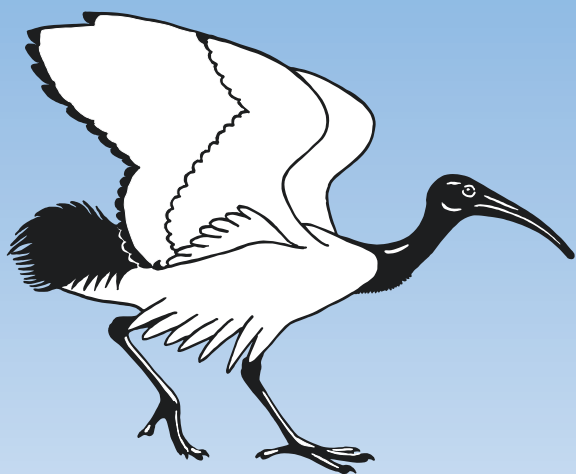


Bulletin of the British Ornithologists' Club



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Bulletin of the British Ornithologists' Club

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Bulletin of the BRITISH ORNITHOLOGISTS' CLUB

Vol. 139 No. 4

Published 16 December 2019

CLUB ANNOUNCEMENTS

The 995th meeting of the Club was held on Monday 16 September 2019 in the upstairs room at the Barley Mow, 104 Horseferry Road, London, SW1P 2EE.

Twenty-eight people were present: Miss H. Baker, Ms. A. H. Belman, Mr P. J. Belman, Mr R. Bray, Mr S. Chapman, Dr R. Cheke, Mr G. de Silva Wijeyeratne, Mr D. J. Fisher, Mr G. M. Kirwan, Mr R. Langley, Mr R. Malin, Dr C. F. Mann, Mr D. J. Montier, Mrs M. Montier, Dr P. Morris (*Speaker*), Ms E. Pilanen, Mr A. Pittman, Dr R. Prÿs-Jones, Mr R. Prytherch, Mr N. J. Redman, Dr P. Rudge, Dr D. G. D. Russell, Mr S. A. H. Statham, Mr C. W. R. Storey (*Chairman*), Ms. Z. Varley, Ms. J. White, Mr P. Wilkinson, Ms. A. Wilson.

Pat Morris gave a talk entitled *The Hastings Rarities—taking the long view*. He explained that it is now more than 50 years since hundreds of bird records were dismissed as potentially fraudulent on the grounds that it was unlikely that so many rare species would turn up within a short period of time and a limited area around Hastings, in south-east England. Statistical analysis confirmed a significant difference between the number of records within that area and time compared to other areas of Kent / Sussex, and with later periods. In ornithological terms, it makes limited difference, as many of the suspect species have been found subsequently in the same area. It has long been widely accepted that fraud occurred and that a local taxidermist, George Bristow, was responsible for perpetrating this. Bristow was unable to defend himself, having died, and the taxidermy profession was besmirched. Although protests were made at the time the issue appears closed. However, there remain worrying doubts when the evidence is examined closely. At the same time, in retrospect there may be further evidence to confirm Bristow's guilt. A lively debate followed Pat's talk.

The 996th meeting of the Club was held on Monday 18 November 2019 in the upstairs room at the Barley Mow, 104 Horseferry Road, London SW1P 2EE.

Thirty-four people were present: Dr Tim Birkhead (*Speaker*), Ms. C. Boutle, Mr R. Bray, Cdr. M. B. Casement, RN, Mr S. Chapman, Ms C. Coull, Mr G. de Silva Wijeyeratne, Mr R. Dickey, Ms R. Dunne, Mr D. J. Fisher, Mr M. Grigson, Mr P. Harris, Mr M. Howard, Ms. J. James, Dr C. F. Mann, Mr A. Merritt, Mr G. Micali, Mr D. J. Montier, Mr A. Morgan, Mrs R. Morgan, Ms. A. Nixon, Mr C. Ozog, Dr D. Prÿs-Jones, Dr R. Prÿs-Jones, Dr A. Richford, Dr P. Rudge, Dr D. G. D. Russell, Mr J. Salmon, Mr S. A. H. Statham, Mr C. W. R. Storey (*Chairman*), Dr J. Verhelst, Mr P. Ward, Ms. J. White, Mr P. Wilkinson.

Prof. Tim Birkhead gave a talk entitled *The wonderful Mr Willughby—the start of scientific ornithology*. The first scientific bird book was *The ornithology of Francis Willughby*, named in Willughby's honour by his friend John Ray after Willughby's death at the age of just 36 in 1672. These two men were pioneers of the scientific revolution and changed the way we think about birds. Until recently it was widely assumed that Ray was the brains and Willughby a mere 'talented amateur', but after a decade of research Tim has been able to show that Willughby was every bit as brilliant as his co-author and friend John Ray. In his talk he told the story of Willughby's short but spectacularly productive life—a story every ornithologist should know. Those wishing to learn more can consult the following two books on the topic that Tim has produced: Birkhead, T. R. (ed.) 2016. *Virtuoso by nature: the scientific worlds of Francis Willughby*. Brill, Leiden (contributions by specialists on different aspects of Willughby's life and work); and Birkhead, T. 2018. *The wonderful Mr Willughby: the first true ornithologist*. Bloomsbury Publishing, London.

Report on the joint meeting on Neotropical birds with the Neotropical Bird Club and Natural History Museum, in the Flett Theatre, NHM, London, 26 October 2019

For the third time in nine years, these three organisations came together to spend a day reflecting on the biology and conservation of the astonishingly diverse Neotropical avifauna. Whereas the morning session focused on critical conservation needs in three diverse areas of South America, the afternoon comprised three more wide-ranging talks on avian biology, encompassing mimicry, behavioural physiology, and discoveries, including new species, feats of vagrancy, remarkable behaviour, etc. We were particularly fortunate to have one of Brazil's foremost ornithologists, Luís Fábio Silveira, to open the event by delivering an outstanding plenary lecture on a key threatened area, the Pernambuco Centre of Endemism, in relation to which he currently holds a major grant to research conservation requirements. This was followed by a succession of

high-quality presentations, much appreciated by an enthusiastic audience of some 70 people. Outlines for each talk are provided below, and both the BOC and NBC are grateful to the NHM for providing an excellent London venue for the event to take place.

Luis Fábio Silveira (University of São Paulo, Brazil)

Avoiding extinctions in the most threatened area in the Neotropics: the Pernambuco Centre of Endemism, Brazil

The Brazilian Atlantic Forest is a hotspot with very rich biodiversity but also a high level of deforestation and degradation. The Pernambuco Centre of Endemism (PCE), originally distributed to the north of the São Francisco River in the states of Paraíba, Alagoas and Pernambuco, is today the most endangered Atlantic Forest region and one of the most threatened ecosystems in the world, as only tiny and isolated habitat fragments remain (c.3% of its original distribution). Moreover, this is also the least studied Atlantic Forest region. Whereas in recent years four bird species there have been recognised as extinct, new bird and mammal species are still being described. Our lack of knowledge concerns not only the composition of the biodiversity, but also 'where' and 'why' it is concentrated. It is therefore essential to not only research the taxonomy and systematics of birds and mammals in the PCE, much of which is at risk of being lost before scientific recordings can be made, but also to use this knowledge to propose and apply conservation management practices, and to communicate the results of this research and the importance of the PCE to the general public.

Christian Devenish (Manchester Metropolitan University)

Conservation of dry-forest endemic birds in north-west Peru

Conservation ecologists face the dual challenge of working with difficult-to-study species and providing ecological metrics to support both global conservation efforts and local conservation management prescriptions. Christian presented metrics identifying distributions, site-level and global abundance, site-contextualised habitat requirements, and threat analyses for dry-forest endemic birds in the globally important Tumbes region of Peru. Results from his field studies revealed extreme variation in abundance within species across the study area, although species' broad distributions were generally congruent. From this, Christian has been able to recommend key sites for the conservation of threatened Tumbes endemics, including extensions of existing protected areas and unprotected sites, especially in the south of their ranges. Threats and opportunities were discussed within the local economic context, especially export agriculture and farming communities. His research has recently been published as a policy document by the Peruvian National Parks authority, and is available at: <http://sis.sernanp.gob.pe/biblioteca/?publicacion=1917>.

Martin Schaefer (Fundación Jocotoco: www.jocotoco.org)

Using science to protect Ecuador's most threatened birds

Private reserves are effective in protecting threatened biodiversity, yet their owners rarely use science to direct their conservation activities. Martin's talk presented 13 years of ecological work on the globally threatened El Oro Parakeet *Pyrrhura orcesi* and Pale-headed Brush Finch *Atlapetes pallidiceps* in Ecuador. Via targeted conservation actions, Fundación Jocotoco has quadrupled the population of Pale-headed Brush Finch within nine years. Their work has also elucidated the truly cooperative breeding system of El Oro Parakeet, mirroring other *Pyrrhura* species. Cooperative breeding is characterised by delayed nesting and the effective population size is low, with only 42% of adults reproducing in any given season. Moreover, the distributional range of this species has shifted a dramatic 300 m elevationally within just 30 years. Genetic data show that even forested valleys can become dispersal barriers. These data have permitted Fundación Jocotoco to adjust reserve design in order to protect this endangered species and many other endemics in Ecuador.

Alexander Lees (Manchester Metropolitan University)

Diversity in avian mimicry

Apparent cases of visual mimicry – where the plumage of one species converges on that of another unrelated species, are surprisingly common in birds and especially prevalent in the Neotropics. Alex's talk gave an overview of the different forms of mimicry, such as Müllerian, aggressive and Batesian mimicry, which are suspected to occur in birds, and highlighted the cutting-edge science being used to uncover these patterns.

Samuel Jones (Royal Holloway London)

*The physiology / behaviour nexus in a Central American cloud forest songbird, the Black-headed Nightingale-Thrush *Catharus mexicanus**

Very little is known concerning how energy usage relates to season and behaviour in tropical species. Tropical birds are known, however, to have lower metabolisms than temperate species, suggested to be a product of 'slower' lifestyles (such as smaller clutch sizes and greater adult survival). Using a variety of behavioural and physiological techniques, Samuel has explored seasonal shifts in territorial behaviour and physiology in Black-headed Nightingale-Thrushes *Catharus mexicanus*, a Central American cloud forest endemic. His study has offered an intriguing insight into the energy costs of long periods (often 5–6 months) of intense territorial defence, and how energy usage may shift with season in other tropical forest songbirds.

Joseph Tobias (Imperial College London)*Frontiers of knowledge: a quarter-century of Neotropical discovery*

The launch of the Neotropical Bird Club coincided with a period of intense ornithological exploration by field ornithologists, birders and sound-recorderists. Unsurprisingly, the 25-year period since has witnessed some dramatic discoveries, from new species to staggering range extensions and unexpected taxonomic changes. Joe's talk showcased the most spectacular of these discoveries from around the Neotropical region, and made some predictions as to what we might expect from the next quarter century.

Robert Prŷs-Jones

Changes among Associate Editors

After eight years as an Associate Editor of *Bull. Brit. Orn. Cl.*, with this issue we bid farewell to Frank Steinheimer. Frank now heads one of the largest natural history collections in Germany, based at Martin Luther University Halle-Wittenberg. This university institute has been managed by Frank for 11 years, but his duties have increased tremendously in recent years due to engagement with several large third-party-funded projects, the planning of a public museum and new magazine spaces, as well as his political engagements (Frank is a member of Halle's environmental council). We thank Frank most warmly for his considerable contributions to the Bulletin, especially his knowledge of zoological nomenclature.

In his stead, the Club has been fortunate to engage the assistance of Lincoln Fishpool as a new Associate Editor, and he has already been involved with the Bulletin's workload since June 2019. Fishpool began his professional life as an entomologist, working on a number of agricultural pest problems in different parts of Africa, during which time his interest in Afrotropical ornithology steadily grew. In 1993 he joined BirdLife International to coordinate their then Important Bird Areas (IBA) programme for Africa and was lead editor of the resulting directory of sites, published in 2001. Part of his subsequent role for BirdLife included membership of their taxonomic working group, in which capacity he contributed to the *HBW and BirdLife International illustrated checklist of the birds of the world* (2014, 2016). With a particular interest in African bulbuls, he co-authored the account of the Pycnonotidae for *HBW* and has published several papers on the group. Now retired, he maintains an interest in the taxonomy of Afrotropical birds and in birding in the region.

Errata and Addenda

In *Bull. Brit. Orn. Cl.* 139(3): 215–227, as a result of an inadvertent substitution by the lead author, the version of Sydenham Edwards' picture of the Harlequin Hummingbird that appears in Fig. 6 of the published paper (p. 221) is in fact not that from Audebert & Vieillot (1802), but rather the very similar one from Lesson (1829, pl. 72). This has no wider implications for any argument presented in the text.

In *Bull. Brit. Orn. Cl.* 139(3): 272, the legend to Fig. 2 should read: Figure 2. (a) Red-legged Brushturkey *Talegalla jobiensis* and (b) Thick-billed Ground Pigeon *Trugon terrestris*, camera trapped in the Lake Kutubu WMA. (c) New Guinea Vulturine Parrot *Psittrichas fulgidus*, photographed on the Agogo Range. (d) Greater Melampitta *Megalampitta gigantea*, camera trapped on the Agogo Range. In addition, since publication, Brown Quail *Coturnix ypsilophora* (August 2019) and Golden-backed Whistler *Pachycephala aurea* (December 2019) have been recorded in disturbed habitats at Moro, bringing the Lake Kutubu WMA tally to 218 species.

REFEREES

I am grateful to the following, who have reviewed manuscripts submitted to the Bulletin during the last year (those who refereed more than one manuscript are denoted by an asterisk in parentheses): Juan Ignacio Areta, Bruce M. Beehler (*), Tim Birkhead, K. David Bishop, Walter Boles, Vincent Bretagnolle, Michael Brooker, Rod Cassidy, Alice Cibois, Nigel Cleere, Nigel J. Collar, Marco Aurélio Crozariol, Nicholas Daudt, Ron Demey (*), Edward C. Dickinson, Paul Donald, Simon Dowell, R. J. Dowsett (*), Guy Dutton, Chris Filardi (*), Brian Finch, Clemency Fisher, L. D. C. Fishpool, Harold F. Greeney, Floyd Hayes, David Holyoak, Colin Jackson, David James, Justin Jansen, Flemming Pagh Jensen, Leo Joseph, Peter Lack, Łukasz Ławicki, Mary LeCroy, Yang Liu, Wayne Longmore, Jeff Marks, R. McGowan, Michael Mills, Mark O'Brien, Jente Ottenburghs, Michael Patten, Manuel Plenge, Thane Pratt (*), Robert Prŷs-Jones (*), Roger Safford, Richard Schodde (*), Manuel Schweizer, Frank Steinheimer (*), Bert Theunissen, Magnus Ullman and André Weller. — THE HON. EDITOR

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. **Talks start at 6.30 pm** and, with questions, last c.1 hour.

Monday 23 March 2020—6.30 pm—Beth Okamura—*How birds shape freshwater biodiversity.*

Abstract.—Ever wondered how volcanic islands, garden ponds and gravel pits develop a rich biota? Or why rowan trees grow near pines? The answers in part involve patterns of bird visitations. Darwin appreciated that avian activities might help to explain the widespread distributions of taxa that live in disjunct habitats. This conundrum famously led him to examine the attachment and survival of recently hatched snails on ducks' feet. This talk will consider how our understanding of dispersal of freshwater invertebrates has improved since Darwin's era. I will particularly focus on evidence for waterbird-mediated dispersal of freshwater animals that are poorly known but that have substantial ecological and practical impacts—colonial invertebrates called bryozoans (or 'moss animals') and their myxozoan parasites ('slime animals'). I will illustrate how these unappealingly-named animals serve as 'model systems' that demonstrate the profound effect of waterbird movements on the development and dynamics of freshwater communities, and consequent impacts on water supply and emerging fish diseases.

Biography.—Beth Okamura is a Merit Researcher at the Natural History Museum, London. Prior to this she held positions at the Univ. of Oxford and Bristol, before becoming a Prof. in Aquatic Biology at the Univ. of Reading. Her Ph.D. from the Univ. of California, Berkeley, focused on the ecology and evolution of marine invertebrates, but her move to Oxford led to her long-term interests in how animals that live in isolated lakes and ponds manage to disperse and persist across the landscape. She has particular interests in the role of waterbirds as vectors of dispersal—a question that she is now beginning address in new ways by analysing DNA contained in faeces of ducks, geese and godwits (*Limosa* spp.).

Monday 18 May 2020—6.30 pm—Speaker and title to be announced.

Friends of the BOC

The BOC has from 2017 become an online organisation without a paying membership, but instead one that aspires to a supportive network of Friends who share its vision of ornithology—see: <http://boc-online.org/>. Anyone wishing to become a Friend of the BOC and support its development should pay UK£25.00 by standing order or online payment to the BOC bank account:

Barclays Bank, 16 High Street, Holt, NR25 6BQ, Norfolk
Sort Code: 20-45-45
Account number: 53092003
Account name: The British Ornithologists' Club

Friends receive regular updates about Club events and are also eligible for discounts on the Club's Occasional Publications. It would assist our Treasurer, Richard Malin (e-mail: rmalin21@gmail.com), if you would kindly inform him if you intend becoming a Friend of the BOC.

The *Bulletin* and other BOC publications

Since volume 137 (2017), the *Bulletin* of the BOC has been an online journal, published quarterly, that is available to all readers without charge. Furthermore, it does not levy any publication charges (including for colour plates) on authors of papers and has a median publication time from receipt to publication of five to six months. Prospective authors are invited to contact the *Bulletin* editor, Guy Kirwan (GMKirwan@aol.com), to discuss future submissions or look at <http://boc-online.org/bulletin/bulletin-contributions>. Back numbers up to volume 136 (2016) are available via the Biodiversity Heritage Library website: www.biodiversitylibrary.org/bibliography/46639#/summary; vols. 132–136 are also available on the BOC website: <http://boc-online.org/>

BOC Occasional Publications are available from the BOC Office or online at info@boc-online.org. Future BOC-published checklists will be available from NHBS and as advised on the BOC website. As its online repository, the BOC uses the British Library Online Archive (in accordance with IZCN 1999, Art. 8.5.3.1).

Notes on the birds of Isabel, Solomon Islands, including the first record since 1927 of Island Leaf Warbler *Phylloscopus maforensis*

by Lucas H. DeCicco, Serina S. Brady, Sati Hamilton, Adrian Havimana, Xena M. Mapel, Jenna M. McCullough, Karen V. Olson, Ikuo G. Tigulu, Scott L. Travers, Albert Tugu, Michael J. Andersen & Robert G. Moyle

Received 19 February 2019; revised 26 August 2019; published 16 December 2019

<http://zoobank.org/urn:lsid:zoobank.org:pub:3C229B98-F44A-47C1-BEFD-9975639A0304>

SUMMARY.—The birds of the Solomon Islands have received ample historical attention by explorers, collectors and researchers. Despite this, knowledge of the region's avifauna is categorised by BirdLife International as 'poor' and multiple new populations of birds have been found in recent years, highlighting our incomplete knowledge of the region's avifauna. Here, we present new information on the elevational occurrence, abundance and natural history for ten bird species we observed on Isabel Island. The data we present are based on three weeks of field work at three field sites that included the restricted montane forests above 1,000 m elevation on the Kubonitu-Sasari massif. In this poorly known montane area we observed multiple Island Leaf Warblers *Phylloscopus maforensis* for the first time since it was discovered on Isabel in 1927.

Archipelagos in the South Pacific are high in inter-island species diversity and endemism. They have contributed to the development of influential theories of evolution, including speciation dynamics and island biogeography (e.g. Mayr 1942, MacArthur & Wilson 1967, Mayr & Diamond 2001). Yet our knowledge of the South Pacific avifauna is incomplete, exemplified by recent discoveries of new populations of birds (DeCicco *et al.* in review, Univ. of Kansas unpubl.) and our understanding of the regional avifauna was categorised as 'poor' by BirdLife International (2015).

The Solomon Islands have a complex and varied geological history that has resulted in a diverse and highly endemic fauna. This archipelago, spanning nearly 1,500 km from north-west to south-east, is oceanic in origin, having never been connected to a continental landmass (Pettersen *et al.* 1999). At times of lower sea levels during the last glacial maximum (e.g. Wickler & Spriggs 1988) some of the major islands were joined to form larger landmasses—e.g., Buka, Bougainville, Choiseul, and Isabel were connected, producing a single landmass termed 'Greater Bukida' (Mayr & Diamond 2001). Connectivity among these islands manifests itself in patterns of shared biodiversity. Isabel shares most of its avifauna at the species and subspecies levels with nearby Choiseul and Bougainville (Kaestner 1987, Mayr & Diamond 2001, Dutson 2011). These patterns contrast starkly with the much higher levels of single-island endemism found on those parts of the Solomon archipelago that do not have a history of connectivity (e.g. Makira Island).

Isabel Island (also known as Santa Isabel, Santa Ysabel, Ysabel, or Bugotu) is the fourth largest island in the Solomon archipelago encompassing 4,095 km² (Mayr & Diamond 2001). Isabel comprises primarily low-elevation tropical forest with a small area of distinct mossy, montane forest above 1,000 m in the south, on the Kubonitu-Sasari massif (nomenclature follows Whitmore 1969, but spelling changed to Kubonitu to reflect common local usage;

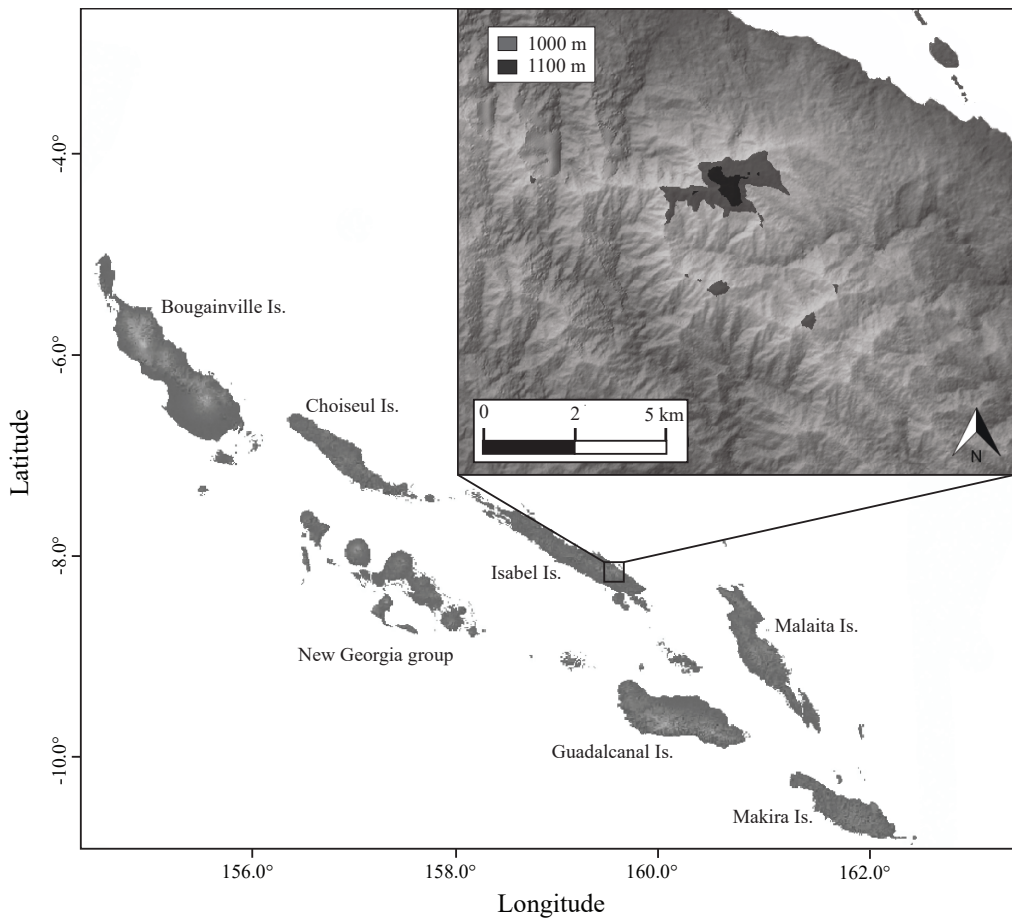


Figure 1. Map of the Kubonitu-Sasari massif (inset), Isabel Island, Solomon Islands, highlighting areas above 1,000 m (4.2 km²) and above 1,100 m (0.7 km²). Mossy montane forests occur above 1,000 m and Island Leaf Warbler *Phylloscopus maforensis* appears to be restricted to this elevation on Isabel Island.

Fig. 1). This massif is the highest elevation on Isabel at 1,186 m. The first bird specimens from Isabel were collected in 1838 (Mayr & Diamond 2001) and further collections of its birds were made in the late 1800s (summarised by Tristram 1892, 1894, 1895). In 1900, A. S. Meek made a thorough collection of 58 bird species from Isabel (Rothschild & Hartert 1902). Members of the American Museum of Natural History's (AMNH) Whitney South Sea Expedition visited Isabel in September 1927 and were the first to collect birds in the highlands (Beck 1927, Drowne 1927, Mayr 1935, Mayr & Diamond 2001). More recently, Webb (1992) and Kratter *et al.* (2001) summarised and updated information on the avifauna of Isabel—Webb (1992) focused on new information from his field observations across the island in 1986–88 and Kratter *et al.* (2001) on lowland coastal forests in 1997–98. The mossy montane forests of the Kubonitu-Sasari massif were visited by ornithologists only twice previously, first by the Whitney Expedition and later by Webb (1992). Dutson (2011) summarised much of this information in his field guide, *Birds of Melanesia*.

Here, we present information that adds to our knowledge of occurrence and elevational abundance of select bird species on Isabel. These data stem from field work on Isabel during a survey of the land vertebrates of the Solomon Islands led by the Univ. of Kansas, the



Figure 2. Examples of mossy montane forest on the Kubonitu-Sasari massif, Isabel Island, Solomon Islands (Lucas H. DeCicco)

Univ. of New Mexico, and Ecological Solutions Solomon Islands in 2018. The information we present improves our knowledge of distribution, abundance and ecology of birds in the region, and on Isabel.

Methods

We spent three weeks on Isabel at three sites: the headwaters of the Kolosita River (7–15 June; 08.159°S, 159.546°E, 550–650 m elevation), Gnulahage and Kolomola villages (6 June and 15–20 June; 08.129°S, 159.538°E, 0–30 m), and the Kubonitu-Sasari massif (12 June and 22–26 June 2018; 10.564°S, 161.905°E, 1,050–1,160 m). These sites permitted us to survey three general habitats: lowland riparian and gardens / coconut plantations (Gnulahage and Kolomola villages), mid-elevation primary hill forest (headwaters of the Kolosita River), and mossy montane forest (above 1,000 m on the Kubonitu-Sasari massif). We accessed the Kubonitu-Sasari massif via Kolomola village, 5.5 km north-northwest of the massif. Our surveys consisted of daily field observations, audio recordings and daily mist-netting using up to 25 12-m nets per site.

We reference audio recordings made during our field work and archived at the Cornell Lab of Ornithology's Macaulay Library (www.macaulaylibrary.org). Specimens and their associated genetic material and parasites taken during this work are deposited at the Univ. of Kansas Natural History Museum, Lawrence, and the Museum of Southwestern Biology, Univ. of New Mexico, Albuquerque. These specimen vouchers provide a manifold record of the avifauna and will be used in ongoing work on the systematics and evolutionary biology of avifauna of the Solomon Islands. We follow the nomenclature and taxonomy of Gill & Donsker (2019).

Results

Our observations over three weeks of field work recorded 64 species of birds on Isabel Island, from coastal and disturbed lowland habitats to mature mid-montane forest and mossy montane forest above 1,000 m. Our observations from the highlands are of particular note because they provide (1) a modern assessment of the avifauna of this poorly known area and (2) comparison to our observations of the avifauna of mature mid-elevation hill forests. Contradictory reports in the literature claim the highest point on Isabel is either Mt. Sasari or Mt. Kubonitu (e.g. Whitmore 1969, *cf.* Webb 1992). To limit further confusion, we follow Whitmore (1969) and refer to the highest single area as the Kubonitu-Sasari massif and the highest elevation as 1,186 m based on SRTM elevation raster data (USGS) accessed using the R (R Core Team 2014) package 'elevatr' (Hollister & Shah 2017). On Isabel, approximately 4.2 km² of land lies above 1,000 m and just 0.7 km² of land is above 1,100 m in a single area centred on the Kubonitu-Sasari massif (calculated using a custom script in R; Fig. 1). We noted distinct habitat transitions around 1,000 m at which point the forest structure changed, with smaller trees and dense moss growing on tree trunks and branches. Above 1,000 m, moss and epiphytic growth thickened and trees were shorter and the canopy more open. At c.1,100 m habitat transitioned to stunted mossy montane forest including large ferns with a dense contiguous layer of moss covering all surfaces from outer tree branches to the forest floor (Fig. 2). Dense native scrambling bamboo tangles (see Whitmore 1969) were common in openings at this elevation and there was thick understorey growth. Topographically this area was extremely steep, a characteristic also noted by Drowne (1927: 196): 'All this country consists of knife-like ridges and deep canyons...'. The one exception was around the summit itself where there was a small plateau no more than 50 m wide in any direction.

Species accounts

IMITATOR GOSHAWK *Accipiter imitator*

LHD observed a single pied morph on 25 June 2018 at 1,100 m in mossy montane forest on a ridge leading to the summit of the Kubonitu-Sasari massif. He obtained good views using binoculars and recorded >5 minutes of its vocalisations, a series of high-pitched *keek* notes typical of the genus (ML117225041). This rare and elusive species is reported to occur to 1,000 m (e.g. Ferguson-Lees & Christie 2001, Dutson 2011, Debus *et al.* 2019), making ours the highest-elevation report available. Kratter *et al.* (2001) considered the species uncommon in the lowlands of Isabel, and Webb (1992) reported two sightings between Bara and Kologaru villages in July 1988 (but see Debus 1995). *A. imitator*, which occurs on Isabel, Choiseul and Bougainville, is listed as Vulnerable (BirdLife International 2018) and both Dutson (2011) and Gregory (2017) considered it rare and poorly known. Vocalisations were described by Webb (1992) but his identification was questioned by Debus (1995; see also Webb 1995). Kratter *et al.* (2001) also described the vocalisations based on observations from lowland Isabel and audio recordings archived at the Univ. of Florida bioacoustic collection. However, Dutson (2011: 266) still considered the voice of the species 'poorly known', presumably due to discussion and contradictions in the literature. The field identification of *A. imitator* vs. Pied Goshawk *A. albogularis* is not straightforward and the two occur in sympatry on some islands, but *A. albogularis* has not been confirmed on Isabel (see LeCroy *et al.* 2001 for a full discussion on the status of *A. imitator* and *A. albogularis*, plumage morphs of both species, and summary of vocalisations). The pied-morph *A. imitator* that LHD observed in 2018 had white underparts with a black back, head and bib. Although both *A.*

imitator and *A. albogularis* are polymorphic, only *A. imitator* is known to have a pied morph with a black bib; other pied morphs of both species possess a white throat. Our observation of *A. imitator* at 1,100 m is the highest documented for the species and our audio recordings should clarify some of the confusion regarding the species' vocalisations.

CRESTED CUCKOO-DOVE *Reinwardtoena crassirostris*

We detected a single vocalising individual (ML118125161) on 26 June 2018 at 1,050 m on a ridge leading to the summit of the Kubonitu-Sasari massif. We did not find the species at lower elevations. On Isabel, Webb (1992) reported the species to occur from the lowlands to 400 m and Kratter *et al.* (2001) considered the species to be uncommon in lowland forest. Our record at 1,050 m provides evidence that it occurs at nearly all elevations on Isabel. This is unsurprising as the species is known at similar, or higher, elevations on other islands throughout its range (e.g. Dutson 2011, Gregory 2017) and was considered to be a bird of hill and montane forests by Mayr (1945).

WHITE-RUMPED SWIFTLET *Aerodramus spodiopygius reichenowi*

We observed this species uncommonly around the villages of Kolomola and Gnulahage at c.40 m elevation, generally associated with flocks of Uniform *A. vanikorensis* and Glossy Swiftlets *Collocalia esculenta* foraging over open coconut plantations and gardens. Webb (1992) reported the species to be confined to elevations above 700 m on Isabel, but others have also reported it in the lowlands (e.g. Kratter *et al.* 2001) and elsewhere *A. spodiopygius* occurs at all elevations (Dutson 2001, Gregory 2017) making our observations expected.

FINSCH'S PYGMY PARROT *Micropsitta finschii nanina*

M. finschii was observed from c.40 m to at least 650 m in the Kolosita River drainage, but nowhere was it numerous. Our observations agree with those of Kratter *et al.* (2001), who found the species in lowland forests of Isabel, but not with previous suggestions that the species is confined to montane habitat above 900 m (e.g. Webb 1992, Mayr 1945). SH described the species nesting in arboreal termitaria, corroborating Forshaw & Cooper (1989) and Kratter *et al.* (2001). We observed *M. finschii* vocalising near an arboreal termitarium that contained a cavity, but did not observe individuals visiting this termitarium.

BLACK-FACED PITTA *Pitta anerythra anerythra*

Uncommon at the Kolosita River site around 600 m, where we estimated up to five individuals daily. During our visit (7–15 June 2018) the species was very vocal both morning and evening (ML11848441, ML118478931) and was strongly associated with dense leafy undergrowth—typically ginger thickets on gentle slopes of drainage bottoms. Endemic to Buka, Bougainville, Choiseul and Isabel, Black-faced Pitta is rare throughout its range (Dutson 2011) and treated as Vulnerable (IUCN). On Isabel, it has been found regularly near Tirotonga village (Dutson 2011); however, Kratter *et al.* (2001) stated that the species is rare in the lowlands and Webb (1992) did not mention it. On Bougainville, *P. anerythra* is thought to be possibly extirpated (Hadden 2004: 180).

RED-CAPPED MYZOMELA *Myzomela lafargei*

Rare in hill forests along the Kolosita River at 500–700 m where we detected three individuals during nine days of field work. We did not observe the species in the lowlands around Gnulahage and Kolomola villages. In stark contrast, it was one of the most numerous species above 1,000 m on the Kubonitu-Sasari massif where we estimated up to 20 individuals daily. Nearly a century ago, Drowne reported a similar pattern of elevational

abundance: 'the honey sucker [*Myzomela*] being much more common at above 3,000 feet than below it' (Drowne 1927: 196–197). Kratter *et al.* (2001) reported the species to vary from rare to common depending on year in the lowlands of Isabel, Webb (1992) thought it ubiquitous and common, primarily in mid-elevation and lowland areas, and Dutson (2011) reported the species as rare on the island. Given this inconsistency in the literature, we suggest that *M. lafargei* is numerous in montane habitat above 1,000 m with possible seasonal or irruptive movements to lower elevations. These potential movements into the lowlands could have been in response to mature flowering trees, which may no longer exist due to recent, large-scale logging across lower and middle elevations on Isabel.

ORIOLE WHISTLER *Pachycephala orioloides orioloides*

Common in mid-elevation forests of the Kolosita River drainage at c.600 m and present to 1,160 m on the Kubonitu-Sasari massif, where it was less numerous than at lower elevations. We did not find the species in disturbed lowland forests around the villages of Kolomola and Gnulahage. Kratter *et al.* (2001) reported *P. orioloides* to be uncommon in the lowlands and Webb (1992) asserted that it is confined to above 900 m. Our observations corroborate Kratter *et al.* (2001), who suggested that the species is uncommon to common at all elevations on Isabel but is probably restricted to intact forest.

RUFOUS FANTAIL *Rhipidura rufifrons commoda*

We detected just one during nine days of field work along the Kolosita River around 600 m, suggesting that the species is rare in mature hill forest. We did not find it in disturbed coconut plantations and gardens around the villages of Kolomola and Gnulahage. Above 1,000 m along ridges leading to the Kubonitu-Sasari massif the species was common and we estimated up to five individuals daily. Kratter *et al.* (2001) described *R. rufifrons* as rare in the lowlands of Isabel, but Webb (1992) considered it common in lowland forests. Drowne (1927) did not note any change in abundance between the lowlands and highlands of Isabel. These conflicting reports suggest that the species is patchily distributed or has vacated lower elevations in recent years.

STEEL-BLUE FLYCATCHER *Myiagra ferrocyanea ferrocyanea*

Rare in mid-elevation hill forests of the Kolosita River drainage with singles recorded twice during our nine days at this site. It was much more regular on ridges leading to the Kubonitu-Sasari massif at 1,050–1,160 m, where up to three were detected daily. Our observations suggest the species is commoner at higher elevations on Isabel. Webb (1992) and Kratter *et al.* (2001) considered the species to be uncommon in lowland and montane forests.

ISLAND LEAF WARBLER *Phylloscopus maforensis becki*

We found up to four in mossy montane forest around the Kubonitu-Sasari massif between 1,080 and 1,186 m on 12 and 22–26 June 2018. Three of the four were seen only above 1,100 m and were encountered daily during 22–26 June; all were singing and not associated with one another. These three appeared territorial as they were well spaced and only two could be heard at any one time, they were not seen paired, and were present in the same general areas on a daily basis. Non-vocal *Phylloscopus* were not detected. Based on these observations, we estimated at least four territorial, presumably male, *P. maforensis* within the surveyed area (a single ridge leading to the summit, and the summit of the Kubonitu-Sasari massif). LHD obtained nine audio recordings of the birds' songs (ML118513481, ML118354981, ML118354401, ML118256811, ML118256401, ML118152721, ML118152641,

ML118126171, ML118125311). These are the first recordings for the species on Isabel, but no vocal comparison to populations on other islands has been made. None was mist-netted, despite effort. Based on LHD's observations of four individuals over six days, *P. maforensis* is restricted to mossy montane forest above 1,000 m on Isabel, and primarily above 1,100 m. Surveys at lower elevation (7–15 June, c.600 m) did not detect the species. The species was previously known on Isabel from a single specimen (AMNH 218146) collected by R. H. Beck on 19 August 1927 on or near the summit of the Kubonitu-Sasari massif (Beck 1927, Drowne 1927). Despite surveys of the Kubonitu-Sasari massif by the Whitney South Sea Expedition six days after Beck's visit (e.g. Drowne 1927) and by Webb (1992) the species was not observed (see Mayr 1945, Webb 1992, Kratter *et al.* 2001, Mayr & Diamond 2001, Dutson 2011). Clement *et al.* (2018) and Dutson (2011) stated that no recent records are available from Isabel. Our records are the second on Isabel and suggest that it is restricted to mossy montane forest above 1,000 m, an area of less than 5 km² around the Kubonitu-Sasari massif (Fig. 1). Hartert (1929) described, based on plumage differences, the subspecies *becki* from specimens collected on Guadalcanal in July 1927 and restricted this taxon's distribution to Guadalcanal; he did not mention the Isabel specimen, also collected in 1927. Mayr (1935) described, again based on plumage, three additional subspecies of what was then *P. trivirgatus* in the Solomon Islands, still without mentioning its presence on Isabel. A decade later, Mayr was the first to note the species' occurrence on Isabel, when he extended the range of *P. m. becki* to include Guadalcanal, Malaita and Isabel (Mayr 1945: 253). Due to a paucity of specimen material, a thorough taxonomic review of the species in the Solomon Islands is lacking. We refer to the species as *P. maforensis* following Gill & Donsker (2019), although other authorities have split the taxon into multiple species resulting in the Solomons' populations taking the name *P. poliocephalus* (Pratt & Beehler 2015). Clarity in nomenclature and systematics of this complex demands further study.

Discussion

Our data increases our understanding of some rare and poorly known bird species in the Solomon Islands, particularly on Isabel. Our observations from the highlands of Isabel (above 1,000 m) provide a modern perspective on elevational abundance of species in this under-studied and remote region. We found some interesting parallels with Drowne's (1927) observations, patterns that have been largely unrecorded in the literature (e.g., greater abundance of *Myzomela lafargei* in the highlands). Our observations of *Phylloscopus maforensis* provide the first documentation of the species on Isabel since its discovery in 1927. The lack of information concerning this species is symptomatic of our poor understanding of Isabel's montane avifauna.

Mossy montane forest on Isabel is restricted to an area of c.4.2 km² and an elevational envelope of <200 vertical metres. These montane habitats are a product of atmospheric conditions, especially lower temperatures and consistent immersion in the cloud layer (e.g. Still *et al.* 1999, Foster 2001, Hermes *et al.* 2018), and are highly susceptible to the effects of climate change. Given the specialised fauna we documented (Univ. of Kansas unpubl. data), the small area, and threat of habitat reduction from climate change, the Kubonitu-Sasari massif should be of special conservation concern. Future surveys of montane fauna in the Solomon Islands, particularly on Isabel, are required to adequately describe the biodiversity in this unique habitat. Modelling and measuring changes in habitat, and habitat association of species, are needed to determine how species distributions may shift in response to climatological factors.

It is important to continue updating our basic knowledge of the distribution and abundance of birds in the Solomon Islands as this provides the building blocks for ongoing

and future research in the region. Contributions like the present publication provide a record of change in the status and distribution of the archipelago's avifauna and can inform local conservation work aimed to protect critical habitat. Pressure from logging and mining continues to threaten natural habitats across the Solomons, with a dramatic increase in logging licenses and activities since 2000 (Katovai *et al.* 2015) and proposals for nickel mines on Isabel starting in 2016 (Allen & Porter 2016). Much of our knowledge of the Solomons avifauna is restricted to species presence or absence on islands, with few data on elevational abundance, ecology, or more detailed aspects of a species' natural history (Diamond 1975, Mayr & Diamond 2001). Additional documentation of basic natural history information is needed, not only on Isabel, but also for the Solomon Islands and Melanesia as a whole.

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A nest of Yellow-margined Flatbill *Tolmomyias assimilis*

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SUMMARY.—Although it is a common species, almost nothing is known concerning the breeding biology of Yellow-margined Flatbill *Tolmomyias assimilis*. We present the first formal description of the species' nest. It was found in an open area near Manaus, Amazonas state, Brazil, and was, like the nests of other *Tolmomyias* species whose nests have been described, a closed structure, suspended from a branch, with an entrance tunnel.

With eight recognised subspecies, Yellow-margined Flatbill *Tolmomyias assimilis* is widely distributed across much of Amazonia, in *terra firme* and *várzea* forests, including anthropogenically disturbed areas. It forages alone or in pairs in the midstorey and subcanopy, searching for arthropods (Caballero & Kirwan 2019). Currently the species is considered Least Concern (BirdLife International 2019). Despite being a common species, there are no descriptions of its nest, eggs or breeding behaviour (Crozariol 2016, Caballero & Kirwan 2019). Here, we present here the first formal description of its nest, which relates to the subspecies *T. a. examinatus*.

On 12 January 2019, in an open area along Ramal do Italiano (02°49'30"S, 60°03'20"W), in the municipality of Manaus, Amazonas state, we observed two adult *T. assimilis* vocalising and, subsequently, building a nest. On this occasion, the nest consisted of a small quantity of material 2.8 m above ground among the leaves and small fruits near a drooping branch of a *Vismia cayennensis* (Hypericaceae) that was approximately 7 m tall (Fig. 1). Material collected by the birds was carried to the site and woven together around a trifurcation near the tip of the branch. Despite a fairly dense understorey elsewhere in the vicinity of the nest site, the area below the nest was clear of vegetation. Seven days later, nest construction had advanced considerably (it was now 160 mm tall and 80 mm wide), but the nest still lacked an entrance tunnel or egg chamber (Fig. 2). Although nests of *Tolmomyias* spp. often co-occur alongside nests of social insects (Menezes *et al.* 2014), we did not observe any in the vicinity.

On 2 February 2019, the nest had a near-vertical entrance tunnel (35 mm long with an entrance 60 mm in diameter), and a well-formed egg chamber. Its external size had also increased to 230 mm tall and 115 mm wide (Fig. 3). The main materials used to construct the nest were dark vegetable and fungal fibres, as well as tiny twigs and small dry leaves, bound together using spider's web. Our final visit was on 5 March 2019, when the nest had a total height of 260 mm, an external width of 115 mm, a tunnel 75 mm long and 56 mm in diameter at its entrance, and an egg chamber of 62.5 × 80.0 mm, measured externally (Fig. 4). No further observations were possible.

According to the classification scheme devised by Simon & Pacheco (2005), nests of the genus *Tolmomyias* are expected to be of the 'closed / retort / pensile' type. The nest of *T. assimilis* reported here fits this description closely. The nest appeared ready for use by early February, but by the date of our last observation it had not yet been used for breeding, despite that the birds were observed nearby on all of our visits. It is possible that the nest described here was a dormitory, used by the adults only for roosting (Skutch 1956, 1961), or



Figure 1. One of the pair of Yellow-margined Flatbill *Tolmomyias assimilis*, carrying material to the nest, Ramal do Italiano, municipality of Manaus, Amazonas state, Brazil, January 2019 (Gabriel Augusto Leite)



Figure 2. Nest of Yellow-margined Flatbill *Tolmomyias assimilis* with the egg chamber in formation, Ramal do Italiano, municipality of Manaus, Amazonas state, Brazil, January 2019 (Arthur Monteiro Gomes)



Figure 3. Nest of Yellow-margined Flatbill *Tolmomyias assimilis*, still incomplete but with egg chamber and entrance tunnel under construction, Ramal do Italiano, municipality of Manaus, Amazonas state, Brazil, February 2019 (Arthur Monteiro Gomes)

that the pair was delaying clutch initiation, waiting for more conducive weather conditions or a better food supply (Stouffer *et al.* 2013). The nestbuilding period was characterised by heavy rainfall.

There are two previous photographic records of this species carrying nest material. The first was in March 2009, in the municipality of Laranjal do Jari, Amapá state, Brazil (K. M. Aguiar; <http://www.wikiaves.com/615884>), and the second was in August 2018 (K. F. Costa; <http://www.wikiaves.com/3084595>), in the same area as we made our observations. In addition, there is a photograph of a purported *T. assimilis* nest, also from Manaus (M. R. Omena; <http://www.wikiaves.com/218244>), but without further information proving the species involved. In addition, there are two observations of breeding behaviour pertaining to the formerly conspecific Yellow-winged Flatbill *T. flavotectus*. In central Panama, on Barro Colorado Island, in April 1948, Wetmore (1972) observed an individual carrying nesting material, but did not locate the nest site, while a pair was in breeding condition in May in Colombia (Hilty & Brown 1986). In Costa Rica, at the northernmost edge of its range, the latter species breeds in April–June, building a retort-like pear-shaped bag of fine black fibres and fungal rhizomorphs, 9–21 m above ground, often near wasp nests (Stiles & Skutch 1989).

We still know surprisingly little concerning the reproduction of many Neotropical bird species, even basic data such as the structure of nests, size and colour of eggs, breeding season, and clutch size being unknown. Such information aids our understanding of species dynamics and how anthropogenic factors can affect breeding. Moreover, nests can be used to better understand phylogenetic relationships between species (Zyskowski & Prum 1999).



Figure 4. Nest of Yellow-margined Flatbill *Tolmomyias assimilis* in an advanced stage, Ramal do Italiano, municipality of Manaus, Amazonas state, Brazil, February 2019 (Arthur Monteiro Gomes)

It is therefore important that new descriptions of nests be made available, thereby providing basic knowledge about the natural history of species and generating data that can guide their conservation.

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First record of Solomons Nightjar *Eurostopodus nigripennis* for Malaita, with a description of its nest site

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SUMMARY.—Solomons Nightjar *Eurostopodus nigripennis*, listed as Vulnerable by BirdLife International, has previously been recorded only from the north and central Solomon Islands. Even within the species' known range there are few records, limiting knowledge of its ecology. We provide photographic evidence of a Solomons Nightjar nest in a streambed on the island of Malaita at an altitude of c.270 m—the first record on this large island. This observation, combined with traditional local knowledge, suggests that the species may have a wider range of nesting habitat than previously documented, and that further surveys in collaboration with local tribespeople could be important for conservation efforts.

Nightjars are generally crepuscular or nocturnal, and this, combined with their cryptic plumage, results in many gaps in our knowledge of the family as a whole (Holyoak 2001, Hadden 2004). One of the least-known species is Solomons Nightjar *Eurostopodus nigripennis* (Cleere 2010, Dutson 2011). Here, we report the first record of the species for the island of Malaita, in the Solomon Islands, précis the available literature, and summarise what is known by local tribespeople.

On the afternoon of 5 September 2018, while searching for study sites for a collaborative bird survey of East Kwaio, Malaita (Callaghan *et al.* 2019), MA found an unidentified egg (Fig. 1a.) on the ground at 08°59'43.7994"S, 160°58'58.0794"E. MA installed a camera trap in the vicinity (Fig. 1b). When the footage was reviewed, it was discovered that the egg belonged to Solomons Nightjar (Fig. 1c), known as *baababa* in the local Kwaio language. The adult, photographed on 6 September 2018, was identified by the lack of white markings on the wing and tail, and a pale collar extending to the nape (Fig. 1c–e). According to Dutson (2011), the only other potential caprimulgid in this region (based on nearest known range) is Large-tailed Nightjar *Caprimulgus macrurus*, which has white patches in the tail. White-throated Nightjar *Eurostopodus mystacalis* was also excluded based on wing pattern (Dutson 2011). Local tribal people stated there was only one type (species) of *baababa* in the vicinity. The habitat consisted of a streambed, c.270 m above sea level (Fig. 1f), surrounded by secondary forest. The bird abandoned the nest, and the egg remained *in situ* one week post-abandonment before disappearing. A nightjar was subsequently seen in December 2018 and January 2019 in the vicinity. Local tribal leaders stated that the *baababa* is not found any higher in the valley than the September 2018 sighting, and is only occasionally seen along the riverbed and in adjacent abandoned gardens.

This represents the first documentation of the species for the island of Malaita, and one of only a handful of records throughout its global distribution (Hadden 2004). Even within its previously documented range (north and central Solomon Islands; Cleere 2010), its status is poorly known. Solomons Nightjar is classified as Vulnerable by the IUCN, based on its 'very small, declining population, within which all subpopulations are likely to be very small' (BirdLife International 2019). Local people in the vicinity described the *baababa*

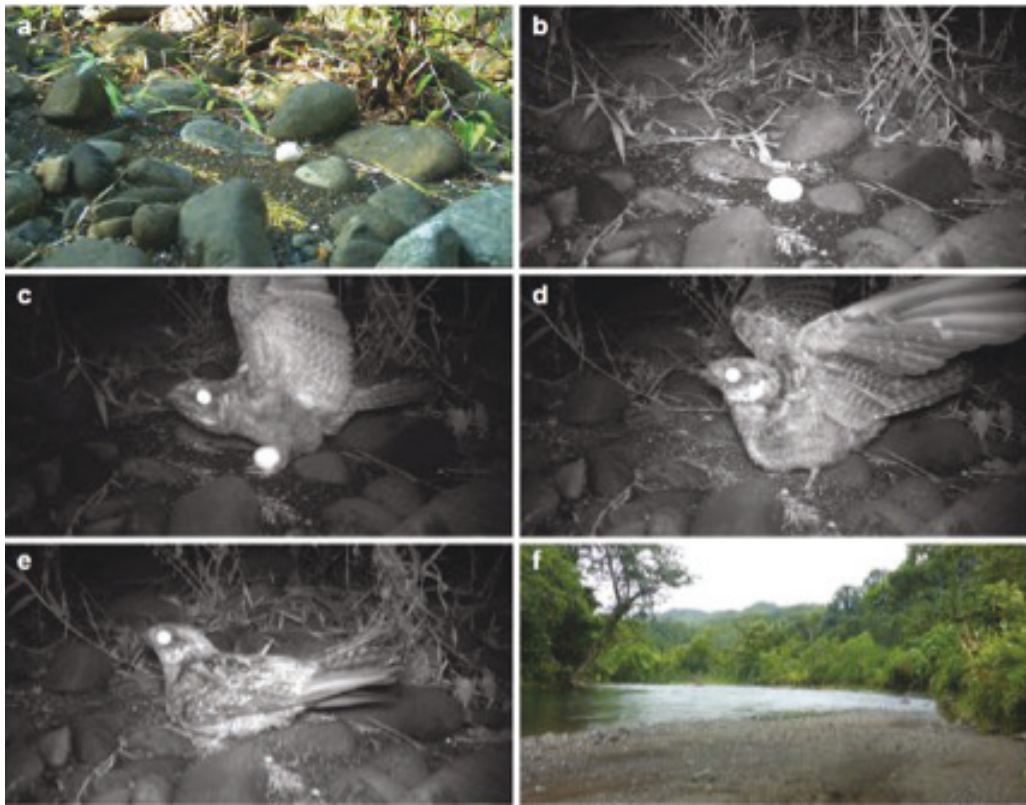


Figure 1. Solomons Nightjar *Eurostopodus nigripennis*, East Kwaio, Malaita, September 2018, showing (a) egg when initially discovered (Maasafi Alabai), (b) egg on camera trap, (c) adult standing over egg, (d) adult showing white throat and lack of white in tail, (e) adult showing pale collar extending to nape, and (f) riverbed where the nest was located (Maasafi Alabai)

as very rare, wary of people, well camouflaged by day and only seen at night. Consistent with this, there are currently only four records in the global database eBird (<https://ebird.org/species/solnig1>). Read (2013) also noted a paucity of records of Solomons Nightjar in the literature, with an apparent hotspot on Tetepare Island which has a long-standing conservation programme. That just one egg is laid matches both traditional and scientific knowledge of this species' behaviour (Cleere 2010). Solomons Nightjar is most commonly found nesting on beaches (Mayr 1945, Coates 1985, Read 2013), but this individual was nesting in a dry streambed, following the seasonal floods. The streambeds are relatively clear areas on sandy / pebble islands within rivers or on the banks of rivers. These small islands are usually vegetated with small shrubs. Local people stated that *baababa* do not venture into gardens with regular human activity or into rainforest. This record suggests that Solomons Nightjar may have a wider range of nesting habitats than previously documented, and that at least on Malaita, the birds adapt their egg-laying schedule based on the wet and dry seasons.

The species is of conservation concern, largely due to the lack of data (BirdLife International 2019). Potentially, this is at least in part because its vocalisations are very poorly known—with two descriptions (Gregory 2017) and no recordings—leading to a potential reduction in records (Mayr 1945). Even local people are unfamiliar with the calls / songs of the species, however they have heard *baababa* chicks uttering a hiss. Interestingly, *baababa* is a 'tabu' bird in Kwaio culture, so this species is not hunted and its eggs cannot be

eaten, meaning that less about its behaviour is known than for other species. Furthermore, the word *baababa* describes the characteristic of the bird that crouches over to 'hide'. Indeed, the Kwaio word for hide is 'baba'. Because of this, this bird is poorly known and only observed when it lays eggs and in the immediate environs of its nest.

In addition to the first record and nesting of Solomons Nightjar on Malaita to be reported in the scientific literature, we also highlight the low detection probability of this species throughout most of its potential range on Malaita because of its elusive behaviour, and the relative lack of scientific visits to the island in search of birds (Callaghan *et al.* 2019). We recommend dedicated surveys for Solomons Nightjar in collaboration with local tribal groups, which could ultimately better elucidate the species' conservation status on Malaita and throughout the Solomons Islands.

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Nesting by dark-bibbed female Beautiful Long-tailed Sunbirds *Cinnyris pulchellus* and occurrence of dark bibs in both sexes of Beautiful Long-tailed and Gorgeous Sunbirds *C. melanogastrus*

by Robert A. Cheke, Clive R. Barlow & Clive F. Mann

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SUMMARY.—Observations on nesting Beautiful Long-tailed Sunbirds *Cinnyris pulchellus* in The Gambia revealed that some females have dark or partially dark bibs, contrary to most accounts in the literature. Furthermore, all fledglings seen in The Gambia also had dark bibs and some males in eclipse plumage or lacking tail-streamers engaged in breeding activity. The conclusion that some adult female *C. pulchellus* have dark bibs and that some, probably all, juveniles have dark bibs was confirmed from museum specimens. It is further demonstrated, based on specimens, that some adult females and juveniles of Gorgeous Sunbird *C. melanogastrus* also have dark bibs.

Beautiful Long-tailed Sunbird *Cinnyris pulchellus* is a widespread species occurring in savanna and Sahelian habitats from Senegal in West Africa to Eritrea in the east, reaching south into parts of Kenya, Uganda and Democratic Republic of the Congo. A close relative, formerly considered a subspecies of *C. pulchellus*, is Gorgeous Sunbird *C. melanogastrus* found in west and central Kenya and parts of Tanzania. Most textbooks describe the black bib on the throats of Beautiful and Gorgeous Sunbirds as characteristic of juvenile and immature males (e.g. Bannerman 1948, the text but not the plates [Figs 10b and 10c of Pl. 42 are transposed] in Barlow *et al.* 1997, Cheke & Mann, 2001, 2008), with females lacking such markings being plain-throated, but sometimes having a yellow wash. An exception is Fry *et al.* (2000) who stated ‘juvenile like adult female but with chin and throat dusky grey’, but this account did not make it explicit that the remark applied to both sexes. It was therefore of interest that between 2010 and 2019 CRB observed that all fledglings from many successful nests of *C. pulchellus* in his garden and vicinity at Brusubi (13.3925°N, 16.7545°W), in the coastal Western Region of The Gambia, were dark-bibbed, this being the standard feature on pulli and fledglings, and apparently also the case at other sites in The Gambia.

In February 2014 CRB observed a dark-bibbed female, accompanied by a male lacking any tail-streamers but otherwise in full breeding plumage, feeding and attending a fledgling. Then on 15 March 2018 he observed and photographed a dark-bibbed female, albeit with a pale-centred throat, carrying nesting material. When this was reported to CFM & RAC they initially surmised that helpers of various ages were involved. CRB’s rejection of this possibility prompted RAC & CFM to examine specimens of both *C. pulchellus* and *C. melanogastrus* at the Natural History Museum, Tring (NHMUK), to re-examine the occurrence of dark-bibbed plumages in these species. Here we describe some breeding observations and the results of our specimen examination, and conclude that (1) some or all of both sexes of fledglings / juveniles of *C. pulchellus* and *C. melanogastrus* have dark bibs; (2) some adult females of *C. pulchellus* retain the bib even when nestbuilding, incubating

and feeding young, and (3) male *C. pulchellus* in breeding plumage without streamers or in eclipse plumage are sometimes involved in breeding activities.

Nesting by *Cinnyris pulchellus* at Brusubi

On 26 February 2014 CRB noted a very recently fledged *C. pulchellus* being fed by a pair of colour-ringed, apparently adult, birds in a *Bougainvillea* hedgerow bordering a road. The adult male (colour-ringed with a single yellow 7, when it had full-grown streamers, on 22 October 2013; Fig. 1.) was in full breeding plumage but lacked tail-streamers and the female had a dark bib, which it also had when initially trapped almost one year earlier (colour-ringed single green on 11 April 2013; Fig. 2). Observations were made for a week and, as both presumed adults were colour-ringed, it was possible to confirm that these were the only birds feeding the single fledgling, which also had a dark bib, thus the possibility of attendant helpers in juvenile plumage was eliminated. Fig. 3 illustrates the dark bib on another recently fledged juvenile but of unknown sex.

On 15 March 2018, during a nesting effort in the same garden an apparently adult female with a black bib, but with a pale-centred throat, was photographed collecting nesting material during multiple visits to leaf litter in a flower pot (Fig. 4). On 12 January 2019 CRB observed a female with a dark bib collecting and carrying away bark fibres from an *Acacia* sp. on a number of visits to the tree's bole at Bantakunku Beach (13.3405°N, 16.8123°W) coastal Gambia, but no nest was located.

Although the bird in Fig. 1 may have simply just lost its streamers, there is other circumstantial evidence that males that are not in full breeding plumage engage in breeding activity. For example, on 27 June 2019 CRB observed a male in almost full eclipse plumage without tail-streamers that was in full song, and he has also seen a male in three-quarters eclipse plumage visiting a nest and displaying to a female.

Museum specimens

Adult female *C. pulchellus* and *C. melanogastrus*.—Fig. 5 shows specimens of adult female *C. pulchellus* from which it is clear that although some females have unmarked throats, the two in the centre of the image have narrow and broad expanses of black on their throats, respectively. All are labelled as females, with NHMUK 1930.3.4.220 reported as containing eggs and having a brood patch. Fig. 6 illustrates two additional black-throated females. There are similar specimens of female *C. melanogastrus*, including one collected by R. E. Moreau (Fig. 7). However, presumably in the belief that all birds with black throats must be males, someone has annotated the label of this bird 'young male'. A similar annotation is present on the labels of black-throated birds claimed as being female by their collectors, including on that of NHMUK 1911.10.16.189 (collected by G. Blaine) and a '?' has been inserted in blue ink ahead of the female symbol on NHMUK 1964.15.1 (collected by C. H. Fry, apparently the only author to suggest that both sexes could have dark throats). This raises the issue of whether some or all of the black-throated birds, claimed as being female by their collectors, were perhaps incorrectly sexed. However, NHMUK 1940.12.4.27 (Fig. 8), collected on 24 June 1939 south-west of Sokoto, Nigeria, which has some black on the throat, but not an extensive amount, was collected at its nest by W. Serle who reported that it had enlarged ovaries. A similar specimen (NHMUK 1926.8.8.350) with a slightly darker throat was collected by G. L. Bates north of Rei Buba, Cameroon, at an altitude of c.400 m on 6 April 1925, and labelled as having small eggs (Fig. 8).

Juvenile *C. pulchellus* and *C. melanogastrus*.—Confirmation that some juvenile females of both species have black throats is provided by the specimens illustrated in Fig. 9.



Figure 1. Breeding male Beautiful Long-tailed Sunbird *Cinnyris pulchellus* without tail-streamers, Brusubi, The Gambia, 11 March 2014 (Dave Montreuil)

Figure 2. Black-bibbed female Beautiful Long-tailed Sunbird *Cinnyris pulchellus* seen nesting, Brusubi, The Gambia, 11 March 2014 (Dave Montreuil)

Figure 3. A very recently fledged black-bibbed Beautiful Long-tailed Sunbird *Cinnyris pulchellus*, Brusubi, The Gambia, 14 February 2016 (C. R. Barlow)

Figure 4. Black-bibbed, but with pale centre to the throat, female Beautiful Long-tailed Sunbird *Cinnyris pulchellus* with nest material, Brusubi, The Gambia, 15 March 2018 (C. R. Barlow).

The label for NHMUK 1930.3.4.219, collected by G. L. Bates, includes the note 'ovary small'. Many similar specimens labelled as juveniles or immatures of both sexes with extensive black throats are also present in the NHMUK collection.

Discussion

As only female *C. pulchellus* are involved in nestbuilding, there is no doubt from the above observations made by CRB (see Figs. 2 and 4) that some females possess dark feathers on their throats. The bird in Fig. 2 was undoubtedly more than one year old, being probably at least 15 months old, and, given that it is unlikely that immatures would build nests, we consider that there is little doubt that some adult females have dark bibs or streaks on their



Figure 5. Female Beautiful Long-tailed Sunbird *Cinnyris pulchellus* specimens, left to right: (1) NHMUK 1929.2.18.377, Bakkendik, North Bank Division, The Gambia, 22 December 1928, coll. W. P. Lowe; (2) NHMUK 1939.12.9.3176, near Thiès, northern Senegal, 29 June 1907, coll. F. W. Riggenbach; (3) NHMUK 1930.3.4.221, Say, River Niger ('Upper Volta' but now in Niger), 21 April 1928, coll. G. L. Bates; (4) NHMUK 1878.10.26.86, Daranka (? = Daranka Island, south-west of Banjul), The Gambia; (5) NHMUK 1913.7.6.24, George Valley, Freetown, Sierra Leone, 12 April 1911, coll. Major Kelsall; (6) NHMUK 1930.3.4.220, east of Kulikoro, French Sudan (now Mali), 18 June 1928, coll. G. L. Bates (R. A. Cheke, © Natural History Museum, London)

Figure 6. Two black-throated female Beautiful Long-tailed Sunbirds *Cinnyris pulchellus*, left: NHMUK 1902.1.20.218, Darella Aila, southern Abyssinia (Ethiopia), 10 December 1900, coll. A. E. Pease; right: NHMUK 1912.10.15.1219, Mensi Wandu, southern Abyssinia (Ethiopia), 18 August 1905, coll. W. N. McMillan / P. C. Zaphiro (R. A. Cheke, © Natural History Museum, London)

Figure 7. Female Gorgeous Sunbird *Cinnyris melanogastrus*, NHMUK 1936.7.2.247, Manyara Plain, north end of Lake Manyara, Tanzania, 2 August 1936, coll. R. E. Moreau (R. A. Cheke, © Natural History Museum, London)

Figure 8. Female Beautiful Long-tailed Sunbirds *Cinnyris pulchellus*, above: NHMUK 1940.12.4.27, shot at nest with enlarged ovaries, south-west of Sokoto, Nigeria, 24 June 1939, coll. W. Serle; below: NHMUK 1926.8.8.350, female with small eggs, north of Rei Buba, Cameroon, 6 April 1925, coll. G. L. Bates (R. A. Cheke, © Natural History Museum, London)

throats. This conclusion is supported by museum specimens (Figs. 5, 6 and 8) and is also the case for *C. melanogastrus* (Fig. 7). However, some females do have completely pale throats, sometimes washed yellow. There is also evidence that males that are not in full breeding plumage may breed or perform activities associated with breeding such as singing, displaying or visiting nests. It is also clear that some juveniles of both sexes and both species may have dark throats but, as yet, we are unsure if this is always true.

Our findings contradict most accounts in the literature. Bannerman (1948) stated of *C. pulchellus* that the 'adult female differs in every particular from the male and lacks any



Figure 9. Specimens claimed as female and described as immature, left: Gorgeous Sunbird *Cinnyris melanogastrus*, NHMUK 1935.10.16, Rusinga Island, Kenya, 14 February 1935, Leakey / Bell coll., or juvenile, middle: Beautiful Long-tailed Sunbird *C. pulchellus*, NHMUK 1930.3.4.219, above Yelwa, River Niger, Nigeria, 1 April 1928, coll. G. L. Bates, and right: NHMUK 1922.12.8.1319, Zalingei, Darfur, Sudan, 29 October 1921, coll. Admiral H. Lynes (R. A. Cheke, © Natural History Museum, London)

metallic colour, the whole plumage being dull' and continues subsequently 'Chin and throat whitish, the rest of the undersurface washed more or less strongly with yellow'. He described immature males as resembling 'the adult female in having upperparts brown but have the throat blackish...' and that immature females are distinguished from immature males 'by not having any dusky black on the chin and throat which is white'. It is probable that these descriptions led to the widespread assumption that only males ever have dark throats. Indeed, it is possible that the female-labelled specimens at NHMUK that were 'corrected' to being assigned to the male sex were so re-labelled by Bannerman. Given this salutary lesson in the dangers of following the literature uncritically (although the account in Fry *et al.* 2000 is an exception, implicitly but not explicitly), we now wish to re-examine the situation in other sunbirds, such as other species of *Cinnyris* with dark throats and *Chalcomitra* spp. that are similarly endowed, and to follow-up whether all or only some juvenile *C. pulchellus* have dark throats, with The Gambia being an ideal location for further such field work.

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A Great Frigatebird *Fregata minor* at Fernando de Noronha archipelago, equatorial Atlantic Ocean

by Robson Silva e Silva & Caio J. Carlos

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SUMMARY.—We report a documented record of a Great Frigatebird *Fregata minor* at Fernando de Noronha, 360 km off the coast of northeast Brazil in the equatorial Atlantic. We presume that the bird at Fernando de Noronha originated from Trindade Island, c.1,800 km to the south, since it is the species' nearest breeding site, and we hypothesise that it moved with the south-east trade winds towards the north-east Brazilian coast.

Four frigatebird species nest on Atlantic Ocean islands: Ascension Frigatebird *Fregata aquila*, Magnificent Frigatebird *F. magnificens*, Great Frigatebird *F. minor* and Lesser Frigatebird *F. ariel*. Whereas Magnificent Frigatebird has a broad breeding distribution, in the Atlantic each of the other species nests on a single island / archipelago (Orta *et al.* 2019a,b,c). The Atlantic populations of Great and Lesser Frigatebirds, respectively referred to as *F. m. nicolli* and *F. a. trinitatis*, are currently restricted to Trindade (Carlos 2009, Mancini *et al.* 2016, Olson 2017), an island of volcanic origin 1,140 km off south-east Brazil (Alves

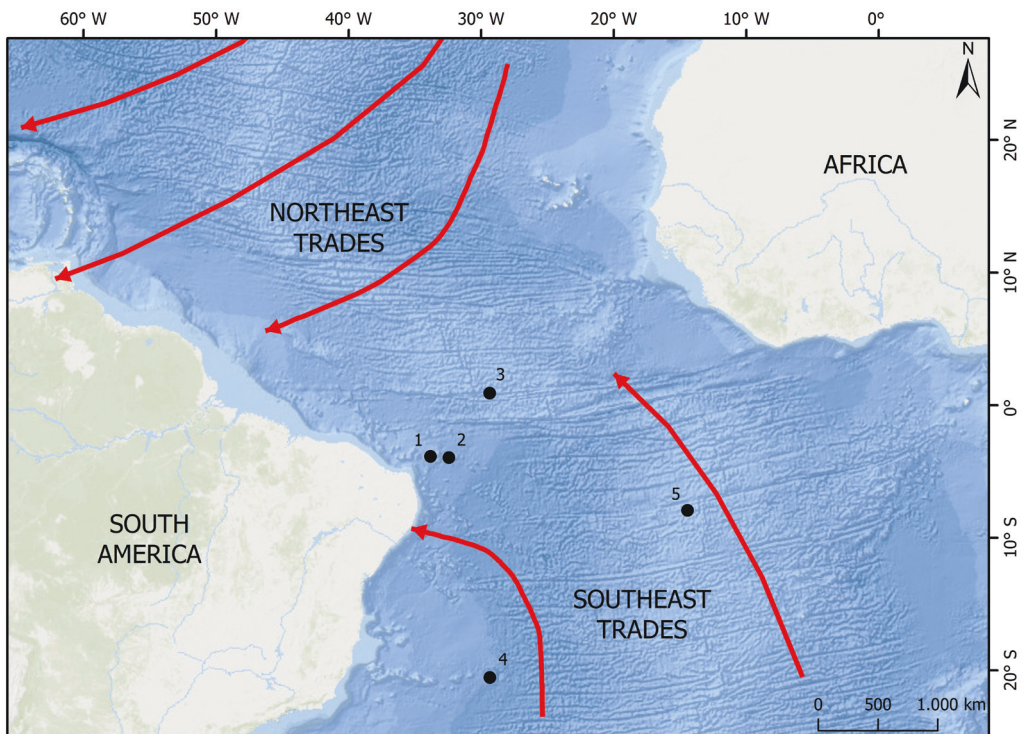


Figure 1. Tropical oceanic islands in the South Atlantic: (1) Rocas Atoll, (2) Fernando de Noronha archipelago, (3) São Pedro e São Paulo archipelago, (4) Trindade and Martim Vaz archipelago, and (5) Ascension Island.

1998; Fig. 1). However, fossil remains attributed to both taxa have been found on St Helena (Olson 1975, 2017), 1,580 km east of Trindade. Elsewhere, Great and Lesser Frigatebirds breed on tropical and subtropical islands in the Indian and Pacific Oceans (Orta *et al.* 2019b,c).

The at-sea ranges of frigatebirds breeding on Trindade are poorly understood. Available observations are from around Trindade itself and nearby Martim Vaz archipelago (e.g. Murphy 1915, Olson 1981, Antas 1991, Fonseca-Neto 2004, Mancini *et al.* 2016, Port *et al.* 2016). There is a possible sighting of an adult female Great Frigatebird from Mar del Plata, Argentina, in January 2007 (López-Lanús & López-Lanús 2011), c.3,300 km southwest of Trindade, perhaps indicating that the species may wander far from its only Atlantic breeding site.

Juvenile and immature Great Frigatebirds exhibit a series of plumages with rusty and white on head and breast, and white underparts, decreasing progressively before they achieve adult coloration. Adult males are mostly brownish black, whereas females have some white below (Harrison 1983, Valle *et al.* 2006, Orta *et al.* 2019c).

Here, we present a documented record of a Great Frigatebird at Fernando de Noronha, a volcanic archipelago 360 km off north-east Brazil in the equatorial Atlantic (Fig. 1). The archipelago consists of a main island, and 20 islands and islets (Silva e Silva 2008).

Between 1999 and 2008, RSS visited Fernando de Noronha almost annually to study its birds. Visits lasted 10–23 days and smaller islands were accessed by motorboat (Silva e Silva 2008). On 7 March 2008, RSS & P. T. Felipe, an inspector with the Brazilian federal protected areas agency (ICMBio), disembarked at 'Pontal da Macaxeira' (03°48'30"S, 32°22'49"W), on Ilha da Rata to ring the seabirds nesting there: Magnificent Frigatebird, Masked Booby *Sula dactylatra* and Red-footed Booby *S. sula* (Silva e Silva 2008). The next day, near a colony of Magnificent Frigatebirds on the island's east side, a juvenile, rusty-headed frigatebird was observed being chased and grasped by other frigatebirds (Fig. 2).

The frigatebird in question had a pale blue bill with yellowish tip, white head and neck with tawny-washed throat, cheeks, forehead and nape, blackish-brown upperparts with pale-barred wing-coverts, a complete, blackish-brown breast-band, a white, egg-shaped belly patch with its narrow end turned rearwards, and blackish underwings (Fig. 2). This plumage is like that described for first-year Great Frigatebird (Harrison 1983, Walbridge *et al.* 2003, James 2004).

The most useful characters for distinguishing frigatebird species are the presence of any tawny or rufous on head and neck and the extent and shape of white markings below (Harrison 1983, James 2004). Juvenile Greater and Lesser Frigatebirds have a rusty or cinnamon head that fades to whitish with age, whereas juvenile Ascension and Magnificent Frigatebirds both possess an all-white head (Harrison 1983, Walbridge *et al.* 2003, James 2004). The white belly patch of juvenile Great Frigatebird is rounded anteriorly, so that the posterior margin of the dark breast-band is concave. In juvenile Lesser Frigatebird, the white belly patch is triangular with a rounded, narrow tip pointing towards the tail and straight base bordering the dark breast-band. Furthermore, juvenile Lesser Frigatebird always has axillary spurs, which are long, narrow, and originate from the anterior corners of the triangular belly patch. Great Frigatebird occasionally has small axillary spurs, but these distinctly originate behind the anterior margin of the belly patch and breast-band (James 2004).

In contrast to the limited published information on the at-sea distribution of Atlantic Great Frigatebirds, their counterparts in the Indian Ocean are better studied. For example, satellite-tracked Great Frigatebirds from Europa Island in the Mozambique Channel make



Figure 2. First-year juvenile Great Frigatebird *Fregata minor*, Fernando de Noronha archipelago, Brazil, 7 March 2008, below being chased by a juvenile Magnificent Frigatebird *F. magnificens*; note the tawny wash to the head and neck, complete dark breast-band, and the egg-shaped white belly patch (Robson Silva e Silva)

long-distance, clockwise loops around the Indian Ocean, taking advantage of the trade winds (Weimerskirch *et al.* 2016).

In the Atlantic, the north-east trade winds blow from subtropical latitudes ($c.30^{\circ}\text{N}$) towards the north-east coast of South America and the Caribbean. South-east trade winds blow from $c.30^{\circ}\text{S}$, along the coast of Africa, then across the Atlantic to the equatorial South American coast (Longhurst & Pauly 1987; Fig. 1). We presume that the juvenile Great Frigatebird at Fernando de Noronha originated from Trindade, $c.1,800$ km to the south, as it is the nearest breeding site. Then, we hypothesise that it moved downwind in the south-east trades to the north-east Brazilian coast. Recently, a satellite-tracked juvenile Ascension Frigatebird from Boatswainbird islet, moved north-west to Brazilian waters within less than 100 nautical miles (190 km) of Fernando de Noronha and the São Pedro e São Paulo archipelago (Williams *et al.* 2017). Ascension lies at $c.8^{\circ}\text{S}$, in the path of the south-east trade winds; therefore, we interpret the record reported by Williams *et al.* (2017) as indirect evidence for our hypothesis.

The Great Frigatebird population on Trindade has undergone severe decline and is estimated at just a few individuals (Mancini *et al.* 2016). It is difficult to know whether Trindade Great Frigatebirds regularly move to equatorial latitudes. Nevertheless, the possible sighting in Argentina (López-Lanús & López-Lanús 2011), as well as the record reported herein, indicate that Trindade Great Frigatebirds possibly undertake long-distance movements, as their counterparts do in the Indian Ocean. Therefore, observers should pay attention to frigatebirds in equatorial and subtropical Atlantic waters to eliminate the possibility of wandering by this species.

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Notes on bird breeding activity in a lowland forest in south-west Brazilian Amazonia

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SUMMARY.—We present data pertaining to the nesting of 12 species of forest birds, based on opportunistic observations made between April and November 2018 in Humaitá Forest Reserve, Acre, in south-west Brazilian Amazonia. For some of these species, knowledge of their reproduction is still little known, e.g. Blue-tailed Emerald *Chlorostilbon mellisugus*, White-shouldered Antshrike *Thamnophilus aethiops*, Black-spotted Bare-eye *Phlegopsis nigromaculata* and Pink-throated Becard *Pachyramphus minor*. The data presented here help to fill gaps in the reproductive biology of these species in an ornithologically poorly known region.

Understanding of the breeding biology of birds is necessary to inform successful conservation programmes, as well as to guide studies of ecology and evolution (Martin 2004). Although study of the biology of Neotropical birds has been increasing, there is still a great gap of knowledge, especially for species in Amazonia (del Hoyo *et al.* 2019). For many bird species in Amazonian Brazil, especially those with restricted geographic ranges or that are specialists of a specific habitat type, basic information concerning their reproduction is still unknown (del Hoyo *et al.* 2019). Here, we contribute novel data regarding the breeding of several Amazonian birds based on opportunistic observations made in a forest fragment in eastern Acre, Brazil.

Methods

Study area.—Humaitá Forest Reserve (HFR) (09°45'19"S, 67°40'18"W) is a forest fragment of approximately 2,000 ha administered by the Federal University of Acre, in the municipality of Porto Acre, south-west Brazilian Amazonia. The fragment comprises relatively open *terra firme* forest containing patches dominated by *Guadua* bamboos, and alluvial *várzea* forest (Acre 2010, IBGE 2012). Mean annual minimum and max. temperatures are *c.*24 to 26°C, respectively (Alvares *et al.* 2013). Mean annual rainfall is *c.*1,900 mm. The wet season extends from October to April, and the dry period from May to September (Duarte 2006).

Field work.—We made opportunistic observations of bird breeding behaviour between April and November 2018 usually using binoculars and, in some cases, documenting it photographically. Some of the nests found under construction, or with eggs or nestlings, were revisited to observe if they were still active. Estimates of height of nests above ground was made visually. When nests became inactive we collected the most accessible ones and took the following measurements: external height, depth of cup, external and internal diameter, wall thickness and mass, using digital callipers (accurate to 0.01 mm) and a digital scale (0.05 g), and these tools were also used to assess the size of some eggs. Nests collected were deposited in the collection of the Laboratory of Ornithology at the Federal University of Acre. We follow the species-level taxonomy and nomenclature of Gill & Donsker (2019). The description of types of nests follows the proposals for standardisation made by Simon & Pacheco (2005).

Species accounts

During the eight-month period, we observed 16 breeding events pertaining to 12 different species in HFR. Details follow.

RUDDY QUAIL-DOVE *Geotrygon montana*

On 21 April we found a nest with an adult incubating. It was constructed of dry leaves and some sticks. The nest was of the simple / platform type and was sited in the fork of a plant c.1.5 m above ground. The nest contained two all-white eggs (Fig. 1A). We did not revisit this nest subsequently. Another nest of this species in eastern Acre was found in Chico Mendes Extractive Reserve on 29 October 2011 by M. A. Freitas (<http://www.wikiaves.com/800524>). Our record coincides with the period in which the species is nestbuilding in the understorey of primary forest in southern Costa Rica (Skutch 1949). In central Amazonia, Stouffer & Bierregaard (1993) demonstrated that this species' abundance around Manaus is correlated to rainfall (annual peak in January–April) during the breeding season. Our nest was similar to those found by Skutch (1949) in Costa Rica, Stratford (2004) in central Amazonia, Greeney *et al.* (2004) and Cadena-Ortiz & Buitrón-Jurado (2015) in Ecuador, and Raine (2007) in south-east Peru.

OCELLATED POORWILL *Nyctiphrynus ocellatus*

On 22 August JML observed a female (Fig. 1B) and a nestling (Fig. 1C) on dry leaves beside a trail. As he approached the nestling, the female performed a distraction display, walking on the ground with its wings lowered and uttering an alarm vocalisation. Other nest records in Acre are in August–September (T. N. Melo, <http://www.wikiaves.com/1456885>; R. A. Plácido, <http://www.wikiaves.com/2260246>; E. Guilherme, <http://www.wikiaves.com/2693387>; D. P. Guimarães, <http://www.wikiaves.com/2862455>). Kirwan (2009) found a nest of this species in August in Mato Grosso. For South America as a whole, Robbins & Ridgely (1992) suggested that breeding is likely to occur in July–September. However, Raine (2007) reported finding an egg in September and a nestling in November, in Madre de Dios, south-east Peru. Anderson (2000) found that Ocellated Poorwill prefers to nest close to trails in the forest and in open areas, as was also true of the observation reported here.

PAURAQUE *Nyctidromus albicollis*

On 7 June and 1 August we found two nests on the forest floor. One had two eggs laid at the edge of a trail, while the other involved a single egg laid on dry leaves at the edge of the forest near the reserve buildings (Fig. 1D). The latter was predated a few days later and the first nest was not visited subsequently. The eggs were coloured beige with pale pink spots (Fig. 1E). In Acre, nest records of this species are in August–October (E. Guilherme; <http://www.wikiaves.com/1434453>, <http://www.wikiaves.com/2332636>). Oniki & Willis (1982) reported that the species breeds between May and December in central Amazonia. Kirwan (2009) recorded a nest with eggs in north-east Peru at the end of September and in the Atlantic Forest he found eggs and nestlings between September and February. Further, Alvarenga (1999) reported nesting in October and November in the Taubaté region of São Paulo state, also in the Atlantic Forest.

BLUE-TAILED EMERALD *Chlorostilbon mellisugus*

On 1 June JML found an incomplete nest (Fig. 1F) c.4 m above ground, over a small dry watercourse. He observed a female carrying material to the nest, which was constructed of tiny twigs, dry leaves and fibres on the outside. On the day of the observation he noticed



Figure 1. Breeding records of birds in Humaitá Forest Reserve, Porto Acre, Acre state, south-west Amazonian Brazil: (A) eggs of Ruddy Quail-dove *Geotrygon montana*; (B–C) female Ocellated Poorwill *Nyctiphrynus ocellatus* and nestling; (D–E) adult Pauraque *Nyctidromus albicollis* and egg; (F) female Blue-tailed Emerald *Chlorostilbon mellisugus* on nest; (G) female Little Woodpecker *Veniliornis passerinus* nestbuilding; and (H) nest and eggs of Plain-throated Antwren *Isleria hauxwelli* (A–C and F: Jônatas M. Lima; D, E, G and H: David P. Guimarães)

that the female was completing the nest. The nest was of the high cup / side type and was attached to a vertical branch (Fig. 1F). In northern Amazonia, F. D. Oliveira (<http://www.wikiaves.com/3134129>) found an active nest on 5 September 2018, differing only in that the external material lacked any dry leaves in the wall. In Venezuela, Thomas (1994) observed a cup-shaped nest with two eggs on 23 December 1982. It too was constructed by the female alone. Use of dry leaves on the outside of the nest has also been observed for Glittering-bellied Emerald *C. lucidus* in the Atlantic Forest of Minas Gerais (Lopes *et al.* 2013).

LITTLE WOODPECKER *Veniliornis passerinus*

On 26 April DPG observed a female building in a dead branch of a tree in forest dominated by *Guadua* bamboo, for >5 minutes (Fig. 1G). The female remained pecking at the edges of the opening and seemed to increase the size of the entrance to the nest. This species' breeding biology is still little known. Gussoni *et al.* (2009), found an active nest in the cavity of a Chinaberry tree *Melia azedarach* (Meliaceae) on 5 May in south-east Brazil. That nest had a vertical tunnel, apparently in the same form as the nest reported here.

PLAIN-THROATED ANTWRN *Iseria hauxwelli*

On 29 October DPG found a nest c.0.5 m above ground on a small shrub in forest (Fig. 1H). The nest was the low cup / fork form, constructed entirely of dry and thin malleable twigs. It contained two eggs, which were pale brown and covered with spots concentrated at the larger end (Fig. 1H). On the day of discovery, the male was incubating. When we revisited the nest a few days later, the eggs were no longer present. The nest was collected and measured as follows: external height and depth of cup 40 and 30 mm, respectively; external and internal diameter 68 and 40 mm, respectively; wall thickness 12.05 mm; and mass 3.54 g. The nest size, composition and support resembled nests of Leaden Antwren *Myrmotherula assimilis* in central-west Amazonia (Leite *et al.* 2016), and those of other *Myrmotherula* such as Amazonian Streaked Antwren *M. multostriata* and Cherrie's Antwren *M. cherriei* (Sick 1997, Chaparro-Herrera & Ruiz-Ovalle 2014).

WHITE-SHOULDERED ANTSHRIKE *Thamnophilus aethiops*

On 23 April we recorded two active nests both containing two eggs. They were constructed of fine twigs, small dry leaves, moss and rhizomorphic fungi on the outside (Fig. 2A). The nests were of the low cup / fork type and were inserted into the fork of support plants. Both nests were c.0.5 m above ground. One was at the edge of a trail 3 m from a treefall gap. The eggs were white with brown spots concentrated at the larger end (Fig. 2C). We sporadically followed one of these nests. Both sexes incubated (Fig. 2B). On 27 April at 08.45 h, the female was incubating and at c.12.40 h the male was doing so. On 12 May at 13.15 h, the male was again incubating and two hours later the female took over. After 12 May, we did not notice the pair at the nest and we verified that it had been abandoned. Both nests were collected and their mean measurements were as follows: external height and depth of cup 56 and 53.5 mm (SD = 0.14 and 0.77), respectively; external and internal diameter 72 and 55 mm (SD = 0.72 and 1.41), respectively; wall thickness 14.97 mm (SD = 0.10) and mass 6.68 g (SD = 0.16). The species' breeding biology is poorly known. In Brazil, nests of *T. a. incertus* have been found in October, November and February, a nest of *T. a. punctuliger* in July and one of *T. a. polionotus* in September (Zimmer & Isler 2019). On 10 September 2014, T. N. Melo (<http://www.wikiaves.com/1462017>) documented a female incubating two eggs at the edge of a track in HFR. The characteristics of the nest, colour and shape of the eggs, and parental care by both sexes are similar to those of other species of *Thamnophilus*, not only in Amazonia



Figure 2. Breeding records of birds in Humaitá Forest Reserve, Porto Acre, Acre state, south-west Amazonian Brazil: (A–C) nest, male and eggs of White-shouldered Antshrike *Thamnophilus aethiops*; (D–F) nest, eggs and nestling of Black-spotted Bare-eye *Phlegopsis nigromaculata*; (G–H) nest of Ruddy-tailed Flycatcher *Terenotriccus erythrurus* and adult carrying nesting material; (I) female Pink-throated Becard *Pachyramphus minor* perched above nest; (J) nest of Olive Oropendola *Psarocolius bifasciatus*; (K) female Silver-beaked Tanager *Ramphocelus carbo* with nesting material (B, C, G, H and J: Jônatas M. Lima; A, D–F, I and K: David P. Guimarães)

but also in the Atlantic Forest and Panama (Skutch 1984, Raine 2007, Zyskowski 2008, Silva & Carmo 2015).

BLACK-SPOTTED BARE-EYE *Phlegopsis nigromaculata*

On 11 November JML found an active nest with two eggs in the cavity of a dead tree trunk with an opening c.1 m above ground (Fig. 2D). The base of the nest was 13 cm wide and 20 cm from the entrance. The nest had the shape of a small shallow 'basket' of dried bamboo leaves (*Guadua* sp.) and fine twigs. The eggs were stained dark pink with predominantly purple linear markings (Fig. 2E) and the following dimensions: 25.4 × 20.05 mm and 25.4 × 20.5 mm, mass 5.2 and 5.6 g, respectively. After 15 days, we observed just one nestling c.2 days old (Fig. 2F). The nestling, still with its eyes closed, had completely dark naked skin and whitish labial commissures. After four days we found the nestling dead in the nest and covered by ants. Also in Acre, on 30 May 2007 E. Guilherme (<http://www.wikiaves.com/802797>) documented a nest with two eggs in a cavity at the base of a dead palm (*cf. Attalea* sp.) with the same characteristics as that we found in HFR, that reported by Leite *et al.* (2018) in eastern Amazonia, in late January, and the nest found in a bamboo stalk by Raine (2007) at Tambopata, Peru, on 20 March 2001. Our nest is also similar to those found in northern Amazonia (Cadena *et al.* 2000, Hill & Greeney 2000) and the eggs resembled those reported by Cadena *et al.* (2000) in Colombia, by Hill & Greeney (2000) in Ecuador, and by Leite *et al.* (2018). The dark skin and whitish labial commissure of the nestling match the report by Cadena *et al.* (2000).

RUDDY-TAILED FLYCATCHER *Terenotriccus erythrurus*

On 7 August JML found a nest being completed beside a trail (Fig. 2G). Nearby, he observed an individual with material in its bill (Fig. 2H). The nest was closed, constructed of soft fibres, and suspended from the branch of a supporting plant c.1.7 m above ground. We did not collect or subsequently follow the nest's progress. Also in eastern Acre, T. N. Melo (<http://www.wikiaves.com/1821127>) photographed an adult carrying nesting material on 26 August 2015. The nest was spherical and was sited on a palm frond c.1.5 m above ground. Ruddy-tailed Flycatcher nest records date from September and November in Pará and Rondônia, respectively (Kirwan 2009). In Costa Rica, the species' breeding season extends from March to May (Stiles & Skutch 1989). Our record in HFR coincides with the season reported by Hilty & Brown (1986) in north-west Colombia, from February to August. The nest in HFR was similar to Skutch's (1960) description from Panama, where he found nests 1.5–4.0 m above ground between March and May.

PINK-THROATED BECARD *Pachyramphus minor*

On 18 October DPG found an active nest constructed at the tip of a branch 10 m above ground (Fig. 2I). The nest was bound with fibres at the attachment with the supporting tree, constructed of coarser fibres and was of the closed / retort / pensile type (Fig. 2I). The pair was constantly visiting the nest, possibly feeding young. In central Amazonia, on 3 March 2014, R. E. Czaban (<http://www.wikiaves.com/1276432>) recorded a pair constructing a nest c.10 m above ground in an isolated tree.

OLIVE OROPENDOLA *Psarocolius bifasciatus*

On May 26 JML observed an adult feeding a young. At the site, there were at least three closed / retort / pensile nests suspended from branches c.25 m above ground (Fig. 2J) on an emergent tree, in forest dominated by bamboos. In Acre, L. M. Brito (<http://www.wikiaves.com/2280810>) recorded a male building a nest on 10 September 2016. The nests of Olive Oropendola can reach 2 m long (Sick 1997). According to Baksh (2012), nesting in the canopy and colony organisation increase security in the breeding season.

SILVER-BEAKED TANAGER *Ramphocelus carbo*

On 28 September DPG photographed a female carrying material (Fig. 2K) to a nest concealed in bushes c.1.5 m above ground in an open area with human activity near the reserve buildings. E. P. Lima (<http://www.wikiaves.com/228509>) and A. Machado (<http://www.wikiaves.com/2398499>) recorded nests each with two eggs on 8 September 2010 and 15 December 2015, in Acre and Rondônia, respectively. Lopes *et al.* (2013) found nests on 20 and 22 September in eastern Amazonia. Sick (1997) reported that the female builds in dense shrubs as we observed in HFR. The height of the nest in HFR accords with the reports by Osuna (2017) and Lopes *et al.* (2013) who found nests between 0.6 and 2.5 m above ground. This species is well adapted to open environments and human activity, and will nest in urban areas and use non-native plants (Almeida *et al.* 2012).

The available records are still insufficient to accurately determine the seasonality and duration of the breeding period of the species listed. However, they are represent initial data that help to fill gaps in our knowledge for these species in Amazonia.

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The taxonomy of *Tanygnathus sumatranus*

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SUMMARY.—Philippine taxa currently assigned to Blue-backed, Azure-rumped or Müller's Parrot *Tanygnathus sumatranus* are distinctive both morphologically (larger bill, red vs. pale yellow iris, royal blue vs. glossy turquoise-blue rump, paler green head and duller green underparts; and males having darker green mantles and no blue on the carpals and scapulars) and genetically (as distinct from Indonesian *T. sumatranus* as *T. lucionensis* is from *T. megalorhynchus*). We therefore propose *T. everetti* (with subspecies *burbidgii* and *freeri*; race *duponti* synonymised with nominate) to be elevated to species rank with the name Blue-backed Parrot, leaving Indonesian *T. sumatranus* (with subspecies *sangirensis*) as Azure-rumped Parrot. The taxonomic status of *T. e. burbidgii* (Sulu Islands) and *T. s. sangirensis* (Talaud Islands), both notably larger than their respective nominates, deserves study.

Blue-backed, Azure-rumped or Müller's Parrot *Tanygnathus sumatranus* is distributed in five or six subspecies across multiple islands in the Philippines and Sulawesi (plus adjacent archipelagos), Indonesia. These break down as (in the Philippines): *T. s. duponti* on Luzon, *T. s. freeri* on Polillo, *T. s. everetti* on Panay, Negros, Samar, Leyte and Mindanao, *T. s. burbidgii* on the Sulu Islands, and (in Indonesia) *T. s. sangirensis* (Talaud Islands) and *T. s. sumatranus* (Sulawesi and its immediate satellites, the Togian Islands, Banggai Islands and Sula Islands) (Forshaw 1973, Dickinson *et al.* 1991, del Hoyo & Collar 2014, Clements *et al.* 2018); however, some authorities consider *sangirensis* to be a synonym of *sumatranus* (White & Bruce 1986, Dickinson & Remsen 2013, Gill & Donsker 2018).

The distinctiveness of the Philippine taxa from the Indonesian taxa appears to have gone largely unnoticed. Forshaw (1973) illustrated only nominate *sumatranus*, while the portraits of nominate *sumatranus* and *everetti* in Collar (1997) and del Hoyo & Collar (2014) miss some key differences. Those in Juniper & Parr (1997) are rather better but not wholly accurate; the best indication is in Forshaw & Knight (2010). Given that there appears to be a suite of consistent characters separating *duponti*, *freeri*, *everetti* and *burbidgii* from *sangirensis* and *sumatranus*, a more detailed consideration of the evidence is warranted.

Methods

Morphological study.—NJC examined and measured a total of 61 male specimens representing five of the six taxa preserved in the American Museum of Natural History, New York (AMNH), Muséum National d'Histoire Naturelle, Paris (MNHN), Museum für Tierkunde, Dresden (MTD), Natural History Museum, Tring (NHMUK), National Museum of Natural History, Washington DC (USNM) and Zoologisches Museum Berlin (ZMB). The sample involved two *duponti* (both in AMNH), eight *everetti* (four in AMNH, two in NHMUK, one in USNM, one in ZMB), 15 *burbidgii* (four in AMNH, one in MNHN, one in MTD, five in NHMUK, two in USNM, two in ZMB), nine *sangirensis* (two in AMNH, three in MTD, three in NHMUK, one in USNM), 22 *sumatranus* from Sulawesi (all in USNM), plus

four from the Peleng and Banggai Islands (two in AMNH, two in MTD) and four from the Sula Islands (all in AMNH).

The differences by which the subspecies *duponti* was established were not apparent (even though one of the AMNH specimens examined was its type), and we doubt the validity of this taxon; so the two birds from Luzon are lumped in the sample for *everetti*. We were unable to examine specimens representing the insular form *freeri*, but do not regard this as an obstacle to the analysis (four specimens of *freeri* held in the Philippines National Museum, Manila, probably the only museum material available, proved much larger than six specimens of *everetti* but differed only slightly in three plumage characters: Salomonsen 1952). Mensural data were taken from males in mm, using digital callipers accurate to two decimal points for bill from edge of nareal skin to tip, and long rulers for wing (curved) and tail (from point of insertion to tip). The Peleng / Banggai and Sula birds proved mensurally to be mildly untypical and are hence shown independently in Table 2 for interest, but they were included in the sample of *sumatranus* in the analysis of relationships between Indonesian and Philippine taxa.

Iris colour proved to be a significant issue in this case. The potential relevance of this was first noted by TA in 2006 when visiting a private collection of parrots, and he continued to gather evidence both in the field and from photographs and local testimony for as many taxa as possible (*sumatranus*, *sangirensis*, '*duponti*' and *everetti*). For the preparation of this manuscript we put out a call for more photographs from the field (notably for *burbidgii*) and in captivity, and made use of the material supplied in the analysis which follows.

To gauge the degree of difference between taxa in voice, plumage and dimensions we made use of the system of scoring proposed by Tobias *et al.* (2010), in which an exceptional character (radically different coloration, pattern, size or sound) scores 4, a major character (pronounced difference in body part colour or pattern, measurement or sound) 3, medium character (clear difference, e.g. a distinct hue rather than different colour) 2, and minor character (weak difference, e.g. a change in shade) 1; a threshold of 7 is set to allow species status, species status cannot be triggered by minor characters alone, and only three plumage characters, two vocal characters, two biometric characters (assessed for effect size using Cohen's *d* where 0.2–2.0 is minor, 2–5 medium and 5–10 major) and one behavioural or ecological character (allowed 1) may be counted. The notation 'ns' with a score in square brackets equates to 'no score' because of the restriction on the number of characters, but the disallowed score is provided to indicate the further degree of difference.

Molecular study.—Blood samples were obtained from 14 specimens representing three species of *Tanygnathus*, eight from Loro Parque Foundation (LPF; Tenerife, Spain), two from Weltvogelpark Walsrode (Germany), one from Talarak Foundation (Philippines), one from Louisiana State University Museum of Natural Science, Baton Rouge (USA), and one from the Institute of Pharmacy and Molecular Biotechnology, Heidelberg University (Germany), supplemented by a GenBank sample of a specimen held in the Indonesian Institute of Sciences, Bogor. These samples consisted of five *T. lucionensis*, three *T. megalorhynchos* and six *T. sumatranus* (two from the Philippines, four from Indonesia; all origins are indicated in Table 1). Some of these were already available on GenBank, having been obtained from LPF for a thesis (Braun 2014), but they involved no *T. sumatranus* material from the Philippines and were in any case inadequate on their own. For the samples from two living *T. s. everetti* at LPF and the Talarak Foundation respectively we verified their taxonomic identity through photographs and confirmed the former by reference to its CITES documentation.

DNA was isolated from blood samples (stored in a modified EDTA buffer at –20°C, in 80% ethanol, or dried on filter paper). Total DNA was isolated using standard proteinase K (Merck, Darmstadt) and phenol / chloroform procedures (Wink & Sauer-Gürth 2004, Wink

TABLE 1

Samples used in the molecular analysis in this paper, with scientific names, GenBank accession numbers, original voucher numbers and origins (LPF: Loro Parque Foundation, Tenerife, Spain; WVPW: Weltvogelpark Walsrode, Germany; TF: Talarak Foundation, Philippines; LSUMZ: Louisiana State University Museum of Natural Science, Baton Rouge, USA; LIPI: Indonesian Institute of Sciences, Bogor, Indonesia; IPMB: Institute of Pharmacy and Molecular Biotechnology, Department of Biology, Heidelberg Univ., Germany; PH = Philippines; ID = Indonesia; capt., o.u. = captivity, origin unknown). The specimen number in column 3 corresponds to the specimen number in Table 4. ¹ Specimen from Tanahjampea. ² Specimen from Sulawesi. Sample numbers correspond to those in Tables 3 and 4.

Scientific name	GenBank no.	No.	Voucher no.	Source of sample
<i>Tanygnathus lucionensis</i>	MK689343	1	35185	LPF (PH)
<i>Tanygnathus lucionensis</i>	MK689344	2	35188	LPF (PH)
<i>Tanygnathus lucionensis</i>	KM611480	3	36539	LSUMZ (capt., o.u.)
<i>Tanygnathus lucionensis</i>	MK689348	4	53885	WVPW (capt., o.u.)
<i>Tanygnathus lucionensis</i>	MK689349	5	53890	WVPW (capt., o.u.)
<i>Tanygnathus megalorhynchos</i>	KM372555	6	35186	LPF (ID)
<i>Tanygnathus megalorhynchos</i>	KM372556	7	35187	LPF (ID)
<i>Tanygnathus megalorhynchos</i>	MK689351	8	85365	IPMB (ID ¹)
<i>Tanygnathus sumatranus</i>	KM372557	9	35189	LPF (ID)
<i>Tanygnathus sumatranus</i>	MK689345	10	35190	LPF (ID)
<i>Tanygnathus sumatranus</i>	MK689346	11	35191	LPF (ID)
<i>Tanygnathus sumatranus</i>	AB177972	12	—	LIPI (ID ²)
<i>Tanygnathus sumatranus</i>	not yet available	13	78067-20190515n	LPF (PH)
<i>Tanygnathus sumatranus</i>	not yet available	14	96205	TF (PH)

TABLE 2

Measurements of males of four taxa in the *Tanygnathus sumatranus* complex, with the doubtfully valid *duponti* combined with *everetti*. Data for the Banggai and Sula Islands are kept separate simply to illustrate their slightly anomalous measurements, but they were included in the sample for *sumatranus* in the analysis.

	<i>n</i>	bill	wing	tail
<i>everetti</i>	10	33.3 ± 1.24	196.1 ± 6.97	137.3 ± 10.12
<i>burbidgii</i>	14	35.1 ± 2.04	215.6 ± 4.53	154.2 ± 9.46
<i>sangirensis</i>	9	31.8 ± 1.71	213.5 ± 6.64	136.7 ± 2.94
<i>sumatranus</i> (Sulawesi)	22	31.6 ± 1.3	199.4 ± 4.94	123.4 ± 4.19
<i>sumatranus</i> (Peleng / Banggai)	4	31.4 ± 0.98	190.5 ± 5.97	118.5 ± 2.89
<i>sumatranus</i> (Sula Islands)	4	33.1 ± 1.01	194.0 ± 9.76	120.8 ± 6.75

et al. 2009). The mitochondrial cytochrome *b* gene (> 900 nucleotides; nt) was selected and amplified as an informative marker gene. It has been used by MW before for a phylogenetic reconstruction of many other bird taxa, including parrots (Kraus & Wink 2015). The PCR (polymerase chain reaction) amplifications were performed in 50 µl reaction volumes containing 1 × PCR buffer (Bioron, Ludwigshafen), 100 µM dNTPs, 0.2 units of *Taq* DNA polymerase (Bioron, Ludwigshafen), 200 ng of DNA and 5 pmol of primers for cytochrome *b* (as described in Arndt & Wink 2017). Thermal cycling involved five minutes at 94°C, followed by 35 cycles of 40 seconds at 94°C, 40 seconds at 52°C, one minute at 72°C and a final extension at 72°C for ten minutes. Products were precipitated with 4 M NH₄Ac and ethanol and centrifuged for 15 minutes (13,000 rpm). For sequencing, the ABI 3730

automated capillary sequencer (Applied Biosystems, CA, USA) with the ABI Prism Big Dye Terminator Cycle Sequencing Ready Reaction Kit 3.1 (carried out by STARSEQ GmbH, Mainz, Germany) was employed. The same primers were used as for the initial PCR amplifications.

For phylogenetic reconstructions, the nucleotide sequences were aligned manually with BioEdit version 7.0.9.0. No internal stop codons or frame-shifts were observed in the sequences, which were translated entirely by using the chicken *Gallus* mitochondrial code. Phylogenetic trees were reconstructed using the Maximum Likelihood (ML) algorithm in MEGA version 7 (Kumar *et al.* 2016) with related parrot species (three *Eclectus* Parrot *Eclectus roratus*, one Western Corella *Cacatua pastinator*, one Yellow-crested Cockatoo *C. sulphurea*) as outgroups. Initial tree(s) for the heuristic search were obtained automatically by applying Neighbor-Join and BioNJ algorithms to a matrix of pairwise distances estimated using the Maximum Composite Likelihood (MCL) approach, and then selecting the topology with superior log likelihood value. A discrete Gamma distribution was used to model evolutionary rate differences among sites (five categories [+G, parameter = 7.5450]). The rate variation model allowed for some sites to be evolutionarily invariable ([+I], 52.49% sites). The tree is drawn to scale, with branch lengths measured in the number of substitutions per site. The analysis involved 19 nucleotide sequences (14 ingroup and five outgroup taxa). Codon positions included were 1st+2nd+3rd. There were altogether 1,140 positions in the final dataset.

Sequence data have been submitted to GenBank (accession numbers listed in Table 1).

Results

Morphological evidence.—Photographs from the field, including from the Sulu Islands (taxon *burbidgii*) repeatedly confirmed that Philippine birds possess red irides and Indonesian birds yellowish-white irides. We were impressed to note that two engravings made in the 19th century by J. G. Keulemans to illustrate Salvadori (1891)—both currently viewable on the Wikipedia online entry for Blue-backed Parrot—depict *everetti* and *burbidgii* with red eyes, presumably because live specimens were in London Zoo at the time. We were unable, however, to find photographs from the Banggai Islands, from which the subspecies *incognitus* was described by Eck (1976) on the basis of its brown or grey-brown irides. This form was not admitted by White & Bruce (1986) because of the collector's unreliable practices in relation to iris colour annotation.

Accepting that iris colour is a consistent difference, we find that the Philippine forms *everetti* (with '*duponti*') and *burbidgii* differ from Indonesian nominate *sumatranus* and *sangirensis* in at least seven phenotypic characters, which we list here followed by our 'Tobias' score for their perceived degree of difference. In both sexes Philippine forms differ by their larger bills (see Table 2; effect size of *everetti* vs. *sangirensis* 1.62 and vs. *sumatranus* 1.15; effect size of *burbidgii* vs. *sangirensis* 1.75 and vs. *sumatranus* 2.02; as *burbidgii* is here treated as conspecific with *everetti*, the lower values for *everetti* must be considered, hence score 1); blood-red or orange-red vs. yellowish-white irides (3); pale matt royal blue in place of slightly glossy turquoise-blue lower back and rump (2); paler green head (ns[1]); and duller green underparts (ns[1]). Moreover, in males the Philippine forms further differ by their absence of blue in the carpal feathers and scapulars (2); and much darker green mantle (ns[2]). Philippine birds thus reach a total of 8 under the Tobias criteria, and achieve species rank as a consequence.

The difference in wing length between *everetti* and *burbidgii* (Table 2) yields an effect size of 3.32. The difference in tail length between nominate *sumatranus* and *sangirensis* (Table 2) yields an effect size of 3.70. Both these findings point to the distinctness and validity of the

TABLE 3

Tanygnathus parrots: informative sites in the nucleotide dataset. Dots indicate that the base is identical to that in the first line. This table only includes the sites which were sequenced in all individuals; six informative sites were excluded here, because of missing data in a few sequences.

# <i>Tanygnathus lucionensis</i> _35185_MK689343_CAPT	TGCATTTC	TCCCATACT	CGTTCAGTGT	CGCTCTCAAA	GTACAAAACC	GGTCCGGAAA	CTCAA								
# <i>Tanygnathus lucionensis</i> _35188_MK689344_CAPT	..C.....								
# <i>Tanygnathus lucionensis</i> _36539_KM611480_CAPT	A.C.....								
# <i>Tanygnathus lucionensis</i> _53885_MK689348_CAPT	A.C.....								
# <i>Tanygnathus lucionensis</i> _53890_MK689349_CAPT	A.C.....								
# <i>Tanygnathus megalorhynchos</i> _35186_KM372555_CAPT	A.C....CT.	C...TGC.	..C..A.A.CT.G....TA..G.	T.G...								
# <i>Tanygnathus megalorhynchos</i> _35187_KM372556_CAPT	A.C....CT.	C...TGC.	..C..A.A.CT.G....TA..G.	T.G...								
# <i>Tanygnathus megalorhynchos</i> _85365_MK689351_TAN_IND	A.C....C..	CT..TGC.	..C..A.A.CT.G....TA..G.	T.G...								
# <i>Tanygnathus sumatranus</i> _35189_KM372557_CAPT	ATC.....C.	CT..TGC.	..C..A.A.CT.G....TA..G.	T.G...								
# <i>Tanygnathus sumatranus</i> _35190_MK689345_CAPT	A.C....C..	CT..TGC.	..C..A.A.CT.G....TA..G.	T.G...								
# <i>Tanygnathus sumatranus</i> _35191_MK689346_CAPT	ATC.....C.	CT..TGC.	..C..A.A.CT.G....TA..G.	T.G...								
# <i>Tanygnathus sumatranus</i> _AB177962_SUL_IND	ATC..CC...	CT..TGCCTC	AACCTGA..C	T.A..C..CTG..G	A.C..G..G....	CACCTA..G..G	T..AG.								
# <i>Tanygnathus sumatranus</i> _78067-20190515n	A..CTG....T	C..TT.....	C..AACC..AC..	..A..TCTGGG	..CT....GT..	..ACTT..G..G	T..CG..								
# <i>Tanygnathus sumatranus</i> _96205	A..CTG....T	C..TT.....	C..AACC..AC..	..A..TCTGGG	..CT....GGT..	..ACTT..G..G	T..CG..								

TABLE 4

Tanygnathus parrots: estimates of evolutionary divergence (*p* distance) between sequences. The number of base differences per site from between sequences are shown. The analysis involved 14 nucleotide sequences. Codon positions included were 1st+2nd+3rd+Noncoding. All ambiguous positions were removed for each sequence pair. There were a total of 1,140 positions in the final dataset. Specimen number (across top and left column) corresponds to specimen number in Table 3.

[1] # <i>Tanygnathus lucionensis</i> _35185_MK689343_CAPT	1	2	3	4	5	6	7	8	9	10	11	12	13	14
[2] # <i>Tanygnathus lucionensis</i> _35188_MK689344_CAPT	-	0.002	-	-	-	-	-	-	-	-	-	-	-	-
[3] # <i>Tanygnathus lucionensis</i> _36539_KM611480_CAPT	0.005	0.003	-	-	-	-	-	-	-	-	-	-	-	-
[4] # <i>Tanygnathus lucionensis</i> _53885_MK689348_CAPT	0.005	0.003	0.003	-	-	-	-	-	-	-	-	-	-	-
[5] # <i>Tanygnathus lucionensis</i> _53890_MK689349_CAPT	0.005	0.003	0.003	0.000	-	-	-	-	-	-	-	-	-	-
[6] # <i>Tanygnathus megalorhynchos</i> _35186_KM372555_CAPT	0.033	0.031	0.031	0.031	0.031	-	-	-	-	-	-	-	-	-
[7] # <i>Tanygnathus megalorhynchos</i> _35187_KM372556_CAPT	0.033	0.031	0.031	0.031	0.031	0.000	-	-	-	-	-	-	-	-
[8] # <i>Tanygnathus megalorhynchos</i> _85365_MK689351_TAN_IND	0.033	0.031	0.031	0.031	0.031	0.000	0.000	-	-	-	-	-	-	-
[9] # <i>Tanygnathus sumatranus</i> _35189_KM372557_CAPT	0.058	0.057	0.057	0.057	0.055	0.055	0.055	0.055	-	-	-	-	-	-
[10] # <i>Tanygnathus sumatranus</i> _35190_MK689345_CAPT	0.057	0.055	0.055	0.055	0.055	0.055	0.053	0.053	0.053	-	-	-	-	-
[11] # <i>Tanygnathus sumatranus</i> _35191_MK689346_CAPT	0.058	0.057	0.057	0.057	0.057	0.055	0.055	0.055	0.055	0.000	-	-	-	-
[12] # <i>Tanygnathus sumatranus</i> _AB177962_SUL_IND	0.074	0.072	0.072	0.072	0.072	0.067	0.067	0.067	0.067	0.015	0.017	0.015	-	-
[13] # <i>Tanygnathus sumatranus</i> _78067-20190515n	0.060	0.058	0.058	0.058	0.058	0.058	0.062	0.062	0.062	0.041	0.039	0.041	0.057	-
[14] # <i>Tanygnathus sumatranus</i> _96205	0.062	0.060	0.060	0.060	0.060	0.060	0.063	0.063	0.063	0.043	0.041	0.043	0.058	0.002



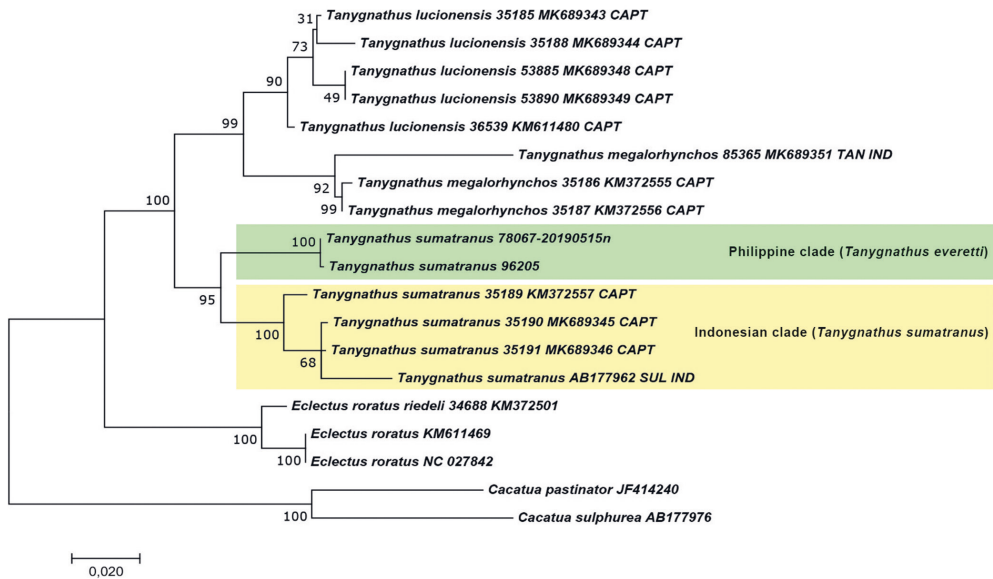


Figure 1. *Tanygnathus* parrots phylogenetic tree. CAPT = captive live bird. IND = Indonesia as the known source. TAN = Tanahjampea. SUL = Sulawesi. Evolutionary history was inferred by using the Maximum Likelihood method based on the General Time Reversible model (Nei & Kumar 2000). The tree with the highest log likelihood (−3897.11) is shown. The percentage of trees in which the associated taxa clustered together is shown next to the branches. Numbers at the branches are bootstrap values (in %) from 500 replications.

forms *burbidgii* and *sangirensis*; *burbidgii* is larger in all dimensions than any other taxon except the little-known *freeri* (see below), while *sangirensis* almost matches it for wing length and almost matches *everetti* for tail length while exactly matching nominate *sumatranus* for bill length. It is also worth noting that the four Peleng and Banggai birds proved to have shorter wings and tails than any other taxa, and that the four Sula birds had larger bills than either *sumatranus* or *sangirensis* (Table 2).

Molecular evidence.—The dataset consisting of all 14 samples of the genus *Tanygnathus* had 224 variable and 106 phylogenetically informative sites (all latter in Table 3). Genetic distances (p distance) are tabulated in Table 4. The phylogeny was reconstructed using Maximum Likelihood (Fig. 1). Birds identified as *T. lucionensis*, *T. megalorhynchos* and Indonesian *T. sumatranus* formed separate clusters within a monophyletic *Tanygnathus* clade (bootstrap support 99% and 95%). The position of the two Philippine birds within the *T. sumatranus* cluster clearly indicates their genetic distinctiveness (as great as that between *T. lucionensis* and *T. megalorhynchos*) and is consistent with evidence above that populations representing *T. sumatranus* in the Philippines in reality constitute a distinct species.

Discussion

On the basis of these results, in which phenotypic and genetic evidence point independently to the same conclusion, we judge that Philippine taxa group together as one species under the name *T. everetti* and Indonesian taxa as another under the name *T. sumatranus* (Fig. 2). Because ‘Azure-rumped Parrot’ *roughly* reflects the colour of

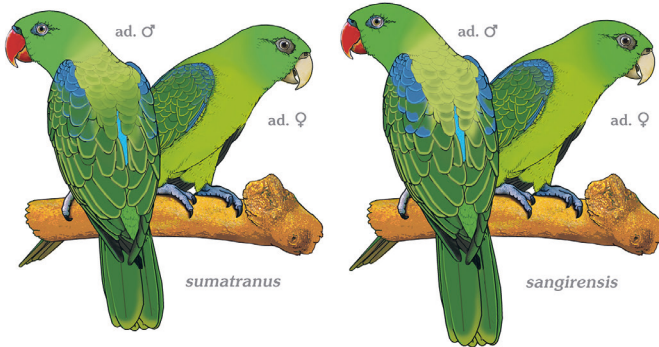
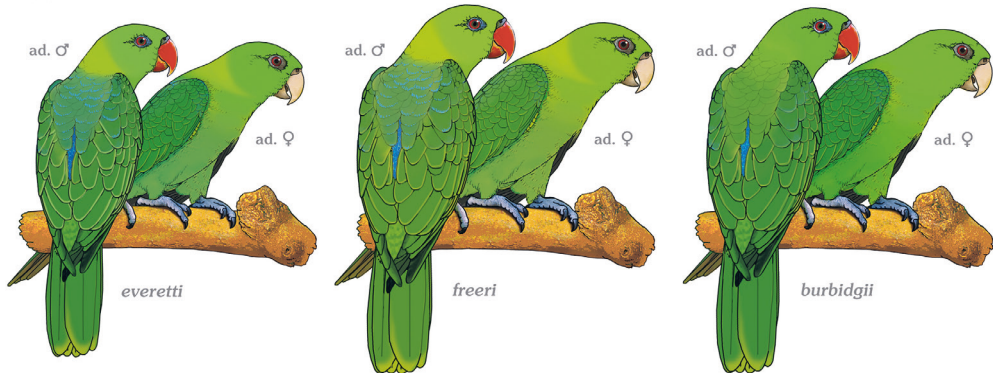
Tanygnathus sumatranus* – Azure-rumped Parrot**Tanygnathus everetti* – Blue-backed Parrot**

Figure 2. Overview of the plumage patterns of all taxa of the *Tanygnathus sumatranus* and *Tanygnathus everetti* complex (Thomas Arndt)

the Sulawesi populations and ‘Blue-backed Parrot’ *roughly* reflects that of those in the Philippines, we suggest that these two names, which hitherto have been used as alternatives for the broader species, be exclusively assigned henceforth to *T. everetti* (Blue-backed Parrot) and *T. sumatranus* (Azure-rumped Parrot).

The distinction between the two species would be more clear-cut were it not for the fact that the two forms with the largest ranges, *T. e. everetti* and *T. s. sumatranus*, each have considerably larger subspecies on small outlying island groups. Consequently the longer wing of *T. s. sangirensis* comes close to matching that of *T. e. burbidgii*, while its longer tail is almost exactly the same as that of *T. e. everetti*. The greater size of *sangirensis* than nominate *sumatranus* (which should ensure its reinstatement as a valid taxon by those who have synonymised it—see Introduction, and Table 2) and of *burbidgii* than nominate *everetti* even raises the issue of whether they might qualify for species rank themselves. However, in plumage *sangirensis* is very close to *sumatranus*, and its classification as a species would seem only to be likely under a fairly extreme application of the phylogenetic species concept. On the other hand, *burbidgii* differs, as noted in its original description, by its slightly yellower green head (Tobias score 1) and lack of blue edges to the mantle feathers (1) (Sharpe 1879), plus a rather weaker pale yellowish edging to the wing-coverts, which thus appear less ‘scaled’ (perhaps 1; greater sample needed); with an effect size of 3.32 for wing length (score 2) these characters accumulate a Tobias score of 5, which indicates a

considerable degree of differentiation. It is also worth noting that the form *freeri* appears to be even larger than *burbidgii*, with Salomonsen (1952) reporting two males and two females having wing 227, 237, 217, 228 mm and tail 157, 174, 159, 165 mm (means 227.3 and 163.8 mm respectively vs. 215.6 and 154.2 mm in *burbidgii* in Table 2). Certainly all three small-island forms merit further taxonomic study—tissue sampling from museum material for additional genetic work is clearly called for—and conservation in their own right; and the differences between *burbidgii* and *everetti* particularly need to be remembered if, as seems likely, *ex situ* endeavours commence in the light of growing evidence, being gathered and reviewed elsewhere, of the newly split species' extreme rarity.

The sample of Peleng / Banggai and Sula birds is far too small for interpretation, but the relatively short wings and tails of the former and the relatively large bills of the latter are worth recalling if the opportunity ever arises to review their taxonomic status. However, any move to reinstate *incognitus* for Peleng / Banggai birds would need to take into account the improbability of the leapfrog pattern in which Sula birds remain with nominate *sumatranus*. Some individuals from all these islands and from Sangihe had the turquoise rump showing touches of the blue found in Philippine taxa, but in other respects their plumages aligned with Sulawesi birds.

The biogeographic affinities between the Philippines and Sulawesi (with or without varying parts of western Wallacea) are indicated in ornithology by the genus *Prioniturus* (involving two dispersal events: Schweizer *et al.* 2012) and by the species Purple Needletail *Hirundapus celebensis* and Citrine Canary-flycatcher *Culicicapa helianthea*. More broadly, Philippine Scrubfowl *Megapodius cumingii* also reaches the islands off northern Borneo while Barred Rail *Hypotaenidia torquata* leapfrogs the Moluccas to the West Papuan islands and north-west New Guinea. Further such correspondence is found in the species pairs Pink-bellied *Ducula poliocephala* and White-bellied Imperial Pigeons *D. forsteni* and the recently split Philippine *Pernis steerei* and Sulawesi Honey-buzzards *P. celebensis* (differences under the Tobias criteria scored in del Hoyo & Collar 2014). The split here of *Tanygnathus sumatranus everetti* may suggest that a fresh consideration of the taxonomic standing of the needletail (usually regarded as monotypic), scrubfowl, rail and canary-flycatcher might result in new arrangements.

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Various *Gallus varius* hybrids: variation in junglefowl hybrids and Darwin's interest in them

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<http://zoobank.org/urn:lsid:zoobank.org:pub:3C87476B-79B4-443D-AAE2-2AF37CB8AC8F>

SUMMARY.—Hybrids between Green Junglefowl *Gallus varius* and domestic fowl *G. gallus domesticus* confused several 19th-century ornithologists. The plumage of these hybrids is so unlike the colours and patterns of either of the parent species that they were considered to be distinct species: *G. aeneus* Temminck, 1825; *G. temminckii* Gray, 1849; and *G. violaceus* Kelsall, 1891. Darwin wanted to understand if *G. aeneus* and *G. temminckii* were hybrids or species, as part of his research on the origin of the domestic chicken. His view was that all domesticated fowl have a single wild ancestor, Red Junglefowl *G. gallus* (formerly *G. bankiva*). A hybrid specimen now present in the bird collection of the Natural History Museum at Tring played an important role in Darwin's reasoning and, although the conclusions he drew from this specimen were incorrect, his single-ancestor origin theory for domesticated fowl stands.

'These hybrids were at one time thought to be specifically distinct, and were named *G. aeneus*. Mr. Blyth and others believe that the *G. Temminckii* is a similar hybrid' (Darwin 1868a: 234–235).

In general, junglefowl species of the genus *Gallus* have a rather confused nomenclatural history. Ceylon Junglefowl *G. lafayettii*, for example, was named three times due both to its sexual dimorphism (males and females were each described as separate species) and to natural variation within the species (van Grouw *et al.* 2017). Other reasons why species were named more than once was that, historically, scientists were less likely to be aware of one another's work or might simply ignore prior descriptions and rename species.

George Kearsley Shaw (1751–1813) was the first to describe and name Green Junglefowl *G. varius* (Fig. 1), which is endemic to Indonesia. The origin of the species, which he called Variegated Pheasant *Phasianus varius*, was unknown to Shaw, but he thought it was probably an Indian bird (Shaw 1798). Whether Coenraad Jacob Temminck (1778–1858), the first director of the State Museum of Natural History (now Naturalis Biodiversity Centre in Leiden, was aware of Shaw's work is unknown, but he subsequently named and described the species both from specimens he had seen in the Paris museum, collected on Java by the French botanist and ornithologist Jean-Baptiste Leschenault de La Tour (1773–1826), and from those in his private collection which he received from the governor of Java (Temminck's own collection helped found the Leiden museum). Temminck named the species *G. furcatus* (from Latin furca: two-pronged fork), 'Cock with the forked tail' (Temminck 1807: 1807, 1813: 261–266, see Fig. 2). Thomas Horsfield (1773–1859) in turn named the species *G. Javanicus*, based on a specimen at that time in the Museum of the Honourable East India Company in London (Fig. 3), despite referring to Shaw's *varius* (Horsfield 1822). Although vols. 1–2 of the *Manuel d'ornithologie* (Temminck 1820a,b) had been Horsfield's guide to most of the genera in his 1822 publication, it nevertheless appears that he was unaware of the



Figure 1. Pl. 353, Variegated Pheasant *Phasianus varius* in Shaw 1798 (Harry Taylor, © Natural History Museum, London)



Figure 2. Lithograph of *Gallus furcatus*, 'ayam-alas', pl. 483 in Temminck's *Planches coloriées* (1829); the lithograph was after a drawing by the French natural history illustrator Nicolas Huet le Jeune (1770–1830) (Harry Taylor, © Natural History Museum, London)



Figure 3 (above). Type specimen of *Gallus javanicus* Horsfield, 1822 (NHMUK Vel.Cat. 34.2a), collected in Java by Horsfield between 1811 and 1817, during which period Java formed part of British possessions in Indonesia (Harry Taylor, © Natural History Museum, London)

Figure 4 (left). Bekisar; a hybrid between a Green Junglefowl cock and a domestic chicken hen; the single throat wattle of Green Junglefowl is dominant in inheritance over the double wattles in chickens and therefore present in hybrids (© Cemani Farms, Subang, West Java, Indonesia)

name *furcatus* for this species mentioned by Temminck (1820a: xc). So overall this junglefowl species was scientifically named three times.

Besides the synonymy in the different pure species, hybrids between Green Junglefowl and domesticated fowl *G. gallus domesticus* added to the nomenclatural chaos in the genus *Gallus*. In Indonesia, especially on Java, these hybrids were deliberately bred. Because of their beautiful, but wholly different plumage, ornithologists believed that they were distinct species and, again, these hybrids were scientifically named three times as distinct taxa: *G. aeneus* Temminck, 1825; *G. temminckii* Gray, 1849; and *G. violaceus* Kelsall, 1891. Here we review these names and present additional information on extant hybrid specimens, including the three different types, of which some were known to Darwin.

Gallus varius hybrids

The first-generation hybrid offspring of a *G. varius* cock and a domesticated chicken hen is called Bekisar in Indonesia (Beebe 1921: 249). The practice of hybridisation to produce Bekisar is ancient and probably commenced on the Kangean Islands in the Java Sea. Only the male hybrids are valued for their peculiar voice while the female hybrids were killed, at least formerly. Their call consists of the prolonged notes of Green Junglefowls combined with the volume of domestic fowl. Each cock has his own unique voice which carries long distances. They were prized by the boat cultures of Indonesia, which placed them in bamboo cages in their canoes and used them to maintain communication with other boats, even in the roughest seas.

While on Java, William Beebe (1877–1962), an American ornithologist, noticed the large diversity in these birds: ‘some of these hybrids are huge creatures, with enormous pendant combs and beautiful plumage, whilst others are small and bantam-like with absurdly short legs’ (Beebe 1921: 249). The large diversity in Bekisar, both in size and colour, is caused predominantly by the domestic fowl parent, depending on the inheritable features present in the breed of chicken used for the cross with Green Junglefowl. All dominant features present in the domestic hen will be present in the hybrid. What all Bekisar have in common, however, is their single throat wattle (Fig. 4), which is also present in *varius* and is dominant in inheritance over the double wattles of Red Junglefowl and its domestic varieties.

Another feature of all Bekisar cocks is their peculiar voice which lacks cadence or definiteness. Their calls are loud prolonged screams which can carry for at least 1 km. In Beebe’s time the value of the bird was usually in the loudness and the piercing quality of its crow, which also needed to be drawn-out and monosyllabic. Among the poorer classes, however, another standard of vocal excellence was common: birds with a short, abrupt crow; more like that of the wild *varius*, but with a persistence which, according to Beebe (1921: 261), ‘would drive a white person insane’, were valued over other individuals.

Besides their use among boat cultures, by others their vocal characters were then mainly used for gambling purpose. Breeding and keeping Bekisar is still common and popular on Java for the latter reason—to match them in vocal competition—and ‘good singing birds’ are highly priced. To gain an impression of the diversity in colour, shape and size of these hybrids, search on the internet for images of ‘bekisar’ or ‘ayam bekisar’.

Bronzed Cock *Gallus aeneus* Temminck, 1825

Temminck (*in* Temminck & Laugier de Chartrouse 1825) described a ‘new species’ of junglefowl, based on a specimen (Fig. 5) he had seen in the ‘Muséum d’Histoire naturelle de Paris’. He named it *G. aeneus*, the bronzed cock (French: coq bronzé), a name originally linked to this specimen by Georges Cuvier (1769–1832) who, however, never described it



Figure 5. Holotype of *Gallus aeneus* Temminck, 1825 (MNHN.ZO.2013.42), collected by Pierre-Médard Diard between December 1818 and August 1819 on Sumatra (© Muséum National d'Histoire Naturelle, Paris)

as such (Voisin *et al.* 2015). The specimen was first figured, together with his description, in Temminck's *Planches coloriées* (1825, pt. 63, pl. 374; see Fig. 6).

The type specimen of *G. aeneus* was sent to the Paris museum by Pierre-Médard Diard (1794–1863), a French naturalist and explorer, who collected it at Pitat-Lanoago in Bencoolen (Lesson 1836: 378). Bencoolen was then a British possession (1685–1824) on the west coast of Sumatra (modern Bengkulu Province, Indonesia). Together with Alfred Duvaucel (1793–1824), another French explorer and a stepson of Cuvier, Diard was invited by Thomas Stamford Raffles (1781–1826), then Governor-General of Bencoolen (1817–22), to accompany him to the Malay Peninsula, Singapore and Sumatra to collect animals. Their first collecting trip started in December 1818, but in March 1820 Diard and Duvaucel fell out with Raffles over the division of the material, effectively terminating their cooperation! The reason for their conflict is explained differently by French and British sources. According to the French (Cuvier 1821) there was an agreement that half of the material collected would be sent to Paris, but Raffles nevertheless requisitioned most of it for the East Indian Company



Figure 6. Lithograph of *Gallus aeneus*, 'the Bronzed Cock', pl. 374 in Temminck's *Planches coloriées* (1825); the lithograph was after a drawing by the French natural history illustrator Nicolas Huet le Jeune (Harry Taylor, © Natural History Museum, London)

Museum. The English explanation (Raffles 1822, Raffles 1830: 372–373, 702–723), however, was that all the collected material belonged to the East Indian Company as the latter paid the collectors a monthly salary for their work, but that nevertheless the French had secretly sent many objects to Cuvier in Paris, including their notes and drawings. Whatever the truth, Diard and Duvaucel did send specimens to France, including this cock supplied to the Paris museum by Diard during his stay in Bangkok (Voisin *et al.* 2015).

Salomon Müller (1804–63), a member of the governmental Natural Sciences Commission for the Dutch East Indies (1820–50), was the first to recognise that Temminck's *G. aeneus* was not a species (Müller 1843: 210). In December 1825 Müller was sent to Java, in the role of taxidermist, to collect and prepare specimens for the Leiden museum. He was the longest-serving member of the Commission and remained in Indonesia collecting specimens until

late 1836, when he was summoned by the government to return to the Netherlands to begin describing the material he and his colleagues had collected during the previous 16 years. Müller became one of the most important ornithologists of his era, and from the material he collected personally (c.6,500 bird skins) and that of his colleagues of the Commission he described and named more than 90 new species, of which at least 65 are still valid taxa (HvG pers. research). While describing and cataloguing the Galliformes, together with Herman Schlegel (1804–84) who was at that time still Temminck's assistant at the Leiden museum, Müller discovered that *G. aeneus* was merely a hybrid between *G. varius* and a domestic chicken (Müller 1843: 210).

Batavian Cock *Gallus temminckii* G. R. Gray, 1849

George Robert Gray (1808–72) also described a new species of junglefowl (Figs. 7–8), based on a specimen purchased by the British Museum in 1849 from the dealer Gustav Adolph Frank (1809–80). The specimen was said to be from Batavia (modern-day Jakarta), but its true provenance was unknown. According to Gray, presumably based on the similarities with *G. aeneus*, 'it has been thought right to name it provisionally *Gallus temminckii*, until it may be proved otherwise than a species' (Gray 1849). In the description, Gray also mentioned a living example in the London Zoological Gardens (Fig. 9) which in some respects agreed with the description of *G. temminckii*, but bore a closer resemblance to *G. aeneus* of Temminck. It is not at all clear if at that point Gray was aware of Müller's (1843) publication and that *aeneus* is a hybrid, as he ends his description: '...that people who have the means of studying these birds [*G. temminckii* and *G. aeneus*] in their native places may be induced to determine whether these examples may justly be considered species, or only hybrids of others that are already known to naturalists.'

Nearly 20 years later, based on the entry in the museum's catalogue ('GALLUS TEMMINCKII. The Batavian Cock. *a.* Batavia, male. '), it appears Gray (1867: 39) still considered his *temminckii* to be a full species. At some point, however, he must have recognised his mistake as on the back of the original label of the type specimen is written '?? Hybrid between *G. varius* & *G. Bankiva* G. R. G'.

Gallus violaceus Kelsall, 1891

In 1891, Harry Joseph Kelsall (1867–1950), a Lieutenant with the Royal Engineers in Singapore, described a new species of junglefowl based on a live bird held in confinement in the botanic gardens of Singapore (Fig. 10). It was obtained in 1890 from a Malay dealer who had at that time two, both males, for sale. According to the dealer, they came from Borneo, but their provenance was uncertain. Based on the conspicuous violet gloss on the hackles and tail feathers, which according to Kelsall was the most distinguishing feature of the bird, he named this 'species' *G. violaceus*. Kelsall further noted that his bird resembled *G. varius* in having only a single throat wattle, and in the hackles being round-tipped, rather than lance-shaped as in other members of the genus. It, however, differed from *G. varius* in its colouring and by having a serrated comb (Kelsall 1891). A few years later, two additional specimens, both males, came to his attention in the possession of an animal dealer in Singapore who thought they came from Java, but again provenance was uncertain (Kelsall 1894).

Darwin's interest in *Gallus varius* hybrids

Charles Darwin (1809–82) was of the opinion that the domesticated chicken descended solely from one ancestor (monophyletic origin), namely Red Junglefowl *G. gallus* (formerly *G. bankiva*, Temminck). He used artificial selection applied by breeders of domestic animals



Figure 7. Holotype of *Gallus temminckii* G. R. Gray, 1849 (NHMUK 1849.3.2.67), provenance unknown, but said to be from Batavia (modern-day Jakarta) (Harry Taylor, © Natural History Museum, London)



Figure 8. Engraving by Joseph Wolf (1820–99) of the holotype of *Gallus temminckii*, in Gray 1849 (Hein van Grouw, © Natural History Museum, London)



Figure 9 (left). Engraving by Joseph Wolf of a hybrid junglefowl similar to *Gallus aeneus*, which was present in the London Zoological Gardens at the time, in Gray 1849 (Hein van Grouw, © Natural History Museum, London)

Figure 10 (below). Holotype of *Gallus violaceus* Kelsall, 1891 (ZRC 3.30131); at the time of description, 1891, this bird was still alive in the Singapore Botanic Gardens, but after it died was donated to the, then, Raffles Museum (© Kelvin Lim Kok Peng, Lee Kong Chian Natural History Museum at the National University of Singapore)



as an important analogy to illustrate the mechanism of variation and selection in nature. The diversity of domesticated breeds all descended from a common ancestor, in this case Red Junglefowl, showed, in Darwin's opinion, how selection could modify a species. And, if artificial selection can be so powerful over a short time, what might natural selection achieve working over much longer periods?

Darwin very briefly mentioned the above poultry example in *On the origin of species by means of natural selection* (1859: 18–19), but described it in more detail in *The variation of animals and plants under domestication* (1868a: 225–275). As part of his poultry research, Darwin was interested as to whether *G. aeneus* and *G. temminckii* were species rather than hybrids (Darwin 1868a: 233–236). If the former, he needed to find arguments to eliminate them as possible ancestors of the domestic chicken in favour of Red Junglefowl. He had already rejected *G. varius* as ancestor, 'which differs in so many characters – green plumage, unserrated comb, and single median wattle – that no one supposes it to have been the parent of any of our breeds' (Darwin 1868a: 234). Regarding the true identity of *G. aeneus* and *G. temminckii*, he correctly relied on others, quoting Crawford (1856: 112): 'These hybrids [between *G. varius* and domestic fowl] were at one time thought to be specially distinct, and were named *G. aeneus*. Mr. Blyth and others believe that the *G. Temminckii* (of which the history is not known) is a similar hybrid' (Darwin 1868a: 234–235).

Darwin may, however, have found his first evidence for *aeneus* being a hybrid in Wagner (1847), as in his unpublished manuscript *Natural selection*, under footnote 13 (Chapter IX; hybridism), Darwin refers to Wagner's statement there that 'S. Müller and Schlegel have remarked that *Gallus aeneus* (pl. col. 374) is merely a hybrid of *G. furcatus* [*varius*] and a tame Hen.' *Natural selection* was the manuscript Darwin had originally intended to publish as the formal presentation of his views on evolution. It was, however, never completed because, prompted by Wallace's letter to him concerning the principles of evolution, Darwin hurriedly wrote and published *On the origin of species*, which was literally only an abstract of the manuscript. Compared to the *Origin*, the original long manuscript has more abundant examples and illustrations of Darwin's argument, plus an extensive citation of sources. *Natural selection* was transcribed after Darwin's death, and first published by Stauffer (1975).

Darwin was also in contact with Edward Blyth (1810–73), curator of the museum of the Asiatic Society of Bengal in Calcutta, about *G. aeneus* and *G. temminckii*. Blyth (1855b) wrote to Darwin that 'The *G. aeneus*, Temminck, is now known to be a hybrid raised in confinement between *G. furcatus* & a common hen.' In following letters he wrote: 'The *Gallus aeneus* of Temminck is a hybrid between *Gallus varius* (vel *furcatus*) & a common hen, often raised in captivity in Java' (Blyth 1856a), and, 'I have just received a large batch of the *Proceedings of the Zoological Society*; and find a *Gallus Temminckii* described by Gray (& it would seem also figured). I have no faith in it; suspecting it *very strongly* to be a hybrid of some kind, probably a cross between male *varius* (v. *furcatus*) and hen of the large Malayan breed of domestic fowls; while *G. aeneus*, Temminck, as we are assured by Schlegel, is mixed *varius* & (small?) common hen' (Blyth 1856b).

William Bernhardt Tegetmeier (1816–1912), Darwin's advisor on domesticated pigeons and fowl, wrote to Darwin: 'Did you ever see a half bred *Gallus Varius*? or *Eneus* [*sic*] with common fowl. – He was some years since in the Zoological Gardens. He was remarkable as having transverse bright blue bands on his tail coverts like a so called "cuckoo cock". I have some of the feathers if you would like to see them' (Tegetmeier 1866a). Darwin (1866a) did like to see them, so Tegetmeier (1866b) sent them to Darwin who, when he returned the feathers by post, commented: 'they are extremely curious' (Darwin 1866b). In his *Variation under domestication*, Darwin briefly discussed 'cuckoo' markings in fowl as cases of analogous or parallel variation: 'the plumage of these birds is slaty-blue or grey, with each



Figure 11. Male hybrid between Green Junglefowl cock and domestic chicken hen, bred and kept in the London Zoological Gardens in the 1850s and after its death donated to the British Museum (Natural History) (NHMUK 1857.11.9.1); the remarkable dark and pale barring on the feathers (the cuckoo pattern) is the result of a colour aberration known as 'sex-linked barring' which was inherited from the domestic hen; compare this specimen with the bird in Fig. 13 (Harry Taylor, © Natural History Museum, London)

feather transversely barred with darker lines, so as to resemble in some degree the plumage of the cuckoo' (Darwin 1868a: 244). By the term 'analogous or parallel variation' Darwin meant that similar characters occasionally occur in different varieties or races descended from the same species or, more rarely, in widely distinct species and was implying that these markings signified a reversion to an ancestral character.

The same hybrid bird from the London Zoological Gardens is discussed in chapter 13, 'Reversion or Atavism', in *Variation* (Darwin 1868b: 39–40). Again he used the term 'reversion' to describe situations where a character previously observed in a taxon disappears in crosses and then resurfaces in later generations. Reversion was for him a form of ancestral inheritance; the return of characteristics of a distant ancestor; 'I owe to the kindness of this same excellent observer [Tegetmeier] the inspection of some neck-hackles and tail-feathers from a hybrid between the common fowl and a very distinct species, the *Gallus varius*; and these feathers are transversely striped in a conspicuous manner with dark metallic blue and grey, a character which could not have been derived from either immediate parent' (Darwin 1868b: 40). Tegetmeier, when asked his opinion about the latter statement, agreed (Darwin 1861, 1865). So both Darwin and Tegetmeier considered these blue transverse bars on the hackles and tail feathers of this *varius* hybrid to be an ancestral trait expressed by crossing, or by analogous variation. The hybrid which caused this discussion, or a very similar bird, was received by the British Museum in November 1857

from the London Zoological Gardens and is currently still in the Natural History Museum's (NHMUK) collection at Tring (Fig. 11).

Both men drew the same conclusions about some additional specimens—skins of domesticated chickens from Borneo—sent to Darwin by James Brooke (1803–68), Rajah of Sarawak, in 1857. 'Sir J. Brooke sent me some skins of domestic fowls from Borneo', Darwin (1868a: 235) wrote, 'and across the tail of one of these, as Mr. Tegetmeier observed, there were transverse blue bands like those which he had seen on the tail-feathers of hybrids from *G. varius*, reared in the London Zoological Gardens. This fact apparently indicates that some of the fowls of Borneo have been slightly affected by crosses with *G. varius*, but the case may possibly be one of analogous variation.' Although we were unable to check this specimen, it is more likely that it was not a hybrid and that the transverse bars were caused by the cuckoo mutation which was, and still is, present in many domestic chicken populations. Cuckoo pattern in chickens is a dominant and sex-linked mutation, known as 'sex-linked barring' among poultry geneticists. This common heritable mutation rhythmically switches the production of melanin on and off during feather growth, resulting in alternating pale and coloured transverse bars over the total length of each feather (Crawford 1990: 126–128; see Figs. 12–13).

These Bornean skins were probably those that Darwin encouraged Tegetmeier to exhibit, together with those of other Asiatic domestic fowl, at a meeting of the Zoological



Figure 12. German Cuckoo, a breed of domestic chicken, male, in the traditional cuckoo pattern, commonly referred to as 'barred' by chicken fanciers, which is the combination of two different mutations; Black (gene symbol *E*), a dominant mutation which turns the wild type colour solid black, and sex-linked barring (gene symbol *B*) which switches the production of melanin on and off during feather growth, resulting in alternating pale and coloured transverse bars over the length of each feather (© Aad Rijs)



Figure 13. Leghorn, a breed of domesticated chicken, male, in the variety 'gold barred', which is the result of the effect of sex-linked barring alone, without any other mutation; as sex-linked barring affects eumelanin (black) more than phaeomelanin (reddish brown), the alternating pale and coloured transverse bars are less conspicuous in the 'golden' parts of the plumage; compare this bird with the specimen in Fig. 11 (© Aad Rijs)

Society (Anon. 1857, Darwin 1857, Tegetmeier 1857). Their current whereabouts, if they still exist, are unknown to us.

Discussion

One of the reasons why Darwin considered Red Junglefowl to be the sole ancestor of domestic fowl was that crosses between domesticated fowl and Red Junglefowl are fertile, while, according to the evidence available to Darwin, crosses with *G. varius*, *G. sonneratii* and *G. lafayettii* are rarely so. 'As I am informed by Mr. Crawford', Darwin (1868a: 234) wrote, 'hybrids are commonly raised between the male *G. varius* and the common hen, and kept for their great beauty, but are invariably sterile; this, however, was not the case with some bred in the Zoological Gardens.' Darwin also referred to Samuel James Augustus Salter (1825–97), who conducted crossing experiments with *varius* hybrids at the London Zoological Gardens during 1861–62, and reported low fertility among them (Salter 1863).

Hybridisation experiments in the London Zoological Gardens during 1884, however, revealed that all four *Gallus* species can produce fertile hybrids with domesticated fowl.

These results persuaded Tegetmeier to repeal his earlier belief in a monophyletic origin of domestic fowl. In an open letter to *The Field*, Tegetmeier (1885, see Appendix) acknowledged that most poultry breeds indeed descended from Red Junglefowl, but suggested that a few large and distinct Asian chicken breeds were descended from some other species of wild junglefowl, now extinct.

So, less than four years after Darwin's death, his advisor Tegetmeier dismissed the single-species origin based on 'new' evidence which had not been available to Darwin. Although Darwin was correct as to the monophyletic origin of domesticated fowl, some of the evidence he used to corroborate his opinion was incorrect. For much of his hypothesis he had to rely on the accounts and observations of others, e.g. Blyth (1855a, 1856a), Crawford (1856: 112) and Salter (1863) regarding the fertility of hybrids, without knowing whether these were true.

Darwin's theory of evolution by natural selection rests on the premise of the heritability of variation, yet Darwin lacked knowledge of the mechanisms for this. Two views on inheritance were commonly embraced at that time: the inheritance of characteristics acquired during the lifetime of an individual (usually referred to as 'Lamarckian inheritance') and blending inheritance, in which the offspring is intermediate between the two parents. Both were at direct odds with natural selection as the mechanism for evolution. Darwin therefore formulated his own 'provisional hypothesis': pangenesis, a modified combination of the inheritance of acquired characteristics and the blending theory (Darwin 1868b: 357–404). In short, according to Darwin, minute particules called gemmules, produced by every cell, circulate around the body and can be modified throughout life. It is these gemmules, he maintained, that are passed to future offspring, subtly changing the information that is inherited. Depending on the number of gemmules received from both parents, the offspring may be more similar to one, or the other, parent. To explain 'reversion' and 'analogous variation', according to Darwin, gemmules could lie in dormancy then re-emerge to be manifest as ancestral forms.

As the transverse blue bars found in the hybrid are not present in *G. varius* and, according to Tegetmeier (Darwin 1861, 1865), neither in the domestic fowl parent, Darwin assumed they represented an ancestral form. The 'laws of inheritance' and the fact that genes are constantly passed from one generation to the next were unknown to Darwin. Whether the domestic hen indeed did not show any sign of 'barring' or Tegetmeier simply had not noticed it, we do not know; in some gene combinations the cuckoo phenotypic barring trait is hardly visible in female plumage, while in others it is completely masked. What we do know is that the plumage colour of the *varius* hybrid male in the London Zoological Gardens was not the result of reversion or analogous variation, but the result of the gene that codes for barring, present in the domesticated hen, being passed to her hybrid son.

While Darwin was still struggling to make pangenesis work, a monk experimenting with inheritance in pea plants in Brno had just discovered that each individual trait is inherited independently; sometimes visibly, sometimes not, depending on the combination of parental types, but remaining unchanged as each passes inexorably through the generations.

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Appendix

Letter of W. B. Tegetmeier, *The Field* 26 September 1885, p. 467

THE ORIGIN OF THE DOMESTIC FOWL.

SIR,—The origin of all the different varieties or breeds of the domestic fowl is usually believed to be the common wild Indian jungle cock, the *Gallus ferrugineus* of modern naturalists, but known also as the Bankiva fowl (*G. bankiva* in the older books). This bird may be readily described as closely resembling a small black-breasted red game-cock, with a tail carried more horizontally than usual.

It may be regarded as most presumptuous in me to dare to contest the conclusions arrived at by the honoured master Darwin, with whom and for whom it was for some years my privilege to work; but a careful and extended consideration of the facts has led me to a different conclusion to that arrived at by him.

There are now existing four distinct and well-marked species of the genus *Gallus*, namely: (1) The common *G. ferrugineus* [*G. gallus*]; (2) the Sonnerat jungle cock (*G. sonnerati* of naturalists), so readily distinguished by the flattened shafts of the feathers in the male; (3) the jungle cock of Ceylon (*G. stanleyi*), which is confined to the island (this was admirably figured by the late T. W. Wood in illustration of a descriptive article of mine in *The Field* of Nov. 29, 1873); and (4) the fork-tailed or single-wattled cock of Java (*G. furcatus*).

That the domesticated fowl in India is derived from the first species is evident from the fact that sportsmen occasionally confound the wild and tame birds. This, taken into conjunction with the fact that hybrids with the other species bred in confinement have not been remarkably fertile, has led probably to the conclusion which has been arrived at; but this want of fertility has been due to the unnatural conditions under which the birds have been placed. Everyone at all conversant with poultry keeping knows that eggs laid by fowls in confined runs are mostly sterile, and it could hardly be expected that cross-breeding with distinct species would, under these conditions, conduce to greater fertility.

The hybrids between the different species of *Gallus* are, in many cases, perfectly fertile. Some years since, I saw at Clumber numerous game bantams roosting in the trees, that had for several generations been bred from a Sonnerat cock and domestic hens.

Last season [1884], at the Zoological Gardens, numerous half-bred birds were reared from *G. stanleyi* [*G. lafayetteii*], and in former years many were bred from a single specimen of *G. furcatus* [*G. varius*]. There is no doubt that the several wild *Galli* will interbreed and produce fertile offspring as readily as do the corresponding and closely allied pheasants, in which the three species, the Chinese, the versicolor, and the Colchican, have become so mixed, that pure birds are rarer than mongrels.

I have no doubt in my own mind that the wild *Galli* have intermixed in not a few instances, and perhaps through not a few centuries, in producing our domesticated breeds.

But it is with regard to the eastern Asiatic type of fowl (absurdly known as Cochins and Brahmas) that my doubts as to the descent from the *G. ferrugineus* [*G. gallus*] are strongest.

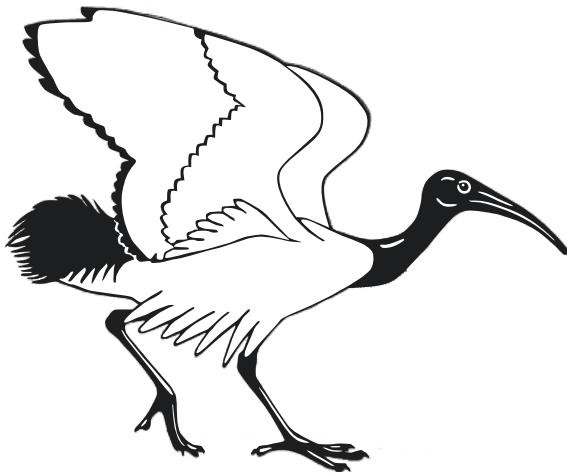
We have in the Cochin a fowl so different from the ordinary domestic birds that, when first introduced, the most ridiculous legends were current respecting it. Putting these on one side, we have a bird with many structural peculiarities that could hardly have been induced by domestication. Thus the long axis of the occipital foramen in the Cochin is perpendicular, in our old breeds horizontal, a difference that could never have been bred for, and which it is difficult to see could be co-relative with any other change. The same may be said respecting the deep sulcus or groove up the centre of the frontal bone. The extraordinary diminution in the size of the flight feathers and that of the pectoral muscles could hardly have been the result of human selection and careful breeding, as the value of the birds as articles of food is considerably lessened by the absence of flesh on the breast. Nor is the extreme abundance of fluffy soft body feathers a character likely

to be desiderated in a fowl. The vastly increased size may have been a matter of selection, although, as the inhabitants of Shanghai feed their poultry but scantily, and, according to Mr. Fortune, mainly on paddy or unhusked rice, it is not easy to see how the size of the breed was obtained if, as generally surmised, it arose from the little jungle fowl [*G. gallus*].

Taking all these facts into consideration, I am induced to believe that the birds of the Cochin type did not descend from the same species as our game fowl. It may be asked what bird I would suggest as the origin of these eastern Asiatic breeds. In reply I would suggest the possibility, or even probability, of their being descended from some easily captured and readily domesticated short-winged species, that may have entirely passed into a state of domestication, as has the camel and the horse. I can see no inherent improbability in this suggestion, nor any fatal objection to the theory I have advanced. W.B. TEGETMEIER.

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