhis striatus*, Liverpool Plains, New South Wales (NSW), east of the lower Namoi, where Gould collected '*A. textilis*'; 'N 1902' represents type localities of *Amytis modesta* in central Australia (CA); 'M 1912' represents the probable type locality of *Diaphorillas textilis inexpectatus*; '*A. t. myall*' indicates the population of Western Grasswren occurring on the Eyre Peninsula and in the Gawler Ranges, South Australia (SA) (modified from Austin *et al.* 2013).

1923) elevated eastern populations to species status, distinguishing them from the much paler isolate in north-western New South Wales, which he included in *A. modestus*. He also included birds from the Gawler Ranges, South Australia, in *D. inexpectatus* under the trinomial *D. i. myall* (= *A. textilis myall*) (Fig. 5). By combining *inexpectatus* with a subspecies of Western Grasswren *A. textilis*, Mathews drew attention to its relatively dark and heavily streaked plumage compared to more typical *A. modestus*. A further attribute of the NBC specimens is that each has the tail >80 mm, thus within the range of *A. m. inexpectatus*, as shown, but above that for all other *A. modestus* subspecies apart from some specimens of the extinct nominate subspecies from central Australia (Black 2011a). Given that these three specimens are also relatively dark and heavily streaked for *A. modestus* an alternative is that they might be *A. textilis*. However, RMNH.AVES.172019 is documented as being from New South Wales and RMNH.AVES.172018 was acquired from Gould (see below) and therefore by implication is also from New South Wales. Furthermore, no specimens of *A. textilis* are known to have been taken in Western Australia between Quoy and Gaimard's visit and the late 1890s (Black 2011b) and, while some were collected in the Gawler Ranges, South Australia, in the 1870s (ABB unpubl.), this is too late to account for RMNH.AVES.172020.

Gould (1848) stated that he had 'killed and dissected many examples' of '*A. textilis*' from New South Wales. Three of his specimens are in ANSP (as above); one went to the British Museum (BMNH 41.2.1496), where it was mounted (Sharpe 1883) but has not survived; another is identified here (RMNH.AVES.172018) and it is possible that RMNH.AVES.172019–020 also came from Gould, since he disposed of many specimens via the

Amsterdam-based (later London-based) Frank family business. Documents reveal that many Australian bird specimens entered the Leiden collection between c.1831 and 1876 via the Frank agency, including known specimens from Gould's collections as well as the 1858 grasswren (RMNH.AVES.172020) (JJFJJ pers. data), but details of their origins and collectors are imprecise or lacking, and we have been unable to locate any documents that show from where the Frank dealership acquired them.

Diagnosis of *A. modestus inexpectatus*.—This subspecies from eastern New South Wales is distinguished by its heavily streaked underparts from the central Australian nominate, whose underparts are barely streaked, and from all other subspecies of *A. modestus* by tail length (range 79.5–91.2 mm, compared to 63.8–78.8 mm in other subspecies and 74.1–83.6 mm in the nominate).

Identification and provenance of the *A. striatus* specimen.—The fourth Leiden specimen (RMNH.AVES.172021) is certainly *A. striatus*. Its label proves that it was received in Leiden before 1850 and evidence for its provenance and that of RMNH.AVES.172018 is held in the NBC archives. These include a list of Australian specimens sent by Gould to C. J. Temminck, inaugural Director of RMNH, which accompanied two copies of Part 1 of Gould's *The birds of Australia*, published in December 1840. The list includes skins and skeletons of mammals, and specimens, skeletons and eggs of birds; 114 species are listed among the birds, including one *Amytis textilis* and one *A. striatus*. From the list of then recently named and yet-to-be-named species in Gould's list, as well as the inclusion of Gould's *The birds of Australia* Part 1, it is evident that these specimens were sent to Temminck in December 1840 or early 1841. With little doubt, Gould had returned from Australia with them but was able to dispose of any material surplus to his immediate needs.

Documentation accompanying both RMNH.AVES.172018 (*A. textilis*) and RMNH.AVES.172021 (*A. striatus*) refers to 'pl 67 f 2' [i.e. Plate 67 figure 2 of Lesson (1831)]. Reference to 'Uranie Zool' (RMNH.AVES.172018) acknowledges Quoy & Gaimard's (1824) zoological account in *Voyage autour du monde sur les corvettes de l'Uranie et la Physicieuue*, including the description of *A. textilis*, which they figured on Pl. 23. Pl. 67 fig. 2 of Lesson (1831) also illustrated *A. textilis* but Gould did not believe that this was the case. He observed (Gould 1848, 1865) that 'the bird figured in the "Voyage de l'Uranie" doubtless represents the present species [*Textile Wren Amytis textilis*]', while that figured by Lesson in the Atlas to his "Traité d'Ornithologie," ... as clearly belongs to *A. striatus*.' Even in his initial description of '*Dasyoruis [=Auytoruis] striatus*' Gould (1840) wrote that it is 'nearly allied to the *Amytis textilis* of Lesson' (but by inference not to *Malurus (=Auytis) textilis* of Quoy and Gaimard). Gould was mistaken; while Lesson's figure shows a more rufous-plumaged bird than is depicted in Quoy & Gaimard (a distinctive feature to which Gould correctly attributed significance), it is still recognisably *A. textilis*, since it lacks the distinctive white throat and black moustachial stripe of the other species.

Possible alternative early specimen sources of *A. modestus* and *A. striatus* in New South Wales.—While it is almost certain that Gould supplied two of the NBC specimens and possibly all four, potential alternative 19th-century suppliers must be considered. Sharpe (1883) listed among specimens of '*A. textilis*' in the British Museum a mount supplied by Governor George Grey of South Australia, and another by Sir Thomas Mitchell who explored New South Wales, which then included Queensland and Victoria, in 1831–36 and again in 1845. Grey's specimen was received by the museum in July 1843 (BMNH 1843.7.14.230) and Mitchell's in August 1847 (BMNH 1847.8.14.135) (ABB pers. obs.) but both are long lost (M. Adams & R. Prÿs-Jones pers. comm.).

Samuel White and his brother William collected extensively in eastern Australia during 1867–68 and three '*Amytis striata*', purportedly from those excursions, were presented to

the South Australian Museum, Adelaide (SAMA) in 1870. Two '*A. striata*' were forwarded from SAMA for the Paris International Exhibition of 1878, of which one, when examined in September 2011 (the other is lost), proved to be *A. modestus*. It is possible that this is one of White's specimens which, if taken in New South Wales in 1868, would represent *A. m. inexpectatus* (Black *et al.* 2013, Horton *et al.* in prep.).

Much of John T. Cockerell's large collection was acquired by F. D. Godman and donated to the British Museum in 1881. Two birds identified as '*Amytornis textilis*' (BMNH 1881.11.7.1229, female, and BMNH 1881.11.7.1230, male) were said to be from South Australia (Sharpe 1883). Later, probably during preparation for the Harold Hall (1962–68) expeditions to Australia, they were labelled *A. modestus inexpectatus*, evidently by curator D. Goodwin, who provisionally assigned all New South Wales and most South Australian examples to that subspecies (R. Prÿs-Jones pers. comm.). In June 1870 Cockerell had acquired via SAMA at least one specimen of what is now *A. m. raglessi* Black, 2011, from the Flinders Ranges, South Australia (Horton *et al.* in prep.). Measurements of the male, but not the female, are consistent with such an origin (Black 2013), so the identity and provenance of both are open to question.

Thomas Campbell Eyton's catalogue (Eyton 1856: 136) listed a specimen of '*Amytis striatus*', labelled only 'Australia'. Henry Baker Tristram's catalogue (Tristram 1889: 158) listed one '*Amytis striata*' from 'S. Australia – S. White' and one '*Amytis textilis*' from Australia, acquired from the Eyton Museum (perhaps the bird listed as '*Amytis striatus*' in Eyton's catalogue).

Of the specimens discussed above, Grey's and Mitchell's cannot be among those in Leiden since they were in the British Museum until at least 1883. White is not known to have obtained grasswrens other than the three identified as *A. striatus* and reportedly taken in New South Wales in 1868 (Horton *et al.* in prep.), but he might have had more than the three presented to SAMA. Indeed, Tristram (1889) attributed one to him (listed as *A. striatus*) and perhaps this was obtained when most of White's collection was sold by his executors in London in December 1885. It is unlikely that White sold any specimens earlier, since his will indicated a wish that his entire collection pass to his son Samuel Albert White (Linn 1989). The provenance and collector of the two Cockerell grasswrens at BMNH are unknown and it is not certain that he obtained any from New South Wales. Cockerell was the probable supplier of specimens sent to the Frank business around 1875, described as from Cape York (JJFJJ pers. data), a locality name frequently used by Cockerell, sometimes misleadingly if not deceptively (Pigott 2004), but there is nothing to show that he supplied the Frank grasswren specimen received in 1873 (RMNH.AVES.172019). Other collectors active in New South Wales could have obtained grasswrens, but E. P. Ramsay (1878), who worked in the colony, though accepting that '*A. textilis*' occurred there, did not include *A. striatus*. Silvester Diggles (1865–70, 1877) painted 325 Australian birds for his never-completed monograph but could find no specimen of *A. striatus* anywhere, even in Eli Waller's extensive collection in Brisbane, Queensland. Diggles resorted to copying an image from one of Gould's plates held by Charles Coxen, who was by then also based in Queensland (Pigott 2004). Both Ramsay and Waller supplied lists of 'desiderata' for SAMA Curator F. G. Waterhouse, among them any '*Amytis*' species. A specimen of '*Amytis striata*' was sent from SAMA to Waller in December 1867, and two to Ramsay in May 1868 (Horton *et al.* in prep.), the latter two known to be *A. striatus* (ABB pers. obs.). The dearth of any grasswren specimens amongst these collectors makes it difficult to suggest an alternative to Gould as the supplier of the two Franks' specimens.

The specimen measured by Gould and the type locality of Amytornis striatus (Gould, 1840).—Stone & Mathews (1913: 166—'Type') and Meyer de Schauensee (1957:

208–209—‘Holotype’) collectively identified ANSP 16890, an adult male from ‘New South Wales’ at the Academy of Natural Sciences, Philadelphia, as the holotype of *Dasyornis striatus* Gould, 1840 [= *Anytornis striatus*]. They perhaps chose this specimen because it is a male and they thought it must therefore be the specimen Gould (1848, 1865) reported collecting himself. These authors recorded the type locality (which they took from Gould’s *Proceedings of the Zoological Society of London* account) as the Liverpool Plains, while Meyer de Schauensee further quoted Gould as taking his specimen while ‘traversing the Lower Namoi’. A designation of ‘holotype’ is only appropriate if there is certainty that Gould described the species from a single specimen but this is not the case and the question of syntypes must be considered; moreover, as will be shown, Gould’s own specimen cannot have been used in the description and therefore lacks type status. But the male (ANSP 16890) designated as the holotype by Meyer de Schauensee (1957) might not have been Gould’s and so could have been the specimen he measured; it will be recognised as the lectotype of *Dasyornis striatus* unless strong evidence can be presented to overturn the Philadelphia curators’ decisions. On the other hand it is far more likely that Gould’s personal specimen, retained and illustrated in *The birds of Australia*, is ANSP 16890.

Gould described *Dasyornis striatus* in a letter he sent to the Zoological Society of London, written on 10 May 1839, on returning to Tasmania from his first visit to New South Wales, read to the society on 8 October 1839 and published in January 1840 (Gould 1840: 143). In the same letter Gould wrote that the furthest he had journeyed into the interior of the continent was the Liverpool Range (part of the Great Dividing Range) north of Yarrundi, the property of his host and brother-in-law Stephen Coxen. In an earlier letter, dated 20 March 1839, to his wife Elizabeth (who, heavily pregnant, had been left with the Franklins in Hobart), Gould recounted that he had climbed one of the highest peaks in the Liverpool Range and had seen the Liverpool Plains below him (Sauer 1982: 111). He did not go there, however, until later in the year and so cannot have collected any specimen with type status himself.

Yarrundi was situated near the Dartbrook, a tributary of the Hunter River draining south-east into the Pacific Ocean, thus prior to May 1839 Gould had collected only on the seaward slope of the Great Dividing Range. The Liverpool Plains lie north of the range and are drained by the Mooki and Peel Rivers (tributaries of the Namoi, which flows north-west and inland within the Darling River Basin—see map in Datta 1997: 123). Stephen’s brother Charles had established a property on the Peel (Datta 1997) and might have provided Gould’s first Striated Grasswrens from nearby, as well as type material of Yellow-throated Miner *Manorina flavigula* (Gould, 1840), which was reportedly taken on the banks of the Namoi itself. An alternative source for the grasswren measured by Gould in his type description was the Australian Museum, Sydney, if he had visited this institution during his first visit to New South Wales; certainly he spent much time there during his second in August–September 1839 (Datta 1997). Gould stayed with George Bennett, who had been appointed the museum’s curator in 1835 and had produced a catalogue of its collections (Bennett 1837). This included several bird specimens presented to the museum by Charles Coxen, among them examples of ‘*Malurus textilis*. The Mouse-bird of the Colonists, male and female. Hunter’s River’ [a probable error of location] and ‘*Dasyornis australis*. The Bristle-bird of the Colonists, male. Scrubs near Liverpool Plains’. *Malurus textilis* Quoy & Gaimard, 1824, is now *Anytornis textilis*, the bird that Gould believed he had collected near the lower Namoi later in 1839. *Dasyornis australis* Vigors & Horsfield, 1827, is a synonym of Eastern Bristlebird *D. brachypterus* (Latham, 1801), which occurs only on the coastal side of the Great Dividing Range, far to the east of the Liverpool Plains. It appears that a specimen Bennett had listed as a bristlebird *Dasyornis* was considered to be a grasswren by Gould,

despite which he used Bennett's genus name *Dasyornis* in his description of what is now *A. striatus*, an uncharacteristic error that otherwise appears inexplicable. These entries in Bennett's catalogue reveal that Charles Coxen had collected (or otherwise obtained) both grasswren species before Gould reached New South Wales in 1839. The three specimens, along with many others listed by Bennett, are no longer extant in the collection of the Australian Museum (W. E. Boles pers. comm., N. W. Longmore pers. comm.).

Gould crossed the Liverpool Range to the Liverpool Plains only during his second and longer journey in October 1839–January 1840, during which he travelled 200 miles down the Namoi (Datta 1997). Therefore, as recognised by McAllan & Bruce (1989), we find that the bird Gould measured in his type description cannot be the male he collected himself. This is not to say it is not ANSP 16890, even though it is a male; as noted earlier, another male presumably of this species, collected by Charles Coxen, was listed in Bennett's (1837) catalogue. Potentially, Gould's measured specimen could be either of the female specimens ANSP 16891 or RMNH.AVES.172021, a now lost or no longer extant specimen including the Coxen / Bennett example, or that acquired by Thomas Eyton. Eyton obtained many birds from John Gould, but his *A. striatus* specimen might have been misidentified as it was considered to be *A. textilis* after it entered the collection of Canon H. B. Tristram, whose primary collection later went to the Liverpool Museum. Unfortunately, Tristram's two grasswren specimens cannot be found in what is now National Museums Liverpool, having probably been destroyed when the museum was firebombed during World War II. The type locality of *A. striatus*, often given erroneously as the lower Namoi River, has been questioned because suitable habitat appears to be absent (Schodde 1982, Rowley & Russell 1997) and the species has not been reported there since Gould's time. Yet Gould's (1848, 1865) description of the habitat, 'a loose sandy soil studded with high rank grass, which, growing in tufts, left the interspaces quite bare', is perfectly typical and could only be bettered by naming the vegetation as porcupine grass of the genus *Triodia*. McAllan (1987) provided evidence that *Triodia* and sandy soils do occur relatively near the Liverpool Plains and listed a series of historical grasswren reports linking the present distribution of *A. striatus* with the lower Namoi c.600 km distant. These included one (possibly two) 19th-century specimens, a sighting from 1974 (Schmidt 1978, recently reaffirmed by the observer: L. Schmidt pers. comm.) and observations by A. J. North in the Coonamble district in 1905, <100 km from the Namoi and 150 km from the Liverpool Plains. Also of interest is that several reports raised uncertainty as to whether the species concerned was *A. striatus* or *A. textilis* (= *A. modestus*), but we concur with McAllan (1987) that the former was more likely. We also find support for the Liverpool Plains as the type locality of *A. striatus* (Fig. 5) and, while it is possible that Gould was mistaken as to where he collected his specimen, we cannot discount his claim to have found and collected the species on the lower Namoi.

Identification of Gould's type series.—Gould (1840) described *Dasyornis* [= *Amytornis*] *striatus* among 18 other new species, each of which was given a short description in Latin, a single list of measurements, a type locality of varying levels of precision, comparative details in some and the name of the collector in 14. Benjamin Bynoe, surgeon aboard HMS *Beagle*, was named as collector of 12 of the new species from the north-west coast of Australia. Gould himself collected two of the 19 while one, *Graucalus phasianellus* [= Ground Cuckooshrike *Coracina maxima*] from the Liverpool Plains, was listed as being from the collection of (and implicitly collected by) Stephen Coxen. As discussed above, Charles Coxen, who had already sent specimens to Gould and who continued to do so subsequently (Datta 1997), was probably the collector of the first *Dasyornis striatus*. It should be observed that, while Gould (1840) gave just one set of measurements for each new species, he did not state that only one specimen was before him. His descriptions were certainly based on more

than one specimen in at least three cases, the two collected by him (*Cypselus australis* [= Fork-tailed Swift *Apus pacificus*] and Rose Robin *Petroica rosea*), where he stated as much, and at least one species collected by Bynoe (Striated Pardalote *Pardalotus [striatus] uropygialis*), as demonstrated by Meyer de Schauensee (1957). When describing *Dasyornis striatus* Gould might have had a single specimen but, equally, might have had others. Gould (1848, 1865) stated that he had procured only one specimen of *A. striatus* 'in a recent state'; this was his own male making it clear that no others were obtained during his journey to the interior in late 1839. He added (Gould *loc. cit.*) that 'all the specimens I have seen from New South Wales were [similar]', thus it is evident that those were collected earlier and that all could have formed the basis for his description earlier in the year. Since Gould disposed of RMNH.AVES.172021 within months of his return to London in August 1840, presumably retaining ANSP 16891 for illustration, it is probable that they were the earliest (or among the earliest) specimens he obtained and would have been included in the type series.

Gould's (1840) description reads: '*Dasyornis striatus*. *Das. fuscus*; *abdomine cinerescente; plumis dorsalibus lineâ centrali albâ notatis; rostro pedibusque nigrescentibus*. Long. tot. 6½ poll.; *rostri*, ⅝; *alæ*, 2⅜; *caudæ*, 3½; *tarsi*, 1. *Hab.* Liverpool Plains, New South Wales. This species is nearly allied to the *Amytis textilis* of Lesson.' An English interpretation of the Latin description is of a dark bristlebird (*sic*) with ash-coloured abdomen, dorsal feathers marked with a white central line, bill and feet almost black. These details do not permit identification of an individual specimen; indeed they would match specimens of several grasswren species (but certainly distinguish it from any species of *Dasyornis*). Measurements were compared with those of the three known, extant specimens that Gould might have measured, ANSP 16890, male, ANSP 16891, female, and RMNH.AVES.172021, female. Respective bill measurements were 12.3, 13.0 and 12.8 mm (Gould's measurement of ⅝ inch [=15.9 mm] is presumably erroneous), wing 60, 63 and 63 mm (Gould's = 60 mm), tail (missing), 88.4 and 89.4 mm (Gould's = 88.9 mm). It is impossible therefore to identify either female as the specimen Gould measured (or indeed unequivocally to dismiss the lectotype status of ANSP 16890) and ANSP 16891 and RMNH.AVES.172021 are better considered paralectotypes of the species and therefore of nominate *A. s. striatus*. Eyton's specimen from 'Australia' (1856: 136) could well have been obtained from John Gould, and could conceivably have been that Gould measured for his type description. However, its identity is in question and it is now lost, as is another possible candidate, the specimen listed by Bennett (1837) in Sydney at the time of Gould's visit.

Two other subspecies of Striated Grasswren are recognised at present, *A. striatus whitei* (Mathews, 1910) of the Pilbara, Western Australia, and *A. s. rowleyi* Schodde & Mason, 1999, which is restricted to central Queensland.

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The taxonomic status of Rwenzori Nightjar *Caprimulgus ruwenzorii* Ogilvie-Grant, 1909, and Benguela Nightjar *C. koesteri* Neumann, 1931

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SUMMARY. — Doubts concerning the species status of Rwenzori Nightjar *Caprimulgus ruwenzorii*, and inclusion of Benguela Nightjar *C. koesteri* in its synonymy, are considered using mensural data for the Afrotropical montane nightjar complex, and by re-examining the plumage of *C. koesteri*. I conclude that both these taxa are subspecies of Montane Nightjar *C. poliocephalus*.

Chapin (1939: 413) realised that the four African montane nightjars appear to be conspecific: Abyssinian Nightjar *Caprimulgus poliocephalus* Rüppell, 1840; Ruwenzori Nightjar *C. ruwenzorii* Ogilvie-Grant, 1909; Usambara Nightjar *C. guttifer* Grote, 1921; and Benguela Nightjar *C. koesteri* Neumann, 1931. They were subsequently treated as conspecific by most authorities, including White (1965), Colston (1978) and Jackson (1984). The current spelling of Ruwenzori is Rwenzori, and of Benguela is Benguela. Jackson (1993: 151) recommended that traditional English names be retained for subspecies, but that the species (*C. poliocephalus*, *sensu lato*) be known as Montane Nightjar.

Chappuis (1981) considered the song of *ruwenzorii*, from a sound-recording made in the Impenetrable Forest (Uganda), to be very different to two songs of *poliocephalus*, recorded in Kenya at Kericho and Nairobi, in that it has a much sharper tonality and the phrases are much shorter.

Prigogine (1984) used *C. p. koesteri* as an example of an isolate representing a distinct subspecies of a polytypic species, but noted that *koesteri* might be more than a subspecies, 'as this taxon shows several differences from the other subspecies'.

In a major review of the skull morphology, song characteristics and systematics of African nightjars, Fry (1988) concluded that *C. ruwenzorii* is a species, separable specifically from *C. poliocephalus* by vocal differences. He noted that determination of the taxonomic status of two other montane isolates, *koesteri* and *gutturalis* (*sic*, a *lapsus calami* for *guttifer*), awaited voice recordings and analysis. In *The birds of Africa*, Fry & Harwin (1988) treated *C. ruwenzorii* as a species, and *guttifer* and *koesteri* as subspecies of *C. poliocephalus*, despite both being closer to *C. ruwenzorii* geographically and morphologically.

Louette (1990) commented on the inconsistency shown by Fry & Harwin (1988) of 'excluding *ruwenzorii* from the species *poliocephalus* on vocal characteristics (compared with all subspecies?), while morphologically it is in fact intermediate between two taxa admitted in the species, namely *guttifer* and nominate *poliocephalus*'. He listed this form as '*C. ruwenzorii*', clearly not accepting the proposed species status. Dowsett & Dowsett-Lemaire (1993) also challenged the specific status of *C. ruwenzorii*, partially on morphological grounds, but mainly as a result of a reconsideration of the vocal evidence. While Fry & Harwin (1988) considered a single voice recording of *ruwenzorii* to be sufficiently distinct from that of nominate *poliocephalus* to warrant specific status, examination of more tapes, not only of *ruwenzorii* but also of *guttifer*, by Dowsett & Dowsett-Lemaire (1993) led them to conclude that vocal variation is no more than dialectal. Consequently they preferred to keep all forms within the same species.

Cleere (1995) re-examined the entire montane nightjar complex and recognised two species, separated mainly by vocal differences, namely monotypic *C. poliocephalus* in the north, and polytypic *C. ruwenzorii*, with two subspecies (*ruwenzorii* and *guttifer*), in the south, and treated *koesteri* as a synonym of *ruwenzorii*. This arrangement was adopted in both major monographs of the Caprimulgiformes (Cleere 1998, Holyoak 2001). However, Cleere (1998) noted that some authorities consider the two species to be conspecific, and Holyoak (2001: 35) explained that he provisionally treated a few controversial forms as species, in order to present all relevant data separately from those of close allies, rather than from any conviction that they merited species rank.

The criticisms by Louette (1990) and Dowsett & Dowsett-Lemaire (1993), along with an examination of the sonograms presented by both the latter and by Cleere (1995), lead me to have serious doubts concerning the species status of *C. ruwenzorii*. Presented here are mensural data that may help to resolve the issue.

Methods

I treat *Caprimulgus palmquisti* Sjöstedt, 1908, as a synonym of *C. poliocephalus* Rüppell, 1840, as did Holyoak (2001); Cleere (1998) made no mention of it. Sjöstedt (1908) considered *C. palmquisti* to be nearest to *C. poliocephalus*, and his illustration of *C. palmquisti* reveals that it has the same full extent of white on the outer rectrices as does *C. poliocephalus*, one of the diagnostic characters of this form. Furthermore, the measurements provided by Sjöstedt for *C. palmquisti* all fall within the mensural ranges of *C. poliocephalus* (Table 1).

Key characters (Jackson 2000) were measured on 68 specimens of three of the subspecies involved: 42 *C. p. poliocephalus*, 21 *C. p. ruwenzorii* and five *C. p. guttifer*, listed north to south (for details of specimens see Appendix). Females, juveniles, feathers in moult and damaged characters were excluded. The data therefore refer only to sound characters on fully grown males.

The lengths of the five outer primaries (pp10–6) were measured by sliding a stopped ruler under the closed wing of the specimen until the stop met the bend of the wing, pressing the primaries flat against the ruler and then reading off the five measurements. The position of the wingbar (an isolated white or buff patch approximately halfway along the feather) was measured on p9 by taking the distance from the tip of the primary to the centre of the patch on the inner web. The extent of the emargination on the leading edge of p9 was measured from the tip of the primary to the point of flexure in the reverse curve, i.e. the neutral point between the inner and outer curves (as illustrated in Jackson 1986).

The length of the inner rectrix (r1) was measured from the skin at the base of the calamus to the tip of the feather. The calamus was exposed by parting the uppertail-coverts

TABLE 1

Measurements (from Jackson 2000, tarsus from Jackson 1984) of some key characters in male Abyssinian Nightjars *Caprimulgus poliocephalus* Rüppell, 1840, and the only known male *C. palmquisti* Sjöstedt, 1908 (measurements from Sjöstedt 1908). R1 and r5 are the inner and outer rectrices, respectively. Note that all *C. palmquisti* measurements fall within the ranges for *C. poliocephalus*.

| Key character | <i>C. poliocephalus</i> Mean (range) <i>n</i> | <i>C. palmquisti</i> <i>n</i> = 1 |
|-----------------------|--|--------------------------------------|
| Length of wing (mm) | 152.3 (139–162) 57 | 155 |
| Length of r1 (mm) | 113.8 (106–124) 52 | 115 |
| Length of r5 (mm) | 110.1 (102–120) 52 | 107 |
| Length of tarsus (mm) | 14.9 (10–19) 83 | 17 |

so that the base was located visually, not by feel. The distance from the tip of r1 to the tip of r5 was measured with the tail closed and the difference was then applied to the length of r1 to derive the length of r5. All rectrix lengths are therefore relative to the base of r1. The pale apical patches on r4 and r5 were measured by taking the maximum dimension parallel to the rachis.

The length of the tomium was measured in a straight line from the tip of the bill to the inside angle of the gape and the width of the gape was measured across the bill from gape flange to gape flange. Tomium \times gape provided an approximate mouth size. The length of the tarsometatarsus was measured posteriorly from the intertarsal joint to the base of the last complete scale before the divergence of the toes. The length of the middle toe (t3) was measured from the base of the last complete scale on the tarsus to the tip of the pectinated claw. Tarsometatarsus + t3 provided the overall length of the foot.

Characters showing clinal variation were set aside. The remaining characters were each subjected to an analysis of variance (ANOVA one-way classification) to test, with a probability of 0.05, the null hypothesis that the three forms represent either a single population or three populations with equal means.

With just two known specimens of *C. p. koesteri*, this subspecies was not included in the analyses of variance. However, measurements made in accordance with the methods above were provided by M. Adams (Natural History Museum, Tring, UK) for the male and J. Trimble (Museum of Comparative Zoology, Cambridge, MA, USA) for the female. These were used to compare *koesteri* with *ruweenzorii*.

Results

Measurements of Benguela Nightjar.—Table 2 shows that, with one very minor exception, all key character measurements in *koesteri* fall within the range of *ruweenzorii*. The following results apply to the other three montane nightjars.

Clinal variation.—Three key characters display clinal variation, with mensural means decreasing from north to south (Table 3): the length of the apical patch on the outer rectrix (r5), the length of the apical patch on the adjacent rectrix (r4) and relative mouth size (tomium \times gape).

Analysis of variance.—An ANOVA was conducted on 12 characters (Table 4); seven for the wing, three for the tail and two for the foot. Tarsus length ($F_{2,64} = 8.86, P = 0.000$, Table 4k) was the only character requiring that the null hypothesis be rejected. It was not rejected by any of the results for the other 11 characters: length of p10 ($F_{2,61} = 1.40, P = 0.254$, Table 4a); length of p9 ($F_{2,60} = 1.55, P = 0.220$, Table 4b); percentage emargination on p9 ($F_{2,60} = 0.65, P = 0.526$, Table 4c); distance of centre of wingbar from tip of p9 ($F_{2,61} = 1.44, P = 0.244$, Table 4d); length of p8 ($F_{2,62} = 2.04, P = 0.139$, Table 4e); length of p7 ($F_{2,62} = 0.15, P = 0.864$, Table 4f); length of p6 ($F_{2,62} = 0.86, P = 0.430$, Table 4g); length of r1 ($F_{2,53} = 0.01, P = 0.993$, Table 4h); length of r5 ($F_{2,54} = 1.62, P = 0.207$, Table 4i); tail (r1) / wing (p9) ratio (%) ($F_{2,49} = 0.41, P = 0.669$, Table 4j); and length of t3 ($F_{2,64} = 0.10, P = 0.908$, Table 4l).

Discussion

Taxonomic status of Benguela Nightjar.—According to Cleere (1995) *C. koesteri* Neumann, 1931, is identical to *C. ruweenzorii* Ogilvie-Grant, 1909, and is best treated as a synonym of the latter. However, these two are not identical. Neumann (1931) described *koesteri* as similar to *ruweenzorii*, but smaller, with the pale bars in the tail narrower and more numerous (eight, including the terminal band) than in *ruweenzorii* (which has six). Also, *koesteri* has less white on the throat than *ruweenzorii* (Hall 1960, Colston 1978). The

TABLE 2

Measurements (mm) and ratios (%) of some key characters in (a) Rwenzori Nightjar *Caprimulgus ruwenzorii* Ogilvie-Grant, 1909, and (b) Benguela Nightjar *C. koesteri* Neumann, 1931. ** = the only *C. koesteri* measurement that does not fall within the range of *C. ruwenzorii* measurements.

| Key character | Mean \pm SD (range) <i>n</i> | Key character | Mean \pm SD (range) <i>n</i> |
|---------------|---|-------------------------|---|
| Length of p10 | (a) 145.3 \pm 4.8 (130–155) 40 (b) 146 (M) and 138 (F) | P9 patch position | (a) 60.2 \pm 3.0 (54–67) 42 (b) 60 (M) and 59 (F) |
| Length of p9 | (a) 154.5 \pm 4.9 (141–163) 40 (b) 152 (M) and 146 (F) | P9 emargination | (a) 67.2 \pm 3.2 (58–73) 41 (b) 65 (M) and 62 (F) |
| Length of p8 | (a) 154.8 \pm 4.7 (144–163) 40 (b) 151 (M) and 149 (F) | Ratio emargination / p9 | (a) 43.6 \pm 1.4 (40.0–47.5) 39 (b) 42.8 (M) and 42.5 (F) |
| Length of p7 | (a) 147.3 \pm 4.9 (136–156) 40 (b) 142 (M) and 141 (F) | Ratio p7 / p10 | (a) 101.4 \pm 2.0 (96.5–105.7) 40 (b) 97.3 (M) and 102.2 (F) |
| Length of p6 | (a) 126.8 \pm 5.0 (116–139) 39 (b) 122 (M) and 120 (F) | Ratio p6 / p9 | (a) 82.1 \pm 2.1 (78.6–87.1) 39 (b) 80.3 (M) and 82.2 (F) |
| R5 patch (M) | (a) 55.0 \pm 5.6 (46–68) 20 (b) 57 | Patch on r5 (F) | (a) 28.1 \pm 3.6 (23–34) 21 (b) 32 |
| R4 patch (M) | (a) 54.8 \pm 5.5 (44–63) 20 (b) 53 | Patch on r4 (F) | (a) 24.2 \pm 4.2 (16–34) 21 (b) 15** |
| Length of r1 | (a) 115.0 \pm 5.0 (105–128) 36 (b) ? (M) and 124 (F) r1 of male is in moult | Length of r5 | (a) 108.6 \pm 4.1 (100–122) 37 (b) 112 (M) and 115 (F) |
| Tomium length | (a) 27.0 \pm 1.3 (24–30) 41 (b) 24 (M) and 27 (F) | Length of foot | (a) 35.9 \pm 1.7 (32–40) 41 (b) 37 (M) and 35 (F) |

TABLE 3

Mensural characters showing marked clinal variation in three Afrotropical montane nightjars, with means decreasing from Abyssinian Nightjar *Caprimulgus poliocephalus* Rüppell, 1840, in the north, through Rwenzori Nightjar *C. ruwenzorii* Ogilvie-Grant, 1909, to Usambara Nightjar *C. guttifer* Grote, 1921, in the south. AP = apical patch. R5 and r4 are the outer and adjoining rectrices, respectively. Mouth = tomium \times gape. Sample sizes are shown in brackets following means.

| Taxon | AP on r5 (mm) | AP on r4 (mm) | Mouth (mm ²) |
|----------------------|---------------|---------------|--------------------------|
| <i>poliocephalus</i> | 90.5 (36) | 87.4 (35) | 703 (41) |
| <i>ruwenzorii</i> | 55.0 (20) | 54.8 (20) | 653 (19) |
| <i>guttifer</i> | 42.8 (5) | 43.2 (5) | 611 (5) |

type specimen of *koesteri* was unsexed, but Neumann (1931) presumed that it was a male, whereas it is now known to be female (Hall 1960). As females are generally smaller than males (Table 2), this may have misled Neumann (1931) into believing that *koesteri* is smaller than *ruwenzorii*, after comparing it with specimens of the latter. Table 2, based on rather more material, shows that virtually all *koesteri* measurements fall within the range of *ruwenzorii*.

Hall (1960) noted that both sexes of *koesteri* have pale brown bars on the inner webs of the outermost rectrices, but gave their number as seven rather than eight (perhaps excluding the terminal band?). As *ruwenzorii* has only six, broader, pale bars (Neumann 1931), this character provides a simple means of separating the two forms.

The plumage differences between *koesteri* and *ruwenzorii*, together with the geographical distance (c.2,300 km) separating them, argue against the proposal by Cleere (1995) to treat *koesteri* as a synonym. While I do not agree with Prigogine (1984) that *koesteri* might be more

TABLE 4

Results of ANOVA to test, with a probability of 0.05, the null hypothesis that three of the Afrotropical montane nightjars (same as Table 3) represent either a single population or three populations with equal means. Degrees of freedom (*df*) between groups (upper) and within groups (lower) are shown. *F* is the calculated *F* statistic, *F crit* the critical value that must be exceeded by *F* in order to reject the null hypothesis. * See (k) for the only character in which the calculated value of *F* exceeds the critical value.

| Taxon (<i>n</i>) | Mean | <i>df</i> | <i>F</i> | <i>P</i> -value | <i>F crit</i> |
|---|-------|-----------|----------|-----------------|---------------|
| (a) Length of outer primary p10 (mm): | | | | | |
| <i>poliocephalus</i> (39) | 143.5 | 2 | 1.401 | 0.254 | 3.148 |
| <i>ruwenzorii</i> (20) | 144.6 | 61 | | | |
| <i>guttifer</i> (5) | 147.0 | | | | |
| (b) Length of p9 (mm): | | | | | |
| <i>poliocephalus</i> (38) | 152.6 | 2 | 1.553 | 0.220 | 3.150 |
| <i>ruwenzorii</i> (20) | 153.7 | 60 | | | |
| <i>guttifer</i> (5) | 156.0 | | | | |
| (c) Emargination on p9 (%): | | | | | |
| <i>poliocephalus</i> (38) | 43.3 | 2 | 0.649 | 0.526 | 3.150 |
| <i>ruwenzorii</i> (20) | 43.7 | 60 | | | |
| <i>guttifer</i> (5) | 43.7 | | | | |
| (d) Distance of centre of wingbar from tip of p9 (mm): | | | | | |
| <i>poliocephalus</i> (38) | 60.2 | 2 | 1.444 | 0.244 | 3.148 |
| <i>ruwenzorii</i> (21) | 60.3 | 61 | | | |
| <i>guttifer</i> (5) | 62.8 | | | | |
| (e) Length of p8 (mm): | | | | | |
| <i>poliocephalus</i> (40) | 152.6 | 2 | 2.039 | 0.139 | 3.145 |
| <i>ruwenzorii</i> (20) | 153.9 | 62 | | | |
| <i>guttifer</i> (5) | 156.4 | | | | |
| (f) Length of p7 (mm): | | | | | |
| <i>poliocephalus</i> (41) | 145.9 | 2 | 0.146 | 0.864 | 3.145 |
| <i>ruwenzorii</i> (20) | 146.6 | 62 | | | |
| <i>guttifer</i> (4) | 146.5 | | | | |
| (g) Length of p6 (mm): | | | | | |
| <i>poliocephalus</i> (41) | 124.8 | 2 | 0.856 | 0.430 | 3.145 |
| <i>ruwenzorii</i> (19) | 126.2 | 62 | | | |
| <i>guttifer</i> (5) | 124.0 | | | | |
| (h) Length of inner rectrix r1 (mm): | | | | | |
| <i>poliocephalus</i> (35) | 113.8 | 2 | 0.007 | 0.993 | 3.172 |
| <i>ruwenzorii</i> (17) | 114.0 | 53 | | | |
| <i>guttifer</i> (4) | 114.0 | | | | |
| (i) Length of outer rectrix r5 (mm): | | | | | |
| <i>poliocephalus</i> (35) | 110.5 | 2 | 1.622 | 0.207 | 3.168 |
| <i>ruwenzorii</i> (18) | 108.2 | 54 | | | |
| <i>guttifer</i> (4) | 109.5 | | | | |
| (j) Ratio (%) of tail (r1) to wing (p9): | | | | | |
| <i>poliocephalus</i> (31) | 74.3 | 2 | 0.405 | 0.669 | 3.187 |
| <i>ruwenzorii</i> (17) | 74.3 | 49 | | | |
| <i>guttifer</i> (4) | 72.8 | | | | |
| (k) Length of tarsus (mm): | | | | | |
| <i>poliocephalus</i> (42) | 15.5 | 2 | 8.855* | 0.000 | 3.140 |
| <i>ruwenzorii</i> (20) | 13.8 | 64 | | | |
| <i>guttifer</i> (5) | 16.4 | | | | |

(l) Length of middle toe t3 (mm):

| | | | | | |
|---------------------------|------|----|-------|-------|-------|
| <i>poliocephalus</i> (42) | 21.3 | 2 | 0.097 | 0.908 | 3.140 |
| <i>ruwenzorii</i> (20) | 21.3 | 64 | | | |
| <i>guttifer</i> (5) | 21.6 | | | | |

than a subspecies, I do believe it merits taxonomic status. In October 2003, an individual of *koesteri* was heard singing at Catunda, Angola, by Michael Mills (Mills & Dean 2007). A sound-recording of this taxon's song might help to resolve its taxonomic status.

Taxonomic status of Rwenzori Nightjar.—*C. ruwenzorii* Ogilvie-Grant, 1909, was until recently treated as a subspecies of Abyssinian Nightjar, *C. poliocephalus* Rüppell, 1840. As the result mainly of distributional and vocal analysis, Fry (1988) recognised *C. ruwenzorii* as a valid species and this was followed by Fry & Harwin (1988). However, Dowsett & Dowsett-Lemaire (1993), with more sound-recordings available to them, demonstrated that the variation in song within *ruwenzorii* is at least as great as that between *ruwenzorii* and *poliocephalus*. They considered them to be conspecific. Cleere (1995) examined plumage patterns of the montane nightjars, including *ruwenzorii* and *poliocephalus*. He noted that variation in the amount of white on the outer rectrices is clinal, decreasing from north to south. He also noted variation in overall coloration and in the size of the white spotting on the four outer primaries. Cleere (1995) gave the song of *poliocephalus* as registering 2.0–3.2 kHz, compared to 2.5–3.8 kHz in *ruwenzorii*. The consistent plumage differences, coupled with the vocal differences, convinced him that two species are involved.

Coloration in nightjars is extremely variable within species, both geographically and individually, and this intraspecific variation is often greater than differences between species. Nightjar plumage patterns have evolved not as species-specific characters, but as camouflage for the bird at rest; as an adaptation to the general environment and particular substrate upon which it roosts and nests. These patterns, which may not accurately reflect historical relationships, are of minimal diagnostic value in devising identification keys; comparative measurements provide a better guide to nightjar relationships (Jackson 2000).

When identifying Afrotropical nightjars in the hand, the single most useful diagnostic character, with a low coefficient of variability, is percentage emargination on p9 (Jackson 1984, 2002). As noted in Jackson (2013), percentage emargination values for *poliocephalus* ($n = 57$) and *ruwenzorii* ($n = 39$) are 43.3 ± 1.5 (40.1–47.6) and 43.6 ± 1.4 (40.0–47.5), respectively, the very close means and ranges suggesting strongly that these two forms are conspecific. Minor differences in morphology and voice noted by Fry (1988) and Cleere (1995) appear to represent intraspecific geographic and individual variation, rather than interspecific variation, so I do not support the elevation of *ruwenzorii* to species status.

Relationships of the Afrotropical montane nightjars.—My measurements of the montane nightjars confirm that clinal variation exists in the apical patches on the rectrices, as noted by Cleere (1995), and also in mouth size (Table 3). The relative sizes of the apical patches provide a simple means of separating *poliocephalus*, *ruwenzorii* and *guttifer*, but not *koesteri* (see Table 2), which may better be separated, especially from *ruwenzorii*, by the number of bars in the tail.

Analyses of variance on 12 other key characters (Table 4) reveal that, with one only exception (length of tarsus, Table 4k), the null hypothesis, treating the montane nightjars as a single population, cannot be rejected. This means that the mensural data, mostly overlooked by previous authors, do not support splitting the montane nightjars into separate species.

DNA analysis will in due course provide a more definitive assessment of nightjar relationships. M Louette and his colleagues in Tervuren and Bonn are currently preparing a biochemical phylogeny of African nightjars, but this will not be published for some years (M. Louette *in litt.* 2013). Meanwhile, we must resort to more traditional methods.

Conclusion

Mensural data, especially analyses of variance, but also the emargination percentages and body mass data (Jackson 2003) provide no justification for separating any of the four montane nightjars of the Afrotropical region as a separate species. My conclusion is that the four forms should be re-united under Montane Nightjar *C. poliocephalus* as a polytypic species, with subspecies Abyssinian Nightjar *C. p. poliocephalus*, Rwenzori Nightjar *C. p. ruwenzorii*, Usambara Nightjar *C. p. guttifer* and Benguela Nightjar *C. p. koesteri*.

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Appendix: Museum specimens of *Caprimulgus poliocephalus* analysed.

Museum acronyms: AMNH = American Museum of Natural History, New York (USA); ANSP = Academy of Natural Sciences, Philadelphia (USA); BMNH = Natural History Museum, Tring (UK); CMNH = Carnegie Museum of Natural History, Pittsburgh (USA); FMNH = Field Museum of Natural History, Chicago (USA); LACM = Los Angeles County Museum (USA); MAK = Museum Alexander Koenig, Bonn (Germany); MCZ = Museum of Comparative Zoology, Harvard Univ., Cambridge, MA (USA); MNHN = Muséum National d'Histoire Naturelle, Paris (France); RMCA = Royal Museum for Central Africa, Tervuren (Belgium); ROM = Royal Ontario Museum, Toronto (Canada); UMMZ = University of Michigan Museum of Zoology, Ann Arbor (USA); USNM = United States National Museum of Natural History, Washington DC (USA).

C. p. poliocephalus ($n = 42$): AMNH 260591, 262388, 262390–262392, 633297, 633300, 633301, 633304–633308, 799939; ANSP 49354, 94967, 94968; BMNH 1901.2.22.361, 1912.10.15.313, 1926.5.3.211–1926.5.3.213, 1926.5.3.216, 1927.11.5.169, 1939.10.1.463, 1939.10.3.194, 1946.5.11.38, 1946.5.11.40; CMNH 139760, 149268, 149560; FMNH 82566, 194477–194479, 298272; MAK B.I.1.b.b; MNHN 1975-8; ROM 102988; UMMZ 211621; USNM 519304, 569273.

C. p. ruwenzorii ($n = 21$): AMNH 262394, 764118–764126; CMNH 145910, 146096; FMNH LD330, 346200; LACM 65122, 65124, 65126, 71353–71355; RMCA 17232.

C. p. guttifer ($n = 5$): BMNH 1932.5.10.716, 1939.2.25.475, 1939.2.25.477, 1939.2.25.478; FMNH 216752.

C. p. koesteri ($n = 2$): BMNH 1957.35.50; MCZ 165862.

Contested spinetail systematics: nomenclature and the Code to the rescue

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SUMMARY.—Nomenclatural confusion in a complex of spinetails (*Synallaxis* spp.; Furnariidae) has arisen from early historical treatments in which new names were proposed for differing reasons. Following an historical evaluation and an examination of the rules of nomenclature we conclude that the name *Synallaxis cinereus* Wied, 1831, was proposed in such a manner as to immediately become a junior subjective synonym of *Parulus ruficeps* Spix, 1824 and that, by lectotypification, Wied's name has validly been made available.

The genus *Synallaxis* was erected by Vieillot in 1818 without designation of a type species. Gray (1840) subsequently designated southern South American Rufous-capped Spinetail *Synallaxis ruficapilla* Vieillot, 1819 (p. 117), as its type. Remsen (2003) considered this species to form a superspecies with *S. cinerea* (Bahia Spinetail) and *S. infusata* (Pinto's Spinetail) and added 'this superspecies suggested by some authors as being most closely related to *S. frontalis* [Sooty-fronted Spinetail], *S. azarae* [Azara's Spinetail] and *S. courseni* [Apurimac Spinetail] on basis of plumage and vocal similarities'. The complex thus described is the background for this re-evaluation of the nomenclature of *S. cinerea* and related taxa.

The name *Synallaxis cinerea*¹ Wied², 1831, was not in use as a valid name for many years; most authors following the opinion of Sclater (1856: 97), who considered the name a junior subjective synonym of *Synallaxis ruficapilla* Vieillot, 1818. However, it was removed from synonymy when Whitney & Pacheco (2001) designated a lectotype for *S. cinerea* from the original type series in the American Museum of Natural History (AMNH), New York. This was accepted by Dickinson (2003), although his footnote referred only to 'Whitney *in litt.*' instead of citing the 2001 paper. It was also accepted by Remsen (2003). However, Stopiglia & Raposo (2006) doubted that the lectotype had been validly designated and based their argument on ICZN (1999) Art. 74.2 (lectotype found not to have been a syntype).

Here we seek to reveal the full complexity of this situation and to untangle it by drawing on the *International code of zoological nomenclature* (ICZN 1999), hereafter 'the Code' ('Art.' referring to articles of the Code). In this respect it is evident that there are not only two levels of approach that must be considered, the historic and the present one, but also two different perspectives which are mutually dependent: taxonomy and

¹ In the original publication Wied used the masculine ending for the Latin adjective *cinereus* (ashy grey). The supposed original labels by Wied consistently use the feminine ending *Synallaxis cinerea*, followed by the remark 'mihī', which means '[name proposed] by me'. The genus name *Synallaxis* being feminine, and the adjective *cinereus* variable, the correct spelling is *S. cinerea* as noted by Whitney & Pacheco (2001a; Art. 34.2. Mandatory change in spelling, agreement in gender).

² In full, Maximilian Alexander Philipp, Prinz zu Wied (1782–1867, Gebhardt 1964: 234). He is historically referred to as Maximilian (as in LeCroy & Sloss 2000) or Pr[inz]. Max (e.g., in Pelzeln 1859: 129); but more formally, the name Wied or zu Wied is used in recognition of his authorship of names at this time. His earlier use of zu Wied-Neuwied was to distinguish two branches of the Wied family—Wied-Neuwied and Wied-Runkel. When the last descendant of the house of Wied-Runkel died in 1824, Wied-Neuwied reunified his shire after 300 years of separation. From that year, Maximilian, Prinz zu Wied did not use his compound appellation again (Tullius 2003; M. LeCroy *in litt.* 2013).

nomenclature. Different taxonomic views necessitate different nomenclatural decisions, yet the nomenclature applied should still serve stability in zoological names as far as possible. Here interpretations of the provisions of the Code affect such nomenclatural decisions, and those 'interpretations' must themselves be used with care, both in assessing the deeper intentions of earlier authors and in applying the relevant articles of the Code.

Names proposed by Lichtenstein (1823), Spix (1824) and Wied (1831)

The nomenclatural history commences with the name *Synallaxis ruficapilla* Vieillot, 1819. Hellmayr (1925: 75) noted that 'the type examined in the Paris Museum had been obtained by Delalande near Rio de Janeiro' and amongst the synonyms listed (Hellmayr 1925: 76) are *Sphenura ruficeps* Lichtenstein ('part, adult') and *Synallaxis cinereus* Wied ('part, Brazil'). These restrictions by Hellmayr are clear signals that the respective type material was thought to comprise specimens of more than one taxon, an opinion shared by most subsequent authors until 2001.

Vieillot's contributions (1818, 1819) were not accessible to Lichtenstein (1823: VIII) when he described *Sphenura ruficeps* from an unknown number of specimens from 'Cayana [French Guiana] and Pará [sic]', including short descriptions of adult and 'juniores' [younger birds]. Four syntypes (SysTax 2013) are currently considered to be held at Zoologisches Museum Berlin (ZMB) and Cabanis (1866: 307) described *Synallaxis poliophrys* based on the single specimen labelled Cayana [= reg. no. 9095; in SysTax 2013]. Hellmayr (1925: 76), who had examined the material, considered the locality Pará erroneous and the adult syntype conspecific with *Synallaxis ruficapilla* Vieillot. However, as no lectotype has been formally designated, the taxonomic identity of *Sphenura ruficeps* remains somewhat questionable. A thorough re-evaluation of the original type series would be desirable, considering also the diaries (1818–31) of the collector Friedrich Sellow and problems originating from inadequate early label transcriptions at ZMB (Stresemann 1948, Rego *et al.* 2013).

Spix (1824: 85) described *Parulus ruficeps* based on two specimens (thought to be one of each sex), figured on pl. 86 (fig. 1: male; fig. 2: female) and originating from the rio São Francisco in Bahia. Spix's material was originally deposited in Munich (Zoologische Staatssammlung München, ZSM). The 'female' syntype (ZSM 151) is still in the collection, and a colour photograph of it was provided by Stopiglia & Raposo (2006: 53, fig. 2). The 'male' syntype was missing by 1906, when Hellmayr (1906: 631) revised Spix's types³. In Hellmayr's opinion, most original labels from Spix had been lost (p. 565), and there is no indication among the four labels of ZSM 151 that any is in Spix's hand. Gray (1840: 17) included the genera *Parulus* Spix and *Sphenura* M. H. C. Lichtenstein within *Synallaxis* Vieillot, whereby the name *S. ruficeps* (Spix) became invalid (Art. 59.1) as a junior secondary homonym of *S. ruficeps* (Lichtenstein). Subsequently Sclater (1856) described *Synallaxis spixi* (Spix's Spinetail) and Pelzeln (1859) *Synallaxis frontalis*, based respectively on the male and female of *Parulus ruficeps* Spix, by bibliographic reference (Art. 72.4.1).

Wied (1831: 685) described *Synallaxis cinereus* [sic] from an unknown number of specimens, including detailed descriptions and measurements of the male, female and young female. He provided no illustrations, but instead referred to the coloured plate

³ Given that Spix's type specimens were exchanged after the Munich museum received fresh Brazilian material in 1855, there is a chance that the 'male' type specimen was sent to another collection that was in exchange with Munich at the time. The fresh material came from the private collection of Maximilian von Leuchtenberg (c.1817–52), whose brother Karl August Eugène Napoleon von Leuchtenberg (1810–35) and sister, Amalie von Leuchtenberg (1812–73), the second wife of Pedro I of Brazil, had sent Brazilian specimens back to Bavaria. In 1855 von Leuchtenberg's collection was donated to the Munich museum, when his family moved to Russia following his death (Steinheimer 2003). Later in the 1860s, Spix specimens were exchanged, *inter alia*, with the museums in Bamberg and Vienna (Schifter *et al.* 2007: 252).

'*Parulus ruficeps*, Spix Tab. 86. Fig. 1 und 2'. Concerning the origin of his material, Wied (1831: 688) mentioned 'virgin forest along the street of Capitao Filisberto' (p. 688)⁴, adding (p. 689): 'This traveller [=Spix] found our bird at the Rio St. Francisco and named it *Parulus ruficeps*.'⁵ The main part of Wied's collection is housed in the American Museum of Natural History, where the type material of *Synallaxis cinerea* has been assessed in detail by Allen (1889) and LeCroy & Sloss (2000)⁶.

Allen (1889: 243) expressly recorded 'five specimens labelled by him [Wied]' and that, although 'evidently a Wied specimen,' only AMNH 5204 lacked an original label. LeCroy & Sloss (2000: 19) nevertheless concluded that, of six supposed Wied specimens, only three (AMNH 6811–6813) unquestionably match Wied's description and could be regarded as syntypes (representing taxonomically *S. ruficapilla* Vieillot). Drawing on diagnostic differences provided by Vaurie (1980), they concluded that the three additional specimens (AMNH 6814, 6815 and 5204) did not belong to the original type series because they were 'so different in size and appearance from the other three'. However, they did not designate a lectotype and retained these specimens with the three syntypes 'because of the uncertainty surrounding them'. Understandably missing from the discussion by LeCroy & Sloss (2000) was a reconsideration of type material included by bibliographic reference (Art. 72.4.1), there being, at that juncture, no reason to expand the subject. On the other hand, the fact that Wied had expressly included *Parulus ruficeps* Spix—currently considered to have been based on two different taxa [male: *S. spixi* P. L. Sclater, 1856; female: *S. frontalis* Pelzeln, 1859]—in his *S. cinereus* makes it evident that the syntype series was composite, i.e. taxonomically mixed. The constant difference between spelling in Wied's (1831) publication (*Synallaxis cinereus*) and on the original labels (*Synallaxis cinerea*) suggests at least that all specimens had been labelled (or relabelled?) at the same time, but whether before publication or (more likely) afterwards remains an open question.

A completely different view concerning the type material of *S. cinereus* was proffered by Stopiglia & Raposo (2006: 49). In their opinion 'Wied [when proposing *S. cinereus*] was merely providing a new name for *Parulus ruficeps* Spix, 1824, to avoid problems of homonymy.' As a consequence they suggested the provisions of Art. 72.7 would apply and both the nominal taxa would have the same name-bearing type. The rationale for this new interpretation was based on their analysis of Wied's German text, with Wied's intention, according to Stopiglia & Raposo (2006), being to replace the prospective junior secondary homonym *Parulus ruficeps* Spix, 1824 (in *Synallaxis* preoccupied by *Sphenura ruficeps* M. H. C. Lichtenstein, 1823) by a *nomen novum*.

However, such express intention in Wied's text is not convincing. In 1831, at the time of the publication of the name *Synallaxis cinereus*, the name *Parulus ruficeps* Spix was not formally preoccupied. Although Wied criticised Spix's attitude of not considering or citing names of other authors, he referred to this matter only in general and in part as an explanation for using his own name *cinereus*. Wied did not cite the name *Sphenura ruficeps*

⁴ The type locality 'Strasse des Capitao Filisberto' refers to the road opened by Tenente-Coronel Filisberto Gomes da Silva, relative of Marechal Felisberto Caldeira who had ordered and paid for this enterprise two years before the travels of Wied. The road linked the harbour of Ilhéus to the border of Minas Gerais, east of the village of Rio Pardo. Wied (1821: 99, 333) left 'S. Pedro d'Alcantara' (= Itabuna) on 6 January 1817 for 'Barra da Vareda' (= Inhobim), where he arrived on 30 January 1817, via the road of Captain Filisberto (Moraes, 2009: 35 footnote). Pacheco & Gonzaga (1995) placed the type locality near Ilhéus, southern Bahia, Brazil.

⁵ 'Dieser Reisende [= Spix] fand unseren Vogel am Rio St. Francisco und nannte ihn *Parulus ruficeps*.'

⁶ No specimen of this taxon has been found in the collection of the Hessische Landesmuseum für Kunst und Natur at Wiesbaden, Germany, which holds a small number of Wied's specimens (Hoffmann & Geller-Grimm 2013).

either in his taxonomic concept of *Synallaxis* (Wied 1831: 683–685) or in his description of *Synallaxis cinereus* (Wied 1831: 685–689). Nor did he suggest any intention to include the genus *Sphenura* M. H. C. Lichtenstein in *Synallaxis*, or touch on the issue of homonymy⁷ in a wording of his own. What Wied actually did write⁸ translates as ‘the name *ruficeps* could equally fit several of these birds’, and that it was therefore an inappropriate name that should be rejected (‘zu verwerfen ist’). The implication is that he felt the name was inaccurate. In our reading of Wied’s original text and *contra* Stopiglia & Raposo (2006, 2008), we understand that Wied disliked the name because the epithet *ruficeps* (red-headed) did not truly characterise the taxon—and not for the reason that the species-group name had already been in use within the same genus (which it actually was not)⁹. Wied was by no means alone at this period in the development of modern zoology in altering a name he felt to be inappropriate, and he said he felt entitled to alter (‘abzuändern’) this one¹⁰. However, the present Code explicitly states that ‘the availability of a name is not affected by inappropriateness’ (Art. 18) and such a name ‘is not to be rejected, even by its author(s), for a reason such as its inappropriateness’ (Art. 23.3.7). The name *Synallaxis cinerea* Wied, 1831, is thus not a new replacement name / *nomen novum* (Art. 60.3) required by the Code for the replacement of a preoccupied name (and denoted by type material as provided by Art. 72.7). In 1831, *Parulus ruficeps* Spix was not a homonymous species-group name. In fact Wied (1831) had proposed a new substitute name not required by the Code, thereby producing a junior subjective synonym denoted by its own type material according to the provisions of Art. 72.4.1 (*contra* Stopiglia & Raposo 2006). Since the type concept was virtually unborn at that point, Wied himself will not have considered this one way or another.

The case of *Synallaxis whitneyi*

If the AMNH syntypes attributable to *Synallaxis cinereus* Wied include AMNH 6813, in agreement with the interpretations by Allen (1889) and LeCroy & Sloss (2000), then the designation of AMNH 6813 as the lectotype for this taxon (Whitney & Pacheco 2001: 35) is valid. In such circumstances we respect their judgement in formally considering *Synallaxis whitneyi* Pacheco & Gonzaga a junior subjective synonym of *Synallaxis cinerea* Wied.

Bearing in mind the possibility of taxonomic changes in the future, we present here synonymies for *S. ruficapilla*, *S. ruficeps* and *S. cinereus* that set out current valid names, synonyms and their status, authors, types and type localities.

Synallaxis ruficapilla Vieillot, 1819: 310 (Rufous-capped Spinetail)

Type locality: near Rio de Janeiro, Brazil.

Type material: [presumably] holotype by monotypy, specimen¹¹ figured in Vieillot (1834: 284, pl. 174), deposited in Muséum national d’Histoire naturelle (MNHN), Paris (*vide* Menegaux & Hellmayr 1906: 69).

⁷ The term homonymy was not in use among zoologists at that time and was still missing in the Stricklandian Code (Strickland *et al.* 1843).

⁸ The original German text reads as (Wied 1831: 689): ‘Wenn ich auch gänzlich davon absehe, daß Spix den großen Fehler beging, sich nirgends an die von andern gegebenen Benennungen zu binden, indem er bei keinem einzigen Thiere der übrigen Schriftsteller gedenkt, so habe ich mich hier selbst berechtigt geglaubt, den Trivialnamen abzuändern, indem die Benennung *ruficeps* auf mehrere dieser Vögel paßt, daher zu verwerfen ist.’

⁹ A new replacement name (*nomen novum*) is not to be proposed in advance, to avoid possible homonymy in the future, but only for an already preoccupied name (Arts 53.3 and 60).

¹⁰ The Stricklandian Code, proposed 12 years later (Strickland *et al.* 1843: 266) included several instances where a name could or should be changed, e. g.: ‘§ 11. Names not clearly defined may be changed.’

¹¹ Collected by ‘Delalande fils’ [= Pierre Antoine Delalande, 1787–1823]

= *Sphenura ruficeps* M. H. C. Lichtenstein, 1823: 42.

Type locality: Cayana [French Guiana], Pará [Brazil].

Type material: syntypes (reg. nos. 9089–9091, 9095, *vide* SysTax 2013), deposited in Zoologisches Museum Berlin (ZMB), now Museum für Naturkunde – Leibniz-Institut für Evolutions- und Biodiversitätsforschung an der Humboldt-Universität zu Berlin.

Junior subjective synonym in G. R. Gray (1846: 135 [originally without pagination]).

Junior subjective synonym (*pro parte*: adult, Brazil) in Hellmayr (1925: 76) and subsequent authors.

Remarks: there should be additional syntypes extant elsewhere, acquired from ZMB or the dealer Eimbeck (Braunschweig) around 1823, which so far have not been recognised. The specimen labelled Cayana (ZMB 9095 [holotype of *Synallaxis poliophrys* Cabanis, 1866: 307; by monotypy]), is currently considered to represent taxonomically *Synallaxis frontalis* Pelzeln, 1859: 117 (Remsen 2003: 277).

= *Synallaxis olivacens* Eyton, 1851: 159, pl. 81 [name on plate: *S. olivascens*]

Type locality: South America, exact locality not known.

Type material: two syntypes (one listed as adult, reg. no. 1881.2.18.173 in Warren & Harrison 1971: 404 [as *S. olivacens*]), deposited in British Museum (Natural History) (BMNH), now Natural History Museum, Tring.

Junior subjective synonym in P. L. Sclater (1874: 5) and subsequent authors.

Remark: correct original spelling (Art. 32.2.1): *Synallaxis olivacens*, following Hellmayr (1925: 76) as First Reviser (Art. 24.2.3).

= *Synallaxis (Barnesia) cururuvi* Bertoni, 1901: 77

Type locality: D Jaguarasapá, Alto Paraná, Paraguay.

Type material: not specified, presumably lost (Hayes 1995: 32).

Junior subjective synonym in Lynch Arribálzaga (1902: 353), Hellmayr (1925: 76) and subsequent authors.

***Synallaxis cinerea* Wied, 1831: 685 (as: *Synallaxis cinereus*) (Bahia Spinetail)**

Type locality: Road of Capitaó Filisberto, near Ilhéus, southern Bahia, Brazil.

Type material: lectotype, reg. no. 6813 (Whitney & Pacheco 2001: 35), deposited in the American Museum of Natural History (AMNH), paralectotypes: AMNH 6811, 6812.

= *Synallaxis whitneyi* Pacheco & Gonzaga, 1995: 3

Type locality: 7 km south-east of Boa Nova, Bahia, Brazil.

Type material: holotype male, reg. no. 74011, deposited in Museu de Zoologia da Universidade de São Paulo (MZUSP), paratypes: females MZUSP 74012, 74013.

Junior subjective synonym in Whitney & Pacheco (2001: 34).

Independently, two papers on *Synallaxis ruficapilla* relevant to this complex of spinetails have recently been published emphasising phylogenetics and biogeography (Batalla-Filho *et al.* 2013, Stopiglia *et al.* 2013); our current paper is restricted to nomenclatural issues only.

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