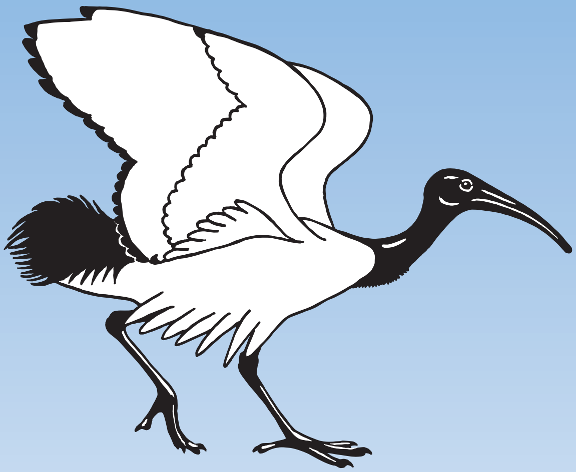
Bulletin of the British Ornithologists’ Club



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CLUB ANNOUNCEMENTS

Chairman's message

At the start of the year we looked forward to celebrating, in conjunction with the Linnean Society, the year of our 1,000th meeting since the inaugural meeting on 5 October 1892. We had planned two talks at the Society's premises: in June, by Prof. Jared Diamond, and in November by Prof. Jon Fjeldså. Alas the pandemic made these and also talks at the Barley Mow impossible. However, like many others, we have been converted to the benefits of Zoom and to date we have hosted two outstanding events. On 21 September Dr Beth Okamura gave our first Zoom talk on *How birds shape freshwater biodiversity* and on 16 November Prof. Jon Fjeldså deliver his presentation on *The evolution of passerine birds explained*. We are very grateful to them both for their willingness to work (and so successfully) in difficult and unfamiliar circumstances.

Whilst we missed the immediacy and companionship of live meetings, in both cases we attracted large audiences and from around the world, which given the Club's large overseas readership is very gratifying. We hope that we may return to something like normality next year, but I believe that even if we meet in person we will continue to Zoom future events. And as is now routine, both these talks are available on YouTube via the BOC site. We are now working on a programme of talks for 2021 and details will be published on the website.

I am very pleased to announce that we are being joined by Sarah Nichols, who will be taking over in early 2021 from Eng-Li Green as our website manager. Eng-Li has decided that she should limit her online work and is delighted that Sarah will be taking over from her. I am pleased that Eng-Li will nevertheless continue to work with Guy Kirwan on the Bulletin. Sarah has recently completed her M.Sc. on Biodiversity, Evolution and Conservation at Univ. College London and the Natural History Museum, London.

I am also delighted that Sarah will be organising and editing a blog. This is a new and important venture and any feedback would be gratefully received. The blog will appear quarterly in synch with the Bulletin. The content of the blog will include summaries of papers published in the Bulletin and posts on other issues in ornithology. It will be launched next month on the Club's website where the News section used to be.

Chris Storey

The 997th meeting of the Club was held on Monday 21 September 2020 via the online medium of Zoom.

Dr Beth Okamura, Merit Researcher, Natural History Museum, spoke on *How birds shape freshwater diversity*. She began by posing the audience questions such as whether they had ever wondered how volcanic islands, garden pools and gravel pits develop a rich biota, or why rowan trees grow near pines. The answers to both in part involve patterns of bird visitations. That avian activities might help explain the widespread distributions of taxa that live in disjunct habitats was appreciated by Darwin, and this conundrum famously led him to examine the attachment and survival of recently hatched snails on ducks' feet. Beth took this as her starting point in considering how our understanding of dispersal of freshwater invertebrates has improved since. In particular, she focused on evidence for waterbird-mediated dispersal of colonial invertebrates called bryozoans (or 'moss animals') and their myxozoan parasites ('slime animals'), freshwater animals that are poorly known but that have substantial ecological and practical impacts. Her explanation of this included illustrating 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. The Club is deeply grateful to Beth for being willing to act as a 'guinea pig' in delivering her fascinating and unusual talk via the medium of Zoom.

The 998th meeting of the Club was held, in conjunction with the Linnean Society of London, on Monday 16 November 2020 via the online medium of Zoom.

Prof. Jon Fjeldså, Professor in Biodiversity at Copenhagen University, where he is also in charge of the bird collections of its Zoological Museum, spoke on *The evolution of passerine birds explained*. Based on his research spanning many decades, Jon explained that classifying birds from morphology has never been easy, and resolving the evolutionary relationships among passerine birds has proven especially challenging. Since the emergence of molecular systematics, many traditionally defined songbird groups, such as 'flycatchers'

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and 'warblers', have been revealed to involve multiple independent lineages of birds with similar lifestyles. Scores of members of these former 'umbrella' groups are now viewed as ancient relictual lineages, and the number of accepted passerine families has increased dramatically, by 40%. Although generating a 'taxonomic mess'—a growing pain resulting from the shift from similarity based taxonomy to taxonomy representing evolutionary relationships—these new relationships also lead to biogeographic insights spanning the globe. His talk revealed novel perceptions and interpretations about the generation of avian diversity and variation over time, and demonstrated that the complex worldwide pattern of bird species diversity was driven by relatively few life-history shifts and geographic expansions. However, despite the immense progress recently made in our understanding, the talk concluded by highlighting remaining problem areas in resolving the passerine tree of life, where further progress requires more and better data. As Jon emphasised, the age of exploration must continue! This was an overview of real scope and detail, in which Jon was kind enough to highlight both the past and the continuing relevance of research published by the Club's *Bulletin* since its inception in 1892. Those interested in learning more will be pleased to know that a comprehensive volume co-edited by Jon, entitled *The largest avian radiation: the evolution of perching birds, or the Order Passeriformes* (Lynx Edicions), will have been published by the time you read this.

FORTHCOMING MEETINGS

Given the uncertainty surrounding the timescale of the current Covid-19 pandemic, details of forthcoming meetings in 2021 will be announced online via the Club's website: https://boc-online.org/meetings/upcoming-meeting, or follow the Club's Twitter (@online_BOC) and Facebook accounts (https://www.facebook.com/onlineBOC). Be sure to keep an eye on them!

BOOK REVIEWS

Kirkconnell, A., Kirwan, G. M., Garrido, O. H., Mitchell, A. D. & Wiley, J. W. 2020. *The Birds of Cuba: an annotated checklist*. BOC Checklist Series 26. British Ornithologists' Club, Tring. 472 pp, 32 pp of colour photographs. ISBN 978-0-9522886-7-1. £44.99.

Those familiar with the BOU, now BOC, checklists will know what to expect in this new publication. The series is renowned for publishing benchmark summaries of the status of each species in a particular country or region. The word 'checklist' might be an example of quintessential British understatement: these checklists represent portable compendia of museum specimen and sighting data, and many of the species accounts in *The birds of Cuba* run to more than a page of concise, informative, densely packed type. If you wish to know the status of a given species, how many records there have been, their geographical spread, or who obtained them, therein lies the answer! If you need to determine which subspecies occur, or if you are delving into a nation's ornithological history, then such a checklist is typically the best starting point. Caribbean ornithology has been the fortunate beneficiary of five previous checklist titles, each an ornithological milestone that has earned its niche in the regional bibliography. This checklist of the birds of the largest and most diverse island will surely take its place among them.

The authors' names will be familiar to those with an interest in the birds of the West Indies, and their individual credentials are impressive. They have accumulated decades of combined field experience, hundreds of publications and a track record of working on similar projects. Jim Wiley's *A bibliography of ornithology in the West Indies* (2000) is a regional researcher's Bible, Garrido and Kirkconnell's field guides to the birds of Cuba (2000, 2011) are the standard national references, and *Birds of the West Indies* (Kirwan *et al*. 2019) is the equivalent for the region. Nevertheless, or perhaps because of that, the task under review has taken the best part of three decades. The extent to which the literature has been reviewed can be judged by the number of bibliographic references, which extend across 58 pages. In passing, the 46 contributions of 'the doyen of Caribbean ornithology' (Parkes 1989), James Bond, take up a double spread. In addition to these published and unpublished sources, museum specimens and observational records have been diligently compiled, and more than 350 individual collectors and observers are cited as a result. Evidently, many of the specimens in both Cuban and the principal foreign museums were personally checked and verified by the authors, who visited every collection holding more than 100 specimens of Cuban provenance.

The content of the 386 species accounts follows and augments that of previous checklists. It comprises sections on global distribution, Cuban records (the meat of the work), breeding data, and as near a comprehensive list of museum specimen holdings as is possible. Where taxonomic differences or points of interest arise they are treated in an additional section. On that subject, taxonomy broadly follows the AOU *Check-list of North American birds* and supplements, with departures where evidence points to a more convincing arrangement. So, for example, Cuban Nightjar *Antrostomus cubanensis*, Cuban Kite *Chondrohierax wilsonii*, and Cuban Palm Crow *Corvus minutus* are all treated as endemic species.

Conservation issues are amply covered, with an optional comments section covering, for example, global and national conservation status according to, respectively IUCN and the national Red List categories of the *Libro Rojo de los vertebrados de Cuba*. In some cases, the accounts themselves present information not readily

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available outside Cuba, which makes the texts for Zapata Rail *Cyanolimnas cerverai* or Cuban Ivory-billed Woodpecker *Campephilus principalis bairdii* invaluable, usefully updating the thorough work of *Threatened birds of the Americas* (Collar *et al*. 1992).

Arguably more important than adding additional species is the task of weeding out inadequately documented records. The authors have performed a vital service in examining afresh the evidence for inclusion of 26 of such 'unconfirmed species', and have set the record straight by dismissing, for example, the extraordinary published claims of Palearctic species Common Kingfisher *Alcedo atthis*, Eurasian Blackcap *Sylvia atricapilla* and White-winged Snowfinch *Montifringilla nivalis* that had found their way on to some national and even regional checklists.

Introductory material that might simply have been a formality to be passed over en route to the species accounts proves to be fascinating, rigorous and not easily found outside this publication. It begins with a history of Cuban ornithology containing brief sketches of the colourful characters who devoted their lives to the pursuit of knowledge, from those, like Gundlach, who are still widely recognised today to fascinating figures not so familiar outside the archipelago like Felipe Poey or José Hernández Bauzá. The long history of home-grown and resident naturalists and ornithologists emerges clearly, right through to the present-day ranks of active guides, park guards and biologists like Pedro Regalado and Nils Navarro. At the same time, it is striking how many leading ornithologists from US museums—among them Cory, Chapman, Barbour, Peters, Bond, Vaurie, Morton—were motivated to undertake field work in Cuba during the 19th and 20th centuries. Sadly, as the story is told, the frequent deterioration, destruction and loss of so many irreplaceable specimens and even entire collections becomes all too apparent; poignantly among them a Gundlach specimen of the extinct Cuban Macaw *Ara tricolor*—the sole example held in Cuba—that I had the good fortune to see while working at the Instituto de Ecología y Sistemática in the early 1990s. The sections on geology, geography and vegetation are similarly well-compiled primers, while the treatment of zoogeography and fossils, reviewed by William Suárez, is exemplary. A 22-page gazetteer is a vital aid in pinpointing localities mentioned in the text. Inserted into the middle of the book is a pleasing selection of photographs that depict, among other things, most of Cuba's endemic and speciality species, including historic specimens of extinct and Critically Endangered birds.

Publication of this survey is timely. International interest in Cuba has increased considerably over the past decade and, prior to the ongoing pandemic and current (though now expiring) US presidency, visitor numbers were growing rapidly at the same time as the old political impediments crumbled. There was therefore no better time for a full stock-take of distributional knowledge to succeed the *Catálogo de las aves de Cuba* published in 1975 (Garrido & García Montaña 1975). Forty-five years on, Orlando Garrido is a co-author of this new book, which is fittingly dedicated to another co-author, the ornithological giant Jim Wiley who sadly died during the final revisions of the manuscript. It is to be hoped that many future ornithologists, both amateur and professional, will find themselves in the happy position to make use of this fine tribute.

Christopher J. Sharpe

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Collar, N. J., Gonzaga, L. P., Krabbe, N., Madroño Nieto, A., Naranjo, L. G., Parker, T. A. & Wege, D. C. 1992. *Threatened birds of the Americas: the ICBP / IUCN Red Data book*. International Council for Bird Preservation, Cambridge, UK.
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Parkes, K. C. 1989. In Memoriam: James Bond. *Auk* 106: 718–720.
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Beehler, B. M. & Laman, T. 2020. *New Guinea: nature and culture of Earth's grandest island*. Princeton Univ. Press, Princeton, NJ & Oxford, UK. 375 pp, *c*.200 colour photographs. ISBN 978-0-691-18030-4. £25.

This is a beautiful and authoritative overview but also a fundamentally accessible one, both in price and content. Belying its 'coffee-table' design and format, it combines the best of both worlds. Bruce Beehler is a veteran of *c*.50 visits to New Guinea, and co-author of both of a recent field guide to the region and a taxonomic handbook worthy of most superlatives (reviewed in *Bull. Brit. Orn. Cl.* 136: 221–222), while Tim Laman is one of the authors of a stunning photographic survey of the birds of paradise and a regular contributor to *National Geographic*.

Subtitled 'Earth's grandest island', a perhaps arguable but certainly not unsubstantiated claim, New Guinea is both 'painfully' remote for most of us and culturally 'beyond our ken'. I suspect that most people around the world, if forced to encapsulate their knowledge of this poorly known part of Australasia, would respond with birds of paradise and scantily but ornately dressed tribespeople. Beehler & Laman escort us on journey that simultaneously underscores and alters our perceptions.

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This lavishly illustrated book comprises 18 chapters, covering among other subjects 'history', 'geology', climate, 'biogeography', plants, invertebrates, fish, reptiles, mammals, birds (of course), 'paleontology', 'people', and 'the future'. A typical chapter covering a biotic group, for example mammals, provides a simple yet informative overview of the families found in New Guinea (including separate coverage of non-natives), with adjunct comments on (in this case) traditional hunting practices, extinctions, and potential future threats. References are eschewed in the text, but a footnote at the start of each chapter briefly lists some of the keynote works used to prepare that section, which the more interested reader can then pursue via the endpapers. The family details for birds are, unsurprisingly, especially detailed, but rather than attempt an overall survey of diversity commence with a general introduction to the geography and ecology of the avifauna, then provide summaries for three keynote families, birds of paradise, bowerbirds, and honeyeaters, before rounding off with the story of the discovery that the feathers and skin of Hooded Pitohui *Pitohui dichrous* are toxic, something which was well known to the region's peoples, but only recently elucidated by Western science.

Although rather more even than *just* a general natural history book, two other chapters should make especially interesting reading for serious birders. The first, that on history, takes us through the early voyages of discovery, the colonial period (British, Dutch, and German), the major expeditions engaged in collecting natural history, some of the institutions harbouring important holdings of specimens, as well as laboratories and research stations currently or recently active, together with some future directions for biodiversity investigations. The illustrations and text highlight that field research was and *is* tough. This reader, at least, would have welcomed more images of the trailblazers, in terms of Western knowledge, although I still struggle to divine whether the young Ernst Mayr half-smirks at the camera in shyness, assuredness in his future, or merely as a result of his having adopted a not entirely comfortable perch, in that famous 1929 photo. The second of my two choices, entitled 'In the field', paints an illuminating picture of the difficulties both in arranging and executing field work in what remains one of the most remote forests in New Guinea, on the Foja Mountains. Over the course of three visits, Beehler and colleagues collected many new taxa, among them at least two birds, with other ornithological novelties still to be described (see Beehler *et al*. 2007, 2012, Beehler & Prawiradilaga 2010).

Even if, like me, you have never set foot on Earth's grandest island, but you share a passion for wild and poorly known places then this book represents an introduction to one such treasure trove, and as already mentioned at an extremely competitive price.

Guy M. Kirwan

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Beehler, B. M. & Prawiradilaga, D. M. 2010. New taxa and new records of birds from the north coastal ranges of New Guinea. *Bull. Brit. Orn. Cl*. 130: 277–285.

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OBITUARY

Robin Wilfrid Woods MBE, FLS (1936–2020)

Falkland Islands ornithology suffered an immeasurable and irreplaceable loss when Robin Woods died on 8 August 2020. He will be remembered for his unrivalled ornithological knowledge especially, but also for his deep understanding of the islands ecology, and his lasting contribution to nature conservation there.

Robin was born on 20 October 1936 in Croydon, Surrey, and grew up in Norbury. His interest in natural history was encouraged by his mother and grandmother and, for his sixth birthday, his father gave him a copy of *The Observer's book of British birds*. Aged 11, Robin wrote to the National Ringing Committee offering to ring sparrows in his loft and, if this 'would be any use', requesting a supply of rings. To his disappointment, he was told tersely that they could not send rings 'to anyone as young as you are'.

After completing O-levels at Mitcham Grammar School in 1953 Robin had to provide another income for the family. He trained as a scientific assistant for the Air Ministry Meteorological Office, and in 1956 volunteered for a post in the Falklands. Part of the appeal, he told me, was that little had been published on the birds of the archipelago. He arrived in Stanley in December of that year. In his spare time Robin gathered information through his own observations, photography, ringing and tape recordings, as well as, critically, from talking to islanders. His natural demeanour with people, inquisitive mind and ability to make meticulous notes were ideal for the role. In 1957 he met Anne, a teacher working in the Senior School for the Colonial Education Service; they married in 1958.

In 1961, on the small, uninhabited Kidney Island, *c*.16 km north-east of Stanley, Robin and a friend discovered a pair of Great Shearwaters *Ardenna gravis* in a burrow; the first proof of the species' breeding in the Falklands. Robin also inspired several small-scale but far-reaching ringing projects. Together with Roddy & Lily Napier of West Point Island, Robin and Anne ringed 3,000 young Black-browed Albatrosses *Thalassarche melanophrys* in 1962–63. Some of them were recovered just a few months later off the coasts of

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Brazil, Angola and the Cape of Good Hope. A Sooty Shearwater *Ardenna grisea* ringed in Stanley in May 1962 was found 28 days later, drowned in a fishing-net in Barbados, having flown at least 9,000 km; the first North Atlantic record of a Falklands shearwater.

Robin left the Falklands in 1963, being posted to RAF Lyneham, Wiltshire. In 1965, he resigned from the Meteorological Office, searching for more challenging and satisfying employment. Alongside his parental and work responsibilities, Robin retrained as a psychologist. He studied for A-levels, then gained a degree, teaching certificate and post-graduate diploma. The family moved to Devon in 1974 and, for the next 21 years, Robin worked as an educational psychologist for the county council, mainly with children in care.

Robin drafted his first book while in the Falklands: *The birds of the Falkland Islands* (1975). With a foreword by Sir Peter Scott, it was the first comprehensive bird guide to the islands. In 1980, Sir Peter asked Robin to serve on the Advisory Council of the newly established Falkland Islands Foundation. The UK-based foundation merged in 1991 with the Falkland Islands Trust, its Stanley-based counterpart, to form Falklands Conservation; Robin was a founding trustee and later became UK Deputy Chairman, UK Chairman and Vice President.

Figure 1. Robin Woods with an adult Striated Caracara *Phalcoboenus australis*, Steeple Jason Island, Falklands, 2012 (Jonathan Meiburg)

He first revisited the Falklands in 1983 to study passerines. Robin told me that the Falklands War and images in the news of places he held dear encouraged him to return. Increased public awareness of the islands brought more visitors and greater interest in wildlife. Additions to the species list prompted Robin to write *Guide to birds of the Falkland Islands* (1988). During his 1983 visit, he initiated a ten-year survey of breeding birds, gathering data and knowledge from islanders, visitors and the military. He collated and analysed the resulting 5,800 breeding records and, with Anne, wrote *Atlas of breeding birds of the Falkland Islands* (1997).

Following early retirement in 1995, Robin visited the Falklands during the austral spring / summer in most years. His work with Falklands Conservation included surveying Striated Caracaras *Phalcoboenus australis* (Fig. 1), excavating subfossil bones from a peat bog, undertaking botanical surveys, eradicating rats from islands, restoring tussac *Poa flabellata*, developing plans to safeguard Cobb's Wren *Troglodytes cobbi*, and writing many reports and articles. I was fortunate to travel with Robin on two of his visits; he was great company, always generous with his knowledge and had a wonderful sense of humour.

In 2005 he was elected a Fellow of the Linnean Society of London and in 2008 awarded an MBE in recognition of his services to nature conservation in the Falklands. True to Robin's character, he chose to receive his medal at Government House in Stanley with his friends, rather than at Buckingham Palace.

Arguably, his most significant publication is *The birds of the Falkland Islands: an annotated checklist* (2017). Robin collated 60 years of knowledge, not only in the 259 species accounts, but also in describing the geography, weather, climate and habitats of the Falklands, the history of local ornithology, human impacts, palaeornithology, and data from more than 4,000 museum specimens. It is an essential reference for anyone interested in the islands' natural history.

Robin found time to publish on other subjects too. Examples include a study of the 1:50,000 DOS Falklands maps resulting in a list of at least 780 (rather than the frequently quoted 'about 200') islands in the archipelago (1986); *Flowering plants of the Falkland Islands* (2000) (his collection forms the basis of the Falklands National Herbarium); *Birds and mammals of the Falkland Islands*, written with Anne (2006, 2018); and a description of a subfossil yet new species of extinct caracara *Phalcoboenus napieri* (*Emu* 2016). He also contributed to *A visitor's guide to the Falkland Islands* (2001, 2005) and *Important Bird Areas of the Falkland Islands* (2006). His final publication was a detailed account of bird ringing in the Falklands since 1949 (*Falkland Islands J.* 2018). It says a lot about Robin that in this paper he paid tribute to the contributions by many others to our understanding of the Falklands avifauna.

Robin's contribution to Falklands ornithology, conservation and education, and help to raise awareness of the Falklands and their wildlife, is immense. His legacy of publications testifies to this and to his love of the islands. He is survived by Anne, sons Alan and Martin, and four grandchildren. He will be greatly missed by his many friends and colleagues across the world.

I am very grateful to Anne and Alan Woods for their help in compiling this tribute.

Mark Adams

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ERRATUM

In a recent paper (Sagot-Martin *et al*. 2020, *Bull. Brit. Orn. Cl*. 140: 218–298) a call in a recording (WA 3300894) was identified as a Swainson's Flycatcher *Myiarchus swainsoni*, which served as one voucher for the inclusion of this species in the Rio Grande do Norte state list. In fact, the vocalisation concerned involves a very similar call of Silvery-cheeked Antshrike *Sakesphorus cristatus* (see similar recordings in Minns *et al*. 2010. *Birds of Brazil / Aves do Brasil*. DVD-ROM. Ed. Avis Brasilis, Vinhedo). As other vouchers are available of Swainson's Flycatcher (e.g., WA 2981660, a sound-recording in which the bird concerned was seen), the misidentified record has no effect on the species' inclusion in the list. However, all other records demonstrate that Swainson's Flycatcher is present in Rio Grande do Norte only during March–August (the austral winter).

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): Jorge Avendaño, Norbert Bahr, Tim Birkhead, K. D. Bishop (*), Murray D. Bruce (*), Donald Buden, Carlos Camacho, Oscar Campbell, Alice Cibois, Anthony Cizek, Nigel Cleere, Kristina Cockle, J. Martin Collinson, Thiago Costa, Marco Aurélio Crozariol (*), Normand David, Carla Dove, J. P. Dumbacher, Guy Dutson, James Eaton (*), Trevor Ellery, Andy Elliott (*), Elise Elliott-Smith, Steven D. Emslie (*), R. L. Flood, Juan F. Freile (*), Peter Garson, Cheri Gratto-Trevor, Harold F. Greeney, Steven M. S. Gregory, Ben Haase, William Hilgartner, Steve Hilty, Steve N. G. Howell, Julian Hume, Alvaro Jaramillo, Sebastian Jiménez, Ron Johnstone, Leo Joseph, Chris Kehoe, Daniel F. Lane (*), Alexander C. Lees, Gabriel Leite (*), Ethan Linck, Wayne Longmore (*), Curtis A. Marantz, Manuel Marín, Jochen Martens, Gerald Mayr, Jeff Marks, Michael Mills (*), Tong Mu, Fábio Olmos, Jente Ottenburghs, José Fernando Pacheco, Marco Pavia (*), Vítor Piacentini (*), Thane K. Pratt (*), Robert Prŷs-Jones (*), Pamela C. Rasmussen, Piero Ruschi, Richard Schodde (*), Edwin Scholes, Thomas S. Schulenberg, Paul Scofield, Chris Sharpe (*), Frank D. Steinheimer, Fernando Costa Straube, Claudia Tambussi, Christophe Thébaud, Lazaro William Viñola, David R. Wells (*), Iain Woxvold, John van Wyhe, and Kevin J. Zimmer.—The Hon. Editor

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).

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Phenotypic variation and polymorphism confirmed among white-bellied swiftlets of the *Collocalia esculenta* group (Apodidae, Collocaliini) by mitochondrial and nuclear DNA evidence

Sian E. W. Davies[*], *Wei Lim Goh*[*], *Sarah P. Ball, Earl of Cranbrook, Wei Sheng Siew & Michael Tarburton*

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http://zoobank.org/urn:lsid:zoobank.org:pub: 3826C787-5FC7-4863-BF0F-251EC206A1E0

Summary.—Among white-bellied glossy swiftlets of the *Collocalia* group, A. R. Wallace was first to recognise the Makassar Strait, separating Borneo and Sulawesi, as a geographical barrier between different phenotypes: plain-tailed to the west and spot-tailed to the east. Other morphological characters used to define species within the group have been blue or green gloss to the dorsal plumage, and the presence or absence of a single minute tufted feather on the hallux. The value of these characters as taxonomic markers is now known to be unreliable due to the discovery of phenotypically mixed populations east of the Makassar Strait, from North Maluku province, Indonesia, through Papua New Guinea to New Ireland. We combine field observations of plumage characters with genetic evidence to establish taxonomy of *Collocalia* group swiftlets. Sequencing specific mitochondrial genes (*Cytb* and *ND2*), the nuclear-encoded *Fib* gene, and a subset of mitochondrial genomes provided data for phylogenetic analysis. Genetic divergence of *c.*4.7% is observed between two *Collocalia* clades either side of the Makassar Strait: the plain-tailed *C. affinis cyanoptila* sampled at Fraser's Hill, Peninsular Malaysia, and a phenotypically mixed population of *C. esculenta spilura* from North Maluku, Indonesia. Each population formed high-affinity genetic clades, within which divergence was <0.5%. These findings are consistent with geographic but not phenotypic separation between populations. We therefore conclude taxonomy based on these plumage features in glossy swiftlets of the Collocaliini is unreliable.

Reviewers of the complex of small, white-bellied glossy swiftlets, for which the oldest available name is *Collocalia esculenta* (Linnaeus, 1758), have given weight to certain phenotypic characters as taxonomic indicators distinguishing species or species groups. One character, first perceived by Wallace (1864), separates 'plain-tailed' and 'spot-tailed' species. The plain-tailed group occurs from the Andaman Islands, India, through Malaysia and Indonesia to Lombok. All members have glossy upperparts that are uniformly dark-coloured including the rump and tail. 'Spot-tailed' populations, from Sulawesi east through and beyond New Guinea, were believed by Wallace (1864), and thereafter by Stresemann (1940) and Somadikarta (1982, 1986), to be differentiated by a white spot on the concealed inner vane of all but the central pair of rectrices. In a review of speciation in the *C. esculenta* complex integrating phenotypic and molecular data, Rheindt *et al*. (2017) broadly confirmed Wallace's ideas, with some revision of species boundaries within these two groups.

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[*]The two first-named authors contributed equally to this work.

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Figure 1. The minute feather tuft on the hallux of *Collocalia affinis cyanoptila* (Earl of Cranbrook)

Among the plain-tailed group of white-bellied swiftlets a second indicator is variation in the green or blue tone to the glossy upperparts. This character has been linked to the presence or absence of a single, small tufted feather on the dorsal side of the hind toe (hallux). Within the western plain-tailed white-bellied swiftlets, excluding those populations in the Philippines, two species groups have been separated by this mix of characters (Somadikarta 1982, 1986). One consists of the species *C. a. affinis* (*sensu* Rheindt *et al*. 2017) on the Andamans, Nicobar and other islands, and *C. a. cyanoptila* from Sumatra, Peninsular Malaysia and Borneo. Within this group, members of three geographically separated colonies of *C. a. cyanoptila* in Selangor, Peninsular Malaysia, exhibited individual age- and wear-related change, from the greenish gloss of fresh plumage to blue gloss of old, worn plumage. Although differently glossed, all individuals in the separate populations were genetically uniform (Lim 1994). Members of this group bear a single, very small tufted feather on the hallux (Fig. 1). In the live bird, this feather is moulted around mid-term during primary moult in the wings, and for a period may be totally absent from one foot or both or, if present, sheathed and inconspicuous (Cranbrook *et al*. 2005). It can also be difficult to confirm presence or absence of this feather on the hallux in specimens. The feet (often tied together) must be separated to allow inspection with a lens, and are often in poor condition due to fungal infestation or other issues of imperfect preservation.

The other group within the western plain-tailed population includes *C. linchi* of Java, Bali, Lombok and intervening small islands. These birds are characterised by permanently green-glossed upperparts including the tail, and being invariably 'bare-toed', i.e., lacking the feather tuft on the hallux. There is more than one instance of sympatry involving the *C. linchi* superspecies and *C. affinis*. In Sabah, Malaysia, the endemic *C. dodgei*, a member of the *linchi* superspecies (Rheindt *et al*. 2017), overlaps in daily activity range with the more numerous local population of *C. affinis cyanoptila* (Cranbrook *et al*. 2005, Moyle *et al*. 2008). On Sumatra, Somadikarta (1986) reported overlapping ranges of *C. affinis cyanoptila* and *C. linchi ripleyi*, with a mixed colony in a cave at Talangpadang, South Lampung. Separation at species level is confirmed by divergence in *Cytb* mtDNA sequences of 6.03–7.20% (Table 3 in Rheindt *et al*. 2017).

On the grounds of exhibiting a spotted tail, Christmas Island white-bellied swiftlet *C. natalis* was regarded by Stresemann (1940) and Somadikarta (1986) as a geographically anomalous member of the *C. esculenta* group, lying west of the main boundary of separation, named 'Stresemann's Line' by Somadikarta (1986) (Fig. 2). However, mitochondrial *Cytb* sequence divergence from nominate *linchi*, at 1.10–1.45%, is 'shallow' and this island endemic, which displays a morphology unlike any other *Collocalia* species, was considered a member of the *linchi* superspecies (Rheindt *et al*. 2017). Removal of *C. natalis* restores Wallace's concept of the Makassar Strait as a natural boundary between western plain-tailed and eastern spot-tailed white-bellied swiftlets. Molecular studies support divergence

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between the clades separated by this boundary at 4.66–8.59% in mtDNA, regarded as 'deep' by Rheindt *et al*. (2017).

The possibility that plain-tailed white-bellied swiftlets might cross this boundary was raised by Mayr & Camras (1938); who noted a specimen of a plain-tailed, greenish-glossed, 'apparently young' bird resembling *C. linchi* of Lombok, among spot-tailed, blue-glossed *C. esculenta manadensis* on Sangihe (Sangir) Island, Sulawesi (also discussed by Salomonsen 1983: 31). S. Somadikarta (*in* Cranbrook *et al*. 2005) examined six additional specimens from Sangihe in the Bogor Zoological Museum, all of which had spotted tails. Rheindt *et al*. (2017) did not assess the implications of this single plain-tailed specimen east of Stresemann's Line, but did report a personal communication by Cranbrook, with photographs of four individuals at a single colony on Ternate, North Maluku province, Indonesia. These shared intensely blue upperparts and the lack of a feather tuft on the hallux, but two were plain-tailed and two spot-tailed. This contrasted with 24 specimens from North Maluku seen by Rheindt *et al*. (2017: 421), all with spotted tails, leading these authors to conclude that: 'the new, unpublished findings from Ternate suggest that the morphological division across Stresemann's Line may not be as clear-cut as previously assumed'.

Here we present the results of collective efforts from different research employing both field observations and genetic studies, with the aim of testing the taxonomic significance of the phenotypic characters that are conventionally used in *Collocalia* identification.

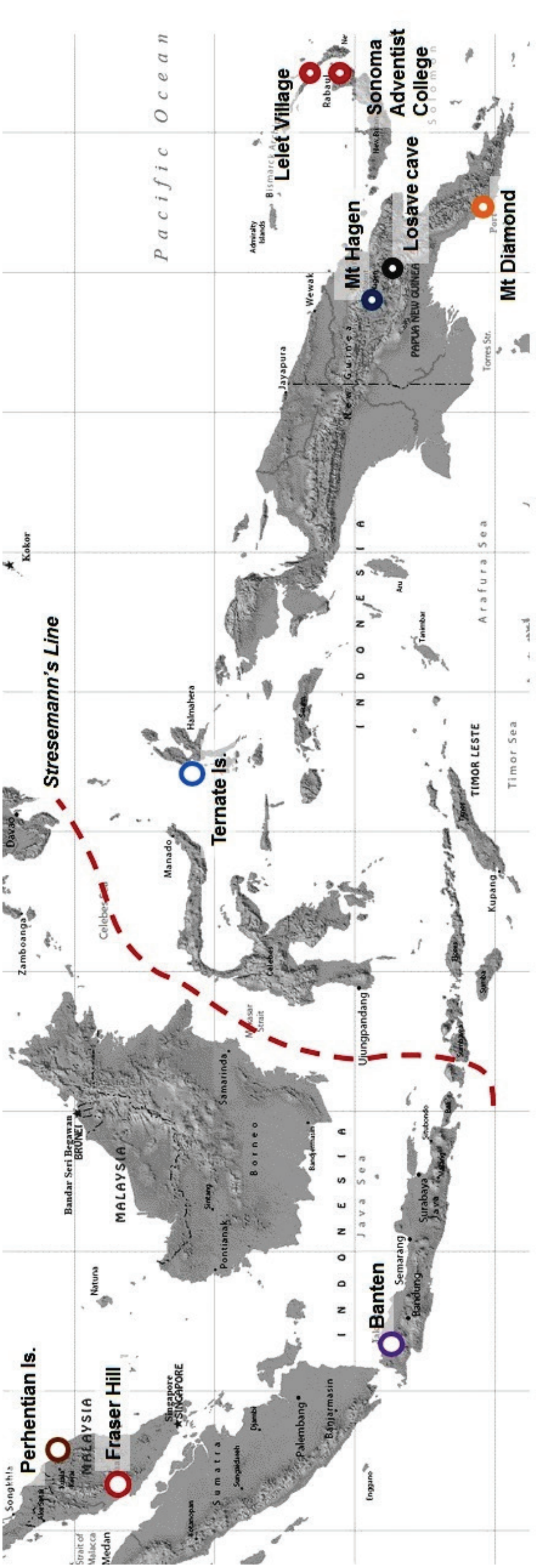

Figure 2. Locations where field observations and DNA material collection were undertaken, showing 'Stresemann's Line' as defined by Somadikarta (1986).

Materials and Methods

Field observations.—Scientific nomenclature *sensu* Rheindt *et al*. (2017) is followed. Locations are given as coordinates, usually taken directly from GPS readings, and elevation as metres above sea level (m). Fig. 2 shows the locations mentioned in the text.

East of the Makassar Strait, in Papua New Guinea, on nine occasions between August 2000 and August 2005, MT, with students from the Pacific Adventist University, handled 275 *C. esculenta nitens* at the abandoned copper mines on Mt. Diamond, Central province (*c*.09º46.4362″S, 147º32.4446″E; 68 m). Smaller samples were taken at Losave Cave, near the Chimbu / Eastern Highlands province border (06º64.8333″S, 145º15.8889″E; 1,425 m); at a cave 5 km west of Kumul Lodge in Western Highlands province (05º77.9853″S, 143º95.9424″E; 2,614 m), and from one bird caught on the western peak of Mt. Hagen (05º76.4172″S, 144º02.1167″E; 3,670 m) (Table 2). From four nests of *C. esculenta tametamele* in the Japanese tunnels at Sonoma Adventist College, New Britain (*c*.04º42.7326″S, 152º23.9931″E; 171 m) one adult was caught and measured. At a cave near Lelet village (03º25.1350″S, 151º96.1743″E; 200 m) on New Ireland, 65 *C. esculenta heinrothi* were caught and examined. All of these birds were released after handling. Additionally, in 2016, four birds, identified on geographical grounds as *C. esculenta spilura* (see Coates & Bishop 2000) were caught using a mist-net at a nesting colony below a road bridge over a deep and precipitous river gully on the lower flank of Gunung Gamalama (07º97.182″S, 127º36.8507″E; 204 m) on Ternate, North Maluku province, Indonesia.

Plain-tailed swiftlets were sampled as follows: in 2015, one bird, taken from a small colony of Linchi Swiftlets *C. l. linchi*, at a swiftlet house-farm at Cacaban, Banten Residency, Java, Indonesia (06º10.8828″S, 106º00.1381″E; 61 m); and in 2016, five White-bellied Swiftlets *C. affinis cyanoptila* at a colony in the garage of Buona Vista (Stephen's Place), Fraser's Hill, Pahang, Peninsular Malaysia (03º71.5903″N, 101º75.0444″E; 1,292 m). As outgroup (for complete mitochondrial genome analysis), one Black-nest Swiftlet *Aerodramus maximus* was included from the Perhentian Islands, Terengganu, Peninsular Malaysia (05º96.3306″N, 102º68.3333″E; 3 m).

DNA materials.—Samples for genetic analysis were obtained by plucking one feather from each of the left and right wings in the primary tract; preferentially p3 or p4 (numbered centrifugally). Approximately 0.5 cm at the base of the rachis was cut off with fine scissors and immediately preserved in 70% or 90% ethanol. The birds were then released, apart from five, which were humanely killed by compression of the thorax; breast muscle was excised and immediately preserved in 90% ethanol.

Molecular procedures.—DNA was extracted from preserved material using standard procedures—HiYieldPlus DNA Mini Kit (Real Biotech Corporation) and Wizard Genomic DNA Purification Kit (Promega), following the manufacturers' instructions. Polymerase chain reactions (PCRs) were set up following the primers and conditions in Price *et al*. (2004) for the mitochondrial cytochrome-b (*Cytb*) and NADH dehydrogenase 2 (*ND2*), and Thomassen *et al*. (2005) for the nuclear beta-fibrinogen gene *(Fib*) region, which spanned the partial exon 8, complete intron 7 and partial exon 7 regions. Direct sequencing was performed commercially by FirstBase Laboratory Sdn. Bhd. Samples for next-generation sequencing were prepared using the Nextera DNA Sample Preparation Kit (Illumina, #FC-121-1031), according to the manufacturer's instructions. Next-generation sequencing was performed with a 4nM library on an Illumina MiSeq 600 bp v3 (2×300 bp) following standard procedures.

Data analysis.—We employed both multi-gene phylogenetic and phylogenomic analyses. The former was performed based on the mitochondrial *Cytb* and *ND2* regions, and the nuclear *Fib7* region; published DNA data from other congeners was incorporated into our analyses. Phylogenomic analysis, based on the mitochondrial genomes, was also performed for a subset of samples.

Phylogenetic analysis for Cytb+ND2 and Fib genes.—Twelve DNA sequences of *C. affinis*, *C. esculenta* and *C. linchi* published in previous studies were randomly retrieved from GenBank (Table 1) and added to our phylogenetic analyses based on *Cytb* and *ND2*. Two house-farm white-nest swiftlets, *Aerodramus* sp., and a white-nest swiftlet *A. fuciphagus vestitus* from a Middle Baram cave, Sarawak, Malaysia (Goh *et al*. 2018) were included as outgroups. MtDNA data from the other *Collocalia* taxa deposited by Price *et al*. (2004) were also included (Table 1). Analysis based on *Fib7* employed two outgroup species, i.e., the house-farm swiftlets (161803i, 161703f, 151020f; Goh *et al*. 2018) which were newly sequenced for this study, and *A. maximus* M2–M5 (Thomassen *et al*. 2005). All sequences

TABLE 1
Additional DNA sequences (Price *et al*. 2004 and Thomassen *et al*. 2005) included in the present study.

Taxa	**Voucher**	**Locality**	**GenBank accession numbers**		
			Cytb	***ND2***	***Fib7***
A. maximus	DHC03	Sabah	AY294449	AY294511	–
A. maximus	DHC117	Sabah	AY294445	AY294509	–
A. maximus	DHC120	Sabah	AY294446	AY294508	–
A. maximus	DMT040	Sabah	AY294446	AY294509	–
A. maximus	M2	Borneo	–	–	AY513100
A. maximus	M3	Borneo	–	–	AY513098
A. maximus	M4	Borneo	–	–	AY513099
A. maximus	M5	Borneo	–	–	AY513101
C. affinis	DMT059	Selangor	AY294460	AY294522	–
C. affinis	DMT057	Selangor	AY294459	AY294521	–
C. affinis	DMT051	Sandakan	AY294457	AY294519	–
C. affinis	DMT050	Sandakan	AY294458	AY294520	–
C. affinis	DHC88	Lahad Datu	AY294455	AY294517	–
C. affinis	DHC97	Lahad Datu	AY294456	AY294518	–
C. esculenta	FMNH358301	Sibuyan	AY294463	AY294525	–
C. esculenta	FMNH358303	Sibuyan	AY294464	AY294526	–
C. esculenta	ATP92.280	Mindanao	AY294462	AY294524	–
C. esculenta	ATP92.131	Mindanao	AY294461	AY294523	–
C. esculenta	MSP068	New Guinea	AY294466	AY294528	–
C. linchi	DHC72	Bogor	AY294467	AY294529	–

TABLE 2
Morphometric data for *Collocalia esculenta nitens* from Papua New Guinea.

		Mass			**Wing length**		
Location where birds were sampled	**Date of sampling**	**Mass (g) ± se**	**Range**	***n***	**Wing length (mm) ± se**	**Range**	***n***
Mt. Diamond	2005–08	6.6 ± 0.02	6.0–8.5	275	102 ± 0.16	91–109	239
Losave Cave	9 June 2000	6.7 ± 0.07	6.0–7.3	22	105 ± 1.05	94–111	15
5 km west of Kumul Lodge	23 July 2005	6.6 ± 0.08	6.4–6.9	7	111.9 ± 1.14	109–118	7
Mt. Hagen (western peak)	18 July 2005	7.6		1	115.5*		1

* Large size attributed to high-elevation habitat (MT)

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obtained for this study are deposited in GenBank (accession numbers: MH727218–226). All sequences were aligned using ClustalX2 v.2.1 (Thompson *et al*. 1997) and manually edited and trimmed in BioEdit (Hall 1999).

Maximum Parsimony (MP) analysis was performed using PAUP4.0b10 (Swofford 2002). The strict consensus tree was reconstructed using heuristic search with 100 random-sequence additions, tree bisection reconnection (TBR) branch swapping and 1,000 bootstrap replications. Bootstrap support (BS) values >70% were considered reliable.

The best-fit models (GTR+G for mtDNA and HKY for nuclear DNA) for the Bayesian Inference (BI) were identified using MrModeltest2.2 (Nylander 2004). BI analyses were run in MrBayes3.1 (Huelsenbeck & Ronquist 2001), using two runs of four chains each, and run for 10,000,000 generations with trees sampled every 100 generations. The first 2,500 trees were discarded as burn-in. Posterior probabilities (PP) >0.90 were considered a strong support in this study.

Phylogenomic analysis of mitochondrial genomes.—Next-generation sequence data for phylogenomic analysis was generated using an Illumina MiSeq. A novel mitochondrial genome scaffold was constructed using Integrated Genome Viewer (IGV) v2.3.88 (Robinson *et al*. 2011, Thorvaldsdóttir *et al*. 2013) from the consensus sequences of five *Collocalia affinis cyanoptila* sampled at Fraser's Hill. The hyper-variable D-loop region (517 bp) was excluded from analysis, leaving a mitochondrial sequence length of 15,564 bp. For the four birds sampled on Ternate and five *C. a. cyanoptila* from Fraser's Hill, MiSeq data was quality-assessed and re-sequenced against this scaffold using the on-instrument Illumina MiSeq Reporter Software. Additionally, two genetic outgroups were included: one *C. l. linchi* sampled at Cacaban, Java, and one *Aerodramus maximus* from the Perhentian Islands, Malaysia. The *A. maximus* sample was re-sequenced against a novel mitochondrial scaffold constructed from house-farmed birds of the region. Re-sequenced mitochondrial genomes were manually curated in IGV to produce a consensus sequence for each bird. Sequences obtained for this study are deposited in GenBank [accession number(voucher)]: MT123507(bd108_162710a), MT123508(bd109_162710b), MT123509(bd110_162710c), MT123510(bd111_162710d), MT123511(bd112_162810a), MT921253(bd072_160803a), MT921254(bd073_160803b), MT921255(bd074_160803c), MT921256(bd075_160803d), MT921257(bd006_15200618), MT921258(bd097_162003a). Mitochondrial genome sequences for the 11 birds were aligned using MUSCLE (Edgar 2004). The best-fit model (GTR+G) for Maximum Likelihood phylogeny was selected and performed using MEGA7 (Tamura 2013), with 1,000 Bootstrap replications. Bootstrap values >70% were considered strong support. Estimates of genetic divergence (uncorrected *p*-distances) were computed in MEGA7.

Results

Tail spots.—East of Stresemann's Line (Fig. 2), among some 303 glossy swiftlets, *C. esculenta* subspp. examined, from three cave colonies and one mountain peak in mainland Papua New Guinea, and one cave on New Ireland (Table 2), three birds had no spots on the rectrices. Others had spots on one, two, three or four rectrices between rr2–5 (never on the central pair). Moreover, spots were variable in size, sometimes large, sometimes small (1 mm diameter) and not always equal or present on matching feathers on either side of the tail. One bird from Mt. Diamond had a very small spot on one feather on the right side, but none on any of the left rectrices. Another from the same colony had an extremely small spot on just r3. One bird from the Losave colony also had a very small spot on just one rectrix.

The small sample of four birds on Ternate were all mist-netted in flight and evidently adult. One had lost the right r4, but otherwise the flight feathers were entirely unmoulted, and fresh in appearance. Two conformed to the description in Coates & Bishop (2000) of

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C. esculenta spilura, being intensely glossed blue on the upperparts including the dorsal tail-coverts, with white spots on the inner webs of all but the central pair of rectrices. The other two (identical to each other) were similarly intensely blue-glossed above, including the dorsal tail-coverts and tail, but all rectrices were uniform black, glossed blue, with no indication of any white spot on the inner vanes (Figs. 3–4). The hind toes of all four birds lacked a small dorsal tuft.

Green to blue gloss transition.—Repeated sampling of *C. esculenta nitens* at the Mt. Diamond colonies revealed an age-related trend from greenish to blue gloss, as observed for *C. affinis cyanoptila* by Lim (1994). The greenish gloss of a newly moulted bird (Fig. 5) gives way after a few months to a mixture of green and bluish gloss (Fig. 6). Just prior to moult the dorsal plumage exhibits a deep blue surface, with much less gloss, as the feather transmits less light via refraction and reflects more (Fig. 7). Confirmation that these are the stages of change is observed when, at the same nest, a blue adult is perched alongside its young with a green gloss (Fig. 8).

Presence of feather tuft on the hallux.—At three colonies of *C. esculenta* in mainland Papua New Guinea and one on New Ireland, 21% of swiftlets examined had a feather tuft on the hind toe.

Molecular phylogenetic analyses*: Cytb + ND2 *and* Fib7 *dataset.—The *Cytb* + *ND2* sequence data were aligned into a data matrix of 1,213 characters, of which 204 characters are parsimony-informative. For the *Fib7* dataset, 32 of 932 characters are parsimony-informative. For each dataset, phylogenetic analyses using BI and MP methods resulted in largely consistent tree topologies, thus only BI topologies are presented here (Figs. 9–10).

In our phylogenetic tree based on the mitochondrial *Cytb* and *ND2* data (Fig. 10), all five individuals of *C. affinis cyanoptila* sampled at Fraser's Hill form a clade (PP 1.00 / BS 100%) with the *Collocalia* individuals collected from Selangor, Sandakan and Lahad Datu (referred to *C. esculenta cyanoptila* by Price *et al*. 2004). *C. marginata* and *C. isonata bagobo* from the Philippines (named *C. esculenta marginata* and *C. e. bagobo* by Price *et al*. 2004) resolve into a cluster with high support (PP 1.00 / BS 95%). The two plain-tailed *C. esculenta* sampled on Ternate form a clade (PP 1.00 / BS 100%) with three other *C. esculenta*, including the two spot-tailed individuals sampled on Ternate by the present study.

Phylogenetic analyses based on the nuclear *Fib7* marker (Fig. 10) again showed high affinity (PP 1.00 / BS 100%) between all four *Collocalia* individuals sampled on Ternate irrespective of tail pattern. They appeared genetically uniform and distant from the *C. affinis cyanoptila* sampled at Fraser's Hill (where only two representatives could be sequenced for the *Fib7* marker).

Mitochondrial genomes.—Phylogenetic analyses based on 'whole' mitochondrial genomes (excluding the hypervariable D-loop region) of a subset of individuals are shown in Fig. 11. Exclusion of the D-loop did not significantly affect genetic divergence or phylogeny results, and resulted in a sequence length of 15,564 bp of mtDNA. The four *Collocalia* individuals sampled on Ternate form a genetically distinct clade with high support (BS 100%), and the five *C. affinis cyanoptila* individuals at Fraser's Hill form another clade (BS 100%), distinct from Ternate birds. These results corroborate the *Cytb* and *ND2* sequence and nuclear *Fib7* marker phylogenies (Figs. 9–10).

Genetic divergence across the mitochondrial genome between the Ternate *C. esculenta spilura* clade and the Fraser's Hill *C. affinis cyanoptila* clade was estimated at 4.68% (Table 3). Both clades are equally genetically distant from the *C. l. linchi* specimen sampled on Java, with 4.74–5.00% divergence. The genetic outgroup for this study, *Aerodramus maximus*, showed a deep genetic divergence of 9.43–9.86% from all *Collocalia* specimens tested.

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Figure 3. One of two plain-tailed *Collocalia esculenta spilura*, Mt. Gamalama road bridge, Ternate, Indonesia, August 2016 (Sian E. W. Davies)

Figure 4. One of two spot-tailed *Collocalia esculenta spilura*, Mt. Gamalama road bridge, Ternate, Indonesia, August 2016 (Sian E. W. Davies)

Figure 5. Adult *Collocalia esculenta nitens* displaying large tail spots and the green gloss of fresh plumage, Mt. Diamond, Papua New Guinea, October 2000 (Michael Tarburton)

Figure 6. Another adult *Collocalia esculenta nitens* midway through moult, displaying a mix of blue and green, Mt. Diamond, Papua New Guinea, September 2003 (Michael Tarburton)

Figure 7. Adult *Collocalia esculenta nitens* just prior to moulting, showing its deep blue plumage, Mt. Diamond, Papua New Guinea, August 2001 (Michael Tarburton)

Figure 8. A blue-glossed adult of *Collocalia esculenta nitens* with old plumage (on left) perched alongside its young in fresh green plumage, Mt. Diamond, Papua New Guinea, September 1999 (Michael Tarburton)

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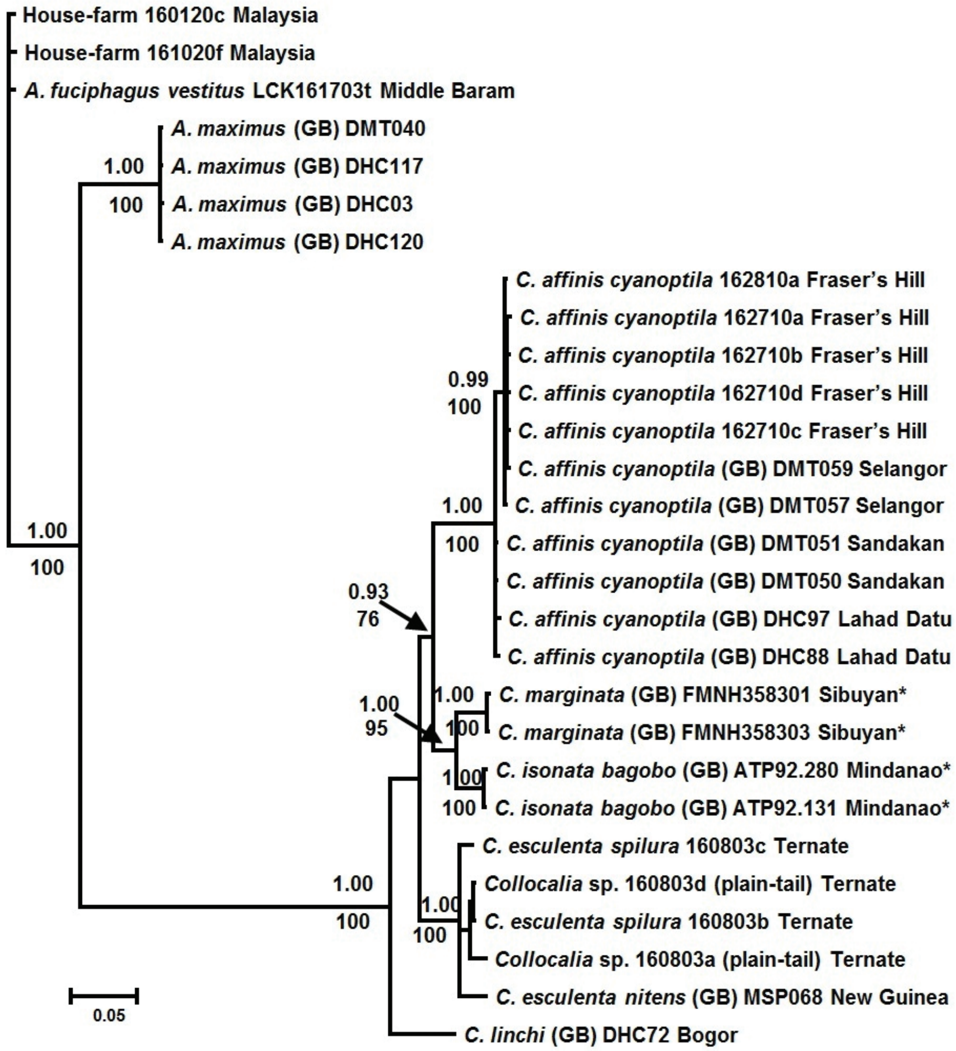

Figure 9. Phylogenetic tree based on the mitochondrial *Cytb* + *ND2* regions (1,213 bp) reconstructed using Bayesian Inference. Numbers above the nodes indicate posterior probabilities >0.90. Bootstrap support values >70% in the maximum parsimony analysis were mapped on the Bayesian topology. Sequences retrieved from GenBank (GB) were published in Price *et al*. (2004). '*' = *Collocalia* taxa from the Philippines not covered in this paper.

As would be expected from near full-length mitochondrial sequences, genetic differences were observed between individuals within both *Collocalia* clades, with divergence of 0.40% within the Ternate group and 0.07% in the Fraser's Hill group. There was high support (BS >70%) for the presence of multiple genetic subclades or maternal lineages within the Ternate group. However, these distinctions did not correlate with the presence or absence of tail spots.

Discussion

Tail spots.—Our observations reveal that, among the population of *C. esculenta spilura* on Ternate, some individuals (50% of the tiny sample of four) were entirely plain-tailed.

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TABLE 3

Genetic (nucleotide) divergence across mitochondrial genomes (total length 15,564 bp, excluding the D-loop region). (A) Genetic divergence between groups: percentage divergences (%) are shown in the lower left of the table, with corresponding standard deviations at the upper right. (B) Genetic divergence within groups. Percentages shown are estimates of evolutionary distance (*p*-distance) over nucleotide sequence pairs, with standard deviations.

(A) Genetic divergence between groups as %, ± standard deviation (s.d.)

	***Collocalia linchi linchi* (Java)**	***Collocalia esculenta spilura* (Ternate)**	***Collocalia affinis cyanoptila* (Fraser's Hill)**	***Aerodramus maximus* (Perhentian Islands)**
***Collocalia linchi linchi* (Java)**		± 1.3 × 10^{-3}	± 1.8 × 10^{-3}	± 2.6 × 10^{-3}
***Collocalia esculenta spilura* (Ternate)**	4.739 %		± 1.3 × 10^{-3}	± 2.9 × 10^{-3}
***Collocalia affinis cyanoptila* (Fraser's Hill)**	5.001 %	4.677 %		± 2.9 × 10^{-3}
***Aerodramus maximus* (Perhentian Islands)**	9.430 %	9.516 %	9.858 %	

(B) Genetic divergence within populations as %, ± standard deviation (s.d.)

	Evolutionary distance	**Standard deviation**
***Collocalia esculenta spilura* (Ternate)**	0.400 %	± 3.4 × 10^{-4}
***Collocalia affinis cyanoptila* (Fraser's Hill)**	0.074 %	± 1.4 × 10^{-4}

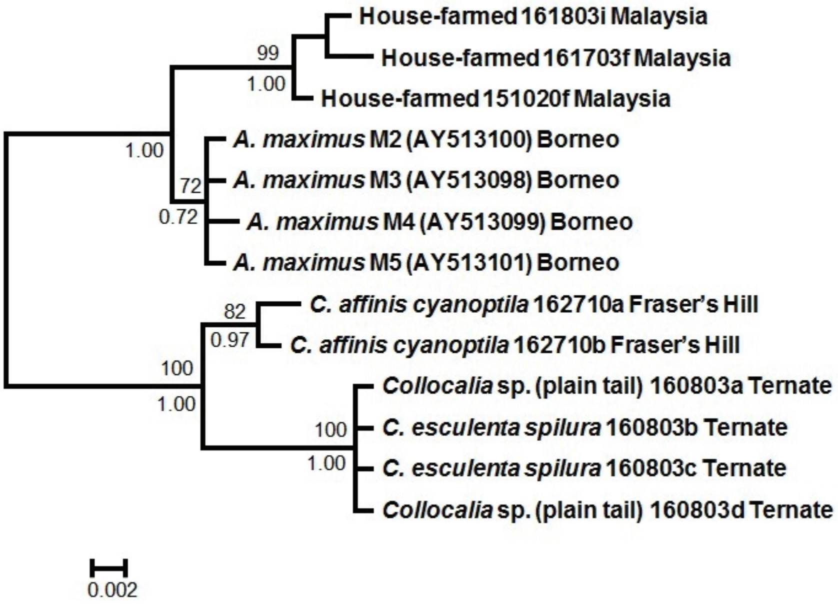

Figure 10. Phylogenetic tree based on the nuclear beta-fibrinogen intron 7 region (935 bp) reconstructed using Bayesian Inference. Numbers above the nodes indicate posterior probabilities >0.90. Bootstrap support values >70% in the maximum parsimony analysis were mapped on the Bayesian topology.

Yet mtDNA sequencing confirms that these two birds were genetically very close to the two spot-tailed swiftlets at the same colony (genetic divergence of 0.40% among the four). Variation in the phenotypic expression of this character among a larger sample of *C. esculenta* in Papua New Guinea was very diverse, and included three with plain (unspotted) tails. i.e., *c*.1% of all birds examined. Although genetic information is not available for these Glossy Swiftlets, the observations are convincing evidence of phenotypic polymorphism among these populations.

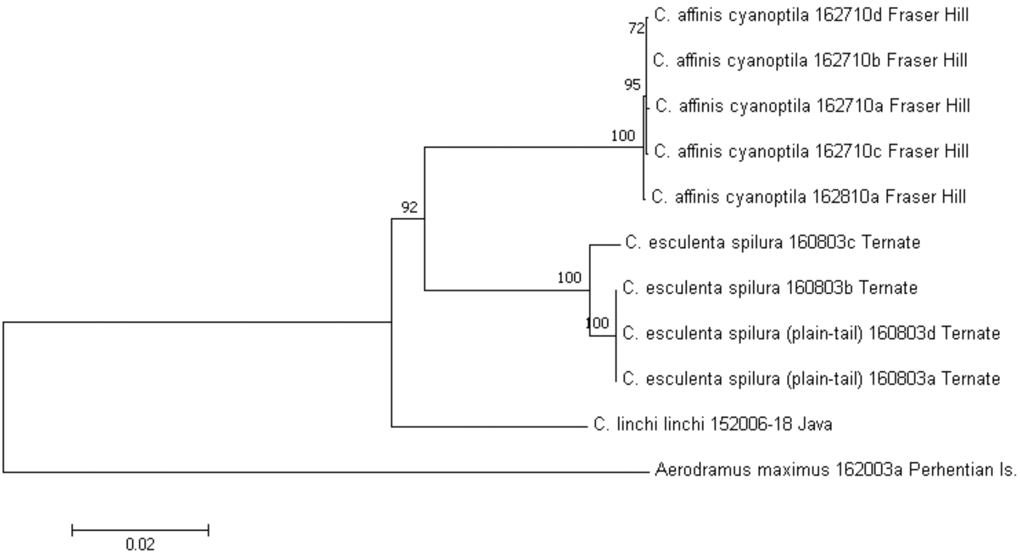

Figure 11. Phylogenetic tree based on novel assembled 'full-length' (with D-loop excluded) mitochondrial genomes (15,564 bp) constructed using Maximum Likelihood with the GTR+G model. Bootstrap support values >70% are indicated above the nodes.

Green and blue gloss.—Between the species (and subspecies) of *C. affinis* and *C. linchi*, variation in the colour of dorsal gloss is supported by genomic evidence (Cibois *et al*. 2018: Fig. 9), and is therefore confirmed as a useful taxonomic indicator. On the other hand, the succession of images of swiftlets at the Mt. Diamond colonies of *C. esculenta nitens* shows age- and wear-related progress from greenish to blue gloss. It is evident that greenish or blue dorsal gloss cannot be considered a character of taxonomic significance among this member of the *C. esculenta* group.

Feather tuft on hallux.—The difficulty of confirming the presence or absence of the single feather tuft on the hallux in *C. affinis cyanoptila*, described by Cranbrook *et al*. (2005), cautions against generalisations as to the prevalence of this character. If this minute feather is shed about mid-term in the slow progression of the moult of the primaries, its absence in an individual should be checked against the moult state of that bird. Variation in New Guinea swiftlets raises doubts that this character is of general taxonomic significance in the *C. esculenta* complex.

Genetic relationships.—Phylogenetic analysis of the mitochondrial markers *Cytb* and *ND2* revealed that the maternal genetic lineages of *Collocalia* may split along geographical lines. This is corroborated by phylogenies produced from the nuclear gene marker *Fib7*. *Cytb* and *ND2* data placed birds sampled at Fraser's Hill within a super-clade of *C. affinis cyanoptila*, comprising two distinct subclades corresponding to Peninsular Malaysia and Bornean Malaysia (Fig. 9).

In both *Cytb* + *ND2* and *Fib7* datasets, the *C. esculenta spilura* sampled on Ternate formed a separate clade. This clade did not cluster with *Collocalia* from the Philippines, which were placed west of Stresemann's Line by Somadikarta (1986), but instead formed a clade with *C. esculenta nitens* from Papua New Guinea (Fig. 9), confirming that plumage variation in Ternate birds does not represent migration from western populations.

This suggestion was corroborated by analysis of mitochondrial genome sequences from a subset of individuals in this study, including the four Ternate *C. e. spilura* and five *C. a.*

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cyanoptila from Fraser's Hill, in addition to *C. linchi* and *A. maximus* outgroups (Table 3). This analysis enabled evaluation of genetic divergence across a larger region (15,564 bp vs. *c*.2,000 bp for *ND2* + *Cytb* combined), thereby increasing confidence in the calculated divergence values: <0.5% within species, *c*.5% between species, and *c*.10% between genera from the sequenced mitochondrial genomes. These are broadly consistent with values from short (*c*.400 bp) mitochondrial fragments (Rheindt *et al*. 2017).

There was a very close genetic relationship between all four Ternate swiftlets, with a within-group evolutionary distance of 0.400%, comparable to that among Fraser's Hill birds (0.074%). The Ternate group was equally distant from *C. l. linchi* on Java (4.739%) and *C. a. cyanoptila* at Fraser's Hill (4.677%). This distance is equivalent to that between *C. a. cyanoptila* and *C. l. linchi* (5.001%), suggesting a species-level divergence of *c*.5% among *Collocalia*, and that these three species are equally distinct from each other. In addition, all three were equally distant from the *Aerodramus maximus* outgroup, each divergent by *c*.10%. These data imply that tail-spot variation within the Ternate population cannot be attributed to genetic input from another species.

Genetic analyses of mitochondrial and nuclear DNA reveal geographic separation of phylogenies, which do not correlate with the phenotypic characters traditionally used as taxonomic indicators, such as tail spots, green and blue gloss, and hallux feather tuft.

Conclusions

Our observations consolidate the deep divergence at 4.66–8.59% mtDNA, reported by Rheindt *et al*. (2017) between the clades of *Collocalia* spp., separated by the Makassar Strait, and further refine it to *c*.5% (4.677–5.001%) via comparison of long mitochondrial sequences (15,564 bp *cf*. *c*.400 bp in Rheindt *et al*. 2017). Our phylogenetic results support the separation by Rheindt *et al*. (2017) of the *Collocalia esculenta* complex into the 'western *linchi*', 'western white-bellied swiftlet' (*C. affinis*) and 'eastern *C. esculenta*' groups. It is, however, now clear that this phylogenetic separation is not expressed phenotypically, by the presence or absence of white spots on the concealed rectrices. The spot-tailed Christmas Island Swiftlet *C. natalis* is a member of the *C. linchi* group. Two plain-tailed birds on Ternate were genetically inseparable from two spot-tailed *C. esculenta spilura* in the same colony, and relatively distantly related to plain-tailed swiftlets *C. affinis cyanoptila* of Peninsular Malaysia and Borneo. *C. esculenta* in Papua New Guinea displayed great variation in the size, distribution and, rarely, absence (<1% of the sample) of concealed white spots on the rectrices, and 21% of the sample had a small feather tuft on the hallux. These comparisons support Somadikarta's (1986) contention that swiftlets of the *C. esculenta* complex cannot be divided into species by single morphological characters.

A comparatively small sample led Rheindt *et al*. (2017) to conclude that all populations of *C. esculenta* throughout mainland New Guinea have intensely blue-glossed dorsal plumage and clearly marked tail spots, and usually no feather tuft on the hind toe. Based on our observations of phenotypic variation in *C. esculenta* subspecies extending from North Maluku through Papua New Guinea to New Ireland, this conclusion needs to be amended, for the benefit of other students of white-bellied swiftlets and to prevent misleading statements in future regional avifaunas.

Genetic data presented by Cibois *et al.* (2018) from Western Pacific glossy swiftlets showed that the white-rumped taxon *albidior* of New Caledonia, rather than being a subspecies of Satin Swiftlet *C. uropygialis* of Vanuatu, was embedded within *C. esculenta becki* of the Solomon Islands, and *C. e. nitens* of New Guinea. This result suggests that further work may reveal that rump coloration is also not a taxonomically significant indicator among some *C. esculenta* species.

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Remarks on extinct giant owls (Strigidae) from Cuba, with description of a new species of *Ornimegalonyx* Arredondo

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Summary.—A revision of large extinct members of Strigidae described from Quaternary cave deposits in Cuba here reduces the number of valid taxa from five to three. *Ornimegalonyx oteroi* Arredondo, 1958a, is the only valid species of the four previously described in the genus. The type series of *Bubo osvaldoi* Arredondo & Olson, 1994, is revealed to be a composite, comprising two different species in the genera *Bubo* Duméril, 1805, and *Ornimegalonyx* Arredondo, 1958a, with the latter described herein as a new, diminutive species.

Confused with a terror bird (Phorusrhacidae Ameghino) because of its gigantic size (Arredondo 1954, 1955, 1956, 1957a,b, 1958a,b, Koopman 1958), the extinct genus *Ornimegalonyx* was erected by Arredondo (1958a) on the basis of post-cranial elements from Cueva de Pío Domingo, Pinar del Río province, western Cuba. The material was collected from the floor of the cave on 2 January 1954 by members of the Sociedad Espeleológica de Cuba (SEC). Subsequently, Brodkorb (1961) realised that this taxon actually belonged to the family Strigidae due to the presence of an ossified supratendinal bridge in the tarsometatarsus. He designated a lectotype for the type species: *Ornimegalonyx oteroi* Arredondo, 1958a. Arredondo (1975) later summarised the taxonomic history of *O. oteroi*, including synonyms, new material and localities. He believed that a number of specimens that were larger or smaller than the type material (a single individual) represented new species (*contra* Brodkorb's opinion, see Arredondo 1975: 140). Apparently discarding the possibility of considerable intraspecific variation in so large a raptor (see also Kurochkin & Mayo 1973: 59), those specimens, mostly from western Cuba, were described as *O. acevedoi*, *O. minor* and *O. gigas*, respectively, with the result that four synchronic species in the genus were recognised as having occurred sympatrically in Cuba during the Quaternary (Arredondo 1982: 45–47).

In 1947, a decade prior to the description of *Ornimegalonyx*, A. Moreno of the Museo Felipe Poey, La Habana, sent to A. Wetmore, at the Smithsonian Institution, Washington DC (USNM), two fossil bones of a large bird from eastern Cuba for study (Arredondo & Olson 1994: 436). Wetmore (1959: 15) identified them as a giant barn owl, Tytonidae, but this was never published. Thirty-five years later, Arredondo & Olson (1994) reassessed the material (Fig. 1B–C)—a near-complete right femur (USNM 447022) and partial humerus (USNM 447023). They identified it with fossils of a large extinct strigid discovered in western Cuba, which was named *Bubo osvaldoi* Arredondo & Olson, 1994. Both east Cuban bones were included in the type series of *B. osvaldoi* because they 'probably belong to the same species as represented by the bones from Pinar del Río [west Cuba], which cannot be referred to any known species of owl, living or fossil' (Arredondo & Olson 1994: 436).

I have now had the opportunity to study fossil and living Strigiformes from the West Indies (Olson & Suárez 2008, Suárez & Olson 2015, 2020) for some years, and have collected and examined material pertaining to *Ornimegalonyx* in Cuba (see, for example, Alegre 2002, Suárez 2020), as well as the type material of *Bubo osvaldoi* including specimens at the Museo

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Figure 1. Left humeri (A–B, palmar view) and right femora (C–D, anterior view) of three large owls: (A) *Bubo bubo* (Linnaeus, 1758), large female (USNM 610384); (B) *Ornimegalonyx ewingi* sp. nov. (paratype, USNM 447023 [paratype of *Bubo osvaldoi*]); (C) *O. ewingi* sp. nov. (holotype, USNM 447022 [paratype of *B. osvaldoi*]); (D) *B. osvaldoi* (paratype, MNHNCu 75.27.3 [formerly MNHN 27.3]). Scale = 2 cm. Modified from Arredondo & Olson (1994: figs. 2 and 4) with permission of the *Proceedings of the Biological Society of Washington*.

Nacional de Historia Natural de Cuba (MNHNCu), La Habana. After comparisons with living and extinct taxa, including *Bubo*, I have discovered that the type series of *B. osvaldoi* is a composite, comprising two different large strigid owls that are similar in size. The holotype of *B. osvaldoi*, a right tarsometatarsus (MNHNCu 75.27.1), and two topotypical paratypes (cited here with their original numbers), a femur (MNHNCu 75.27.3) and a shaft of tarsometatarsus (MNHNCu 75.27.2), are from western Cuba, assigning the name *Bubo osvaldoi* to that form. However, the two remaining USNM bones, from the eastern extreme of the archipelago, belong to a species that agrees with *Ornimegalonyx* and differs from *Bubo* Duméril, 1805, by the following qualitative characters (see Arredondo & Olson 1994: figs. 2A, 3A–D; Fig. 1): (1) humerus small, having (2) shaft (palmar and / or anconal aspect) thinner proximally (also unlike large extinct Tytonidae), with (3) marked curvature and (4) impression of brachialis anticus reduced; femur (anterior and / or posterior aspect) with (5) shaft wider at ends (less expanded in *Bubo*), (6) anterior intermuscular line crossing (transversal) completely the anterior face of the shaft, from proximal (more lateral) to distal (medial) margins of the bone, not parallel with borders of the shaft (parallel, or almost

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TABLE 1

Measurements (mm) of the holotype femur of *Ornimegalonyx ewingi* sp. nov. (USNM 447022) compared to those of the type species of the genus, *O. oteroi*. Measurements by WS unless otherwise stated. Sequence: range (mean, sample size).

Character	***O. ewingi* sp. nov.**[a]	***O. oteroi***
Femur		
Total length	112.4	130.0*–168.0 (163.0, n = 6)
Proximal width	27.7	32.2–45.9 (40.1, n = 10)
Midpoint shaft width	11.5	13.6–20.0 (16.6, n = 10)
Midpoint shaft depth	9.9	12.4–17.6 (14.4, n = 6)
External condyle depth	21.9	24.3–33.4 (31.6, n = 10)

[a] Arredondo & Olson (1994: 439, table 1).

[*] Arredondo (1982: table 6).

parallel in *Bubo*), (7) anterior face of the shaft very flat above condyles (more rounded or convex in *Bubo*; some characters, including this one, were incorrectly depicted in Arredondo & Olson 1994: fig. 3), (8) rotular groove extremely wide, with condyles placed far apart (closer together in *Bubo*), and (9) external condyle bent laterally (not, or less bent in *Bubo*).

I was unable to detect any diagnostic character, or distinction, between the highly variable material of *O. oteroi* (with chronoclines at some localities; WS unpubl.) and specimens of the other three species described in the genus (see Arredondo 1982: 45–47). But all of the material agrees in intraspecific variation observed in skeletons of modern Strigidae. The most enigmatic of the extinct taxa is *O. minor*, of which the type material, two fragmentary proximal femora (Arredondo 1975: fig. 9; 1982: fig. 14), was unavailable to me until recently. These fossils were sent to B. Patterson at the Museum of Comparative Zoology (MCZ), Harvard Univ., MA, by O. Arredondo (see Arredondo 1975: 139). Thanks to S. L. Olson, this material and that of other Cuban taxa at MCZ, were sent on loan to USNM, were I examined it. No differences other than sexual were observed in *O. minor*, of which material named by Arredondo appears to represent the male (smaller sex) of *O. oteroi*. The holotype, a proximal right femur (SEC P-37), is the smaller of the two specimens, and Arredondo (1982: table 6) estimated its total length at 130 mm. The paratype, a proximal left femur (SEC P-38), is larger than the holotype, with a fractured trochanter. This fragment of bone is similar in size to other specimens previously identified by Arredondo (in some cases in my company) as *O. oteroi*; but its measurements (see Table 1) were not included in the original description of *O. minor*. If we take the above-mentioned estimated length of the holotype of *O. minor* as correct, which persuaded Arredondo to describe it as a new species, we have a strigid too large for the *Ornimegalonyx* material previously included within *Bubo osvaldoi* (see Table 1).

In conclusion, of the species previously referred to *Ornimegalonyx* only *O. oteroi* Arredondo, 1958a, is valid; the other three described by Arredondo (1982) are junior subjective synonyms. The much smaller species *Bubo osvaldoi* Arredondo & Olson, 1994, is represented solely by material from the type locality in Pinar del Río in western Cuba, whereas two other specimens from its type series, collected in eastern Cuba, are representative of a previously undescribed *Ornimegalonyx*, as diagnosed above. This is named below, in the following taxonomic arrangement:

Order STRIGIFORMES
Family STRIGIDAE Leach
Genus *Bubo* Duméril, 1815
***Bubo osvaldoi* Arredondo & Olson, 1994**

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Bubo osvaldoi Arredondo & Olson, 1994 (part), *Proc. Biol. Soc. Wash*. 107: 438.
Tyto riveroi: Salgado *et al*. 1992: 28, table 1.

Holotype.—Right tarsometatarsus lacking proximal end, MNHNCu 75.27.1 (see Arredondo & Olson 1994: fig. 1B–D).

Paratypes.—Complete right femur without internal condyle, abraded about the trochanter, MNHNCu 75.27.3 (see Arredondo & Olson 1994: fig. 2B) (Fig. 1D); shaft of left tarsometatarsus without proximal portion and digital trochleae, MNHNCu 75.27.2 (not illustrated).

Type locality.—All of the above material is from Cueva del Mono Fósil, Sierra de Galeras, municipality of Viñales, Pinar del Río province, western Cuba. This is the type locality of *Paralouatta varonai* Rivero & Arredondo, 1991.

Distribution.—Restricted to the type locality in western Cuba (see above).

Remarks.—The humerus of *Bubo osvaldoi* is unknown, as USNM 447023, described as a paratype in the original description, represents a new taxon described below. The species is a large Bubonini, similar in size to female *B. bubo* Linnaeus, 1758 (see descriptions in Arredondo & Olson 1994).

Genus *Ornimegalonyx* Arredondo, 1958a (type, by monotypy [*contra* Brodkorb 1961], *O. oteroi* Arredondo)
***Ornimegalonyx oteroi* Arredondo, 1958a**
Ornimegalonyx oteroi Arredondo, 1958a, *El Cartero Cubano* 17(7): 11.

Ornimegalonyx acevedoi Arredondo, 1982: 45, **new synonymy** (type locality 'Cueva de Quinto, Boca de Camarioca, Matanzas' province, Cuba).

Ornimegalonyx minor Arredondo, 1982: 46, **new synonymy** (type locality 'Cueva de Paredones, San Antonio de los Baños [= Caimito], Habana' [= Artemisa] province, Cuba).

Ornimegalonyx gigas Arredondo, 1982: 47, **new synonymy** (type locality 'Cantera de los Hornos de Cal, a unos 4 km al este de la ciudad de Sancti Spíritus', Sancti Spíritus province, Cuba).

Cathartes aura: Arredondo 1984: 9 (see Suárez 2001: 110).

Lectotype.—Left tarsometatarsus lacking distal end, SEC P-383.E (at MCZ; designated by Brodkorb 1961: 634, Arredondo 1958a: 12, fig. unnumbered, 1975: figs. 1–2, 1976: fig. 5, 1982: figs. 5–6).

Type locality.—Cueva de Pío Domingo, Sierra de Sumidero, Ensenada de Pica Pica, Pinar del Río province, Cuba. This is the type locality of other Cuban extinct birds, including *Antigone cubensis* (Fischer & Stephan 1971a) and *Nesotrochis picapicensis* (Fischer & Stephan 1971b).

Distribution.—Common in Quaternary fossil deposits throughout Cuba and Isla de la Juventud (see, *inter alia*, Kurochkin & Mayo 1973, Arredondo 1975, 1976, 1984, 1996, Alegre 2002, Suárez 2020).

Emended diagnosis.—The largest species of the genus *Ornimegalonyx*.

Remarks.—Treatment of the names *arredondoi* and *borrasi* (see Arredondo 1958a: 11; 1964: 21) as *nomina nuda*, in the synonymy of *Ornimegalonyx oteroi* (Arredondo 1975: 145) or *O. acevedoi* (Arredondo 1982: 46), are incorrect. In the original description of *O. oteroi*, Arredondo (1958a: 11), in reference to *arredondoi* stated: 'nombre que ahora declino y propongo el de Oteroi' [= 'a name that now I reject and propose that of Oteroi']. As *arredondoi* was not validly introduced when first published (Arredondo 1958a), it is not

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made available there (ICZN 1999, Art. 11.5). Brodkorb (1961) treated it, incorrectly, as an available name, but as a synonym of *oteroi*. Thus, the name *arredondoi* is not available (ICZN Art. 11.6). On the other hand, *borrasi* was mentioned only conditionally by Arredondo (1964: 21): 'parece tratarse de otra especie, que de lograrse la certeza, llevaría el nombre específico de "Borrasi"...' [= 'it seems to be another species, which if proven, would bear the specific name "Borrasi"...']. Therefore *borrasi* too is not available (ICZN Art. 15.1), but was cited subsequently by Acevedo (1965: 21) for a bird that was never described by Arredondo. The same fossils, to which those names were applied, were explicitly treated as *O. oteroi* by Arredondo (1975), and not mentioned in Arredondo (1984).

Ornimegalonyx ewingi sp. nov.

Bubo osvaldoi: Arredondo & Olson, 1994: 438 (part).

Holotype.—Right femur without anterior surface of head, piece of posterior face of shaft, and internal condyle, USNM 447022 (see Arredondo & Olson 1994: figs. 2A, 3A–C) (Fig. 1C).

Paratype.—Left humerus without proximal end and the external part of the distal articulation, USNM 447023 (see Arredondo & Olson 1994: fig. 3D, 4B) (Fig. 1B).

Type locality.—A 'mine' in the vicinity of Baire, Oriente (= Santiago de Cuba) province, Cuba. The age of both the holotype and paratype, and the precise location of the type locality are unknown. Probably they were collected at the same time as mammal material known from this locality (see Arredondo & Olson 1994: 438). According to Mayo (1980: 223, 225), the 'mine' is in the south of the former Oriente province, and probably a cave (but see Aguayo & Howell Rivero 1955). It is also the type locality of the extinct sloth *Neocnus baireiensis* Mayo, 1980.

Distribution.—Known only from the type locality in eastern Cuba (see above).

Diagnosis.—A diminutive species of *Ornimegalonyx*, slightly larger than *Bubo osvaldoi*.

Etymology.—I take great pleasure in dedicating this new species to my close friend and colleague Dr Gil C. Ewing, in recognition of his great knowledge and passion for birdlife.

Description and comparisons.—Differs from *O. oteroi* by its much smaller size (*c*.30% smaller), with femur shaft more columnar, less constricted bilaterally at the midpoint, and flaring less at both ends. Humerus relatively more robust, with shaft shorter, less curved and more expanded at the distal end; impression of brachialis anticus relatively larger, less vertical, and more distally placed; entepicondylar prominence less projected. For additional comparisons and descriptions, see Arredondo & Olson (1994).

Remarks.—The type series of *O. ewingi* represents the first material pertaining to the genus to be collected (probably pre-1942, see Aguayo 1950). Given its size, the species' prey must have been smaller compared to those of its gigantic congener. Some specimens from the tar seeps Las Breas de San Felipe, Matanzas province, Cuba (Suárez 2020: 32), may also be referrable to this taxon, but additional comparison and study is needed to clarify their identity.

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Further vocal evidence for treating the Bahama Nuthatch *Sitta* (*pusilla*) *insularis* as a species

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Summary.—The case for recognising Bahama Nuthatch *Sitta insularis* as a species separate from Brown-headed Nuthatch *S. pusilla* has been made several times since 2004, based on plumage, morphometrics, voice and genetic distance, but only one of four world lists currently accepts it as such. We assembled three new sets of recordings and recently published evidence on playback responses. We found that *S. insularis* has at least five vocalisations that are homologous to but always much higher pitched (by 2–3 kHz) than those of *S. pusilla*, such that the main calls of the latter are strikingly different from those of the former, and playback studies all suggest a consistently weak response in one species to the calls of the other. Moreover, genetic divergence of *insularis* from mainland *pusilla* is greater than that of another Bahamian taxon, Bahama Warbler *Setophaga flavescens*, recently accepted by all world lists as a species, from mainland Yellow-throated Warbler *S. dominica*. Taken together with the notably larger bill of *Sitta insularis*, these factors reinforce the case for treating Bahama Nuthatch as a (regrettably now almost certainly extinct) species.

A form of nuthatch present in pinelands on the island of Grand Bahama, in the northern Bahama Islands, has long been considered to represent a distinct subspecies, *insularis*, of Brown-headed Nuthatch *Sitta pusilla*. The description of this form, by Bond (1931), was based on two specimens, both of which showed longer bills and 'darker loral and auricular regions' than the mainland, nominate form of *S. pusilla*, whose range (synonymising the undiagnosable *caniceps*) extends through pineland formations from Delaware south to Florida and west to Texas, in the eastern USA (AOU 1998, Harrap 2008).

This arrangement, with the differences between the two taxa considered 'slight' and indeed requiring confirmation (Harrap 1996, 2008; also Smith & Smith 1994), went unchallenged until Hayes *et al*. (2004) confirmed the morphometric distinctiveness of *insularis* (longer bill and tarsi, shorter wing) and supplemented this with evidence that it also possesses a 'warble' call never recorded in nominate *pusilla*. On this basis, although finding the plumages of the two taxa 'virtually indistinguishable (Grand Bahama forms exhibit more white and less gray on the throat and belly)', Hayes *et al*. (2004) argued that *insularis* merits species rank. This and several other taxonomic recommendations were, however, collectively set aside by what was then the American Ornithologists' Union (AOU) 'because of insufficient or conflicting information', albeit with the proviso that 'Action on these proposals awaits further studies that include additional data' (Banks *et al*. 2006). Further data were duly furnished by Metcalf *et al*. (undated [*c*.2009]) who, using two markers from mtDNA, 'estimated that the average level of sequence divergence between individuals collected on Grand Bahama and in the United States was 1.37%'. However, the case was not re-opened by the AOU, leaving Slater *et al*. (2013) to judge that the molecular finding 'likely reflects nothing more than a) the population on Grand Bahama has been

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isolated a long time and b) gene flow between it and mainland populations is minimal (i.e., nothing about reproductive isolation can be inferred).'

This last remark overlooked the report by Hayes *et al*. (2004) of a distinctive call unique to the Bahama population. By contrast, a peer-reviewed molecular study (Han *et al*. 2015) not only pointed out that the unpublished 1.37% genetic difference was 'higher than the genetic divergence reported for Bahama Warbler *Setophaga flavescens*' in McKay *et al*. (2010), a split (from Yellow-throated Warbler *S. dominica*) which *was* accepted by the AOU (Chesser *et al*. 2011), but also reported moderate to high divergence through different genotyping techniques and reported that 'calls of the Bahama population do not elicit a strong territorial response from individuals on the mainland (H. Levy unpubl. data)'. Moreover, an independent vocal analysis (Boesman 2016a) provided the decisive evidence in the acceptance of *Sitta insularis* as a species in del Hoyo & Collar (2016), where the four characters differentiating it from *S. pusilla* were: 'darker brown facial stripe; much longer bill; considerably shorter wings; and unique call, a rapid high "warble", which is apparently the principal vocalisation'.

Del Hoyo & Collar (2016) afforded these four characters scores of 1, 'at least' 2, 'at least' 1, and 3, respectively, hence at least 7 in total, under the system of taxonomic evaluation proposed by Tobias *et al*. (2010), in which a score of 4 represents an exceptional character (radically different coloration, pattern, size, or sound), a score of 3 a major character (pronounced difference in body part colour or pattern, measurement or sound), a score of 2 a medium character (clear difference, e.g. a distinct hue rather than a different colour), and a score of 1 a minor character (weak difference, e.g. a change in shade). Under these criteria, a threshold of 7 is set to allow species status, but 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 is medium, 5–10 represents major and >10 is treated as exceptional) and one behavioural or ecological character (allowed 1) may be counted. The scores given to Bahama birds for bill and wing length were considered minimal ('at least') because they were not based on direct evidence from specimens but inferred conservatively from the highly indicative box-plots in Hayes *et al*. (2004), who, incidentally, also found a longer tarsus in *insularis* but with 'considerable' overlap.

In allowing *S. insularis* species rank, del Hoyo & Collar (2016) omitted to mention the molecular evidence which, as the comparison above with *Setophaga flavescens* shows, only adds to the case. Despite these convergent items of authentication, no other world list has accepted the Bahama Nuthatch as a species (Dickinson & Christidis 2014, Clements *et al*. 2019, Gill *et al*. 2020). We therefore sought to find, preserve and analyse other sound-recordings of the species on Grand Bahama, particularly in the light of its almost certain extinction there, in an attempt to improve the evidence base for a dependable decision on its taxonomic status. We continue to be guided by the Tobias criteria, which remain the only system for taxonomically ranking allopatric taxa under the Biological Species Concept other than voting by experts on a taxonomic committee. While not perfect, the system continues to garner independent support for its decisions (del Hoyo & Collar 2014, del Hoyo & Collar 2016) in peer-reviewed research (del Hoyo 2020).

Methods

The only publicly available recording of *S. insularis* (Macaulay Library [ML] 163289) was analysed in Boesman (2016a). Two other recordings are mentioned in the literature, the first used in playback searches by Hayes *et al*. (2004) and by Lloyd & Slater (2011), and the second made by P. Merritt and used to catch four birds by Han *et al*. (2015). The recording

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used by Hayes *et al*. (2004) was for a time available on a website (https://medicine.llu.edu/research/department-earth-and-biological-sciences/biology/research/william-k-hayes-phd-ms/bahamian-0#brownheadednuthatch) but it could not be accessed, nor could its owner be traced. However, information kindly provided by Jim Cox, John Lloyd and Gary Slater enabled us to contact Peter Merritt and Mark Oberle, who both very generously took the time to recover and format their recordings, and make them available to us. To these we were able to add recordings made during field work in April–June 2018 and kindly sent to us by the recordist, Matthew A. Gardner.

In addition to the single Macaulay Library recording (by Jeff Gerbracht) we therefore now had access to:

- eight sound recordings made by P. Merritt on 15–17 May 2005 in the central pinewoods of Lucaya Estates, extracted from video taken using a Canon XL1 digital camcorder equipped with a Sennheiser ME66/K6 shotgun microphone;
- 35 sound-recordings made by M. Oberle on 18–19 April 2007 near a nuthatch nest in Lucayan National Park, with a Sound Devices 702 recorder and a Telinga PRO 5W stereo parabolic microphone;
- two sound recordings made by M. A. Gardner on 29 May 2018, in the central pinewoods of Lucaya Estates, extracted from video without external microphone, and one recording made on 26 June 2018 in the same area.

These recordings, which have already been submitted to public digital archives (ML 274427–463) and will be available as soon as possible, complement the earlier recordings used by Hayes *et al*. (2004) and made by Gerbracht, all from July–August, and increase the chances of capturing the full vocabulary of this taxon during the breeding and post-breeding periods.

For comparison with mainland *pusilla*, we used the sound-recordings available in the Macaulay Library (https://www.macaulaylibrary.org/) and Xeno-canto databases (https://www.xeno-canto.org). We made sonograms of all recordings using CoolEdit Pro (Blackman-Harris window at 512 band resolution) and, where necessary, we measured sound parameters manually on these using visual rulers for time and frequency on screen. To construct an overview of the full vocabulary of *S. insularis*, we used as a guideline what is known for *S. pusilla* (Harrap 2008, Slater *et al.* 2013, Pieplow 2017). We aligned our descriptions of vocalisations with commonly used terminology in North America (McCallum 2011, Pieplow 2017), considering a 'note' to be any continuous line on a sonogram up to a pause, and the term 'overslurred' to describe a rise and then fall in pitch.

Results

The vocabulary of *S. insularis* was found to be as extensive as that of *S. pusilla*, and most of its vocalisations possess homologous counterparts in the mainland taxon, including the 'warble' call that Hayes *et al*. (2004) considered unique to *insularis*. Five out of six of the counterpart vocalisations were nevertheless found to be much higher pitched in *S. insularis* vs. *S. pusilla* (Table 1). Most calls in *insularis* are faint and unobtrusive, suggesting use in close-range communication between members of a pair or group. From the available sound-recordings we distinguished the following different vocalisations.

1. *Skew-doo* ('rubber ducky' vocalisation).—In *S. insularis* this call type was present in the three sets of sound-recordings from April, May and June, although Hayes *et al*. (2004) heard it only occasionally in July. To the ear, the *skew-doo* of *insularis* sounds much higher pitched and less nasal than in *S. pusilla*. This was confirmed by measurement of all available recordings of *insularis* compared to a random selection of recordings of *pusilla* from six

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TABLE 1
Max. (fundamental) frequency in kHz for five of six homologous vocalisations in the repertoire of Brown-headed Nuthatch *Sitta pusilla* and Bahama Nuthatch *S. insularis* (mean values), and their calculated difference (Δ). Missing in this list is the 'twitter' call (vocalisation 3), which proved too variable in frequency to be worth measuring and testing. With the exception of the commonly heard *skew-doo* call (see Table 2) and high-pitched *pit* calls, sound-recordings of other vocalisations are rare even for *pusilla*, and measurements are based on just 1–2 available recordings, as detailed in the text. * = an estimate, as the fundamental frequency is not fully visible on the sonogram for the available recordings.

	Sitta pusilla	*Sitta insularis*	Δ
Skew-doo call	4.3	6.3	2.0
High-pitched chitter	5.0	8.0	3.0
High-pitched *pit*	3.8	6.2	2.4
High-pitched *tink*	5.0	7.2	2.2
Begging call	3.0*	8.0	5.0*

TABLE 2
Measurements of sound parameters of the *skew-doo* call in Brown-headed Nuthatch *Sitta pusilla* and Bahama Nuthatch *S. insularis*. Means and standard deviation are given. Each sample of *S. pusilla* is from a different state in the USA (ML 207586931, ML 206324781, ML 172477891, ML 120782681, ML 40782, ML 50234281).

	S. pusilla (*n* = 6)	*S. insularis* (*n* = 8)	effect size
Max. base freq. *skew* (Hz)	4,300 ± 161	6,288 ± 653	4.18
Duration *skew* (seconds)	0.147 ± 0.020	0.22 ± 0.039	2.35
Max. base freq. first *doo* (Hz)	1,367 ± 125	3,363 ± 219	11.19
Duration first *doo* (seconds)	0.093 ± 0.021	0.090 ± 0.021	0.14

different states on the mainland (Table 2). An exceptional difference in max. frequency was found for the *doo* note (effect size 11.2, score 4), with a less powerful but still significant difference in the *skew* note, which is both longer in duration and higher in frequency in *insularis* (score 2). A further clear difference is in note shape, as the *skew* is typically overslurred on the mainland and mainly downslurred on Grand Bahama (Fig. 1). The relative importance of these differences in creating a reproductive barrier is unknown, but we follow standard practice in vocal analysis for taxonomic studies by focusing primarily on the quantification of basic spectral and temporal sound parameters.

In *pusilla* this is the commonest call and the only one that carries more than short distances, being used in a variety of situations linked to territorial song, excitement and long-distance communication. It is uttered by both sexes and is heard year-round, although long series uttered in spring may well be produced by the male alone. *Skew-doo* (*ziu-uu* in Harrap 2008, *tyah-dah* or *chee-da* in Slater *et al*. 2013) consists of two notes, but the *doo* can occasionally be absent, or it can occur in series of up to 12 repetitions when a bird is excited (Harrap 2008, Slater *et al*. 2013, Pieplow 2017). Recordings reveal that this call is given in a context similar to that used by *insularis*.

2. High-pitched chitter and 'warble' call.—This was the main vocalisation given by *S. insularis* in July 2004, described by Hayes *et al*. (2004) as 'a rapid, high-pitched "warble" call', and it was also the only vocalisation recorded in July 2011 (ML 163289). By contrast, this call was almost absent in recordings made in April and May, and only a few examples were found in recordings made at the end of May, but it was more frequently heard in

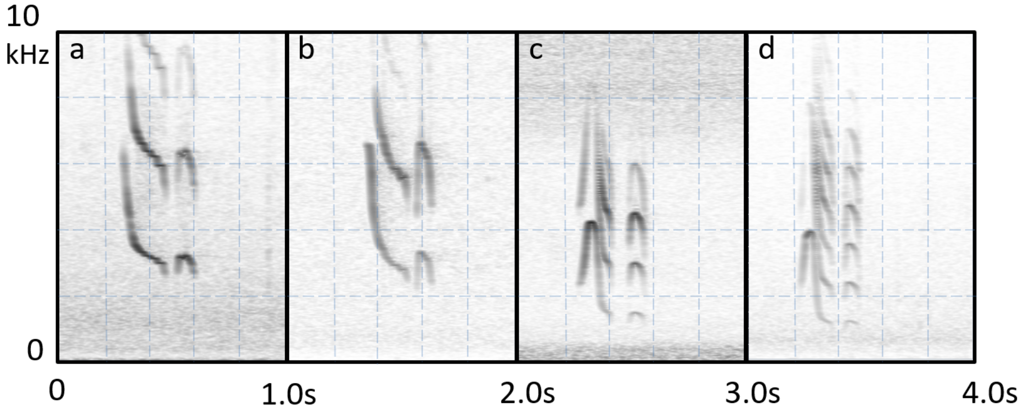

Figure 1. Sonogram of vocalisation 1. Typical *skew-doo* call. Bahama Nuthatch *Sitta insularis* (a–b) and Brown-headed Nuthatch *S. pusilla* (c–d). Extracts from recordings (a) P. Merritt; (b) M. Oberle; (c) ML172477891 (Florida; J. Graham); (d) ML50234281 (Georgia; E. Cormier).

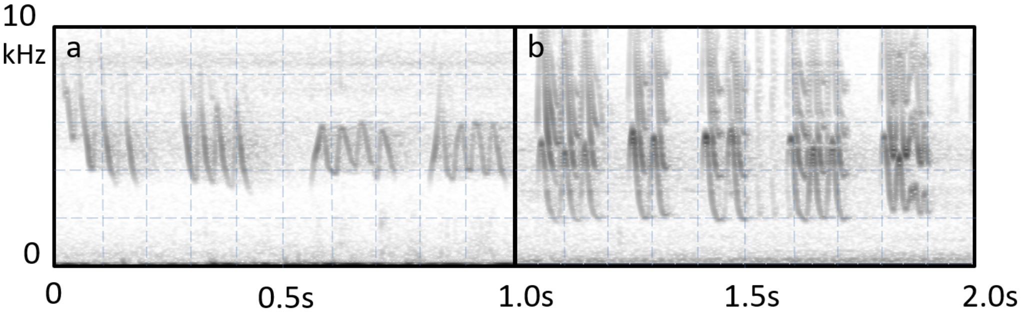

Figure 2. Sonogram of vocalisation 2. (a) High-pitched chitters (first two calls) and warble (second two calls) of Bahama Nuthatch *Sitta insularis* (extract from ML 163289; J. Gerbracht); (b) rarely given, structurally similar vocalisation of Brown-headed Nuthatch *S. pusilla*: ML 196494 (Florida; B. McGuire).

recordings from the end of June. This may well be the primary vocalisation of feeding groups in the non-breeding season, and indeed it was used by Hayes *et al*. (2004) and Lloyd & Slater (2011) to attract feeding flocks with playback. It consists of bursts of short high-pitched chitters that could be transcribed as *tree..tre-ree-ree..tree-tree*. On a sonogram each chitter call consists of 3–7 downstroke elements that are sometimes interconnected, when they appear as a continuous oscillation (hence the 'warble' call) (Fig. 2). Duration is quite variable (0.10–0.40 seconds), depending on the number of included elements, and frequency typically ranges from *c*.3.5 to 8.0 kHz.

We assume this vocalisation is homologous to the 'rattle' described for *S. pusilla* by Pieplow (2017), although we have found surprisingly few sound-recordings of it (e.g. ML 196494) in the extensive material available. While the structure of the bursts is similar to that of *S. insularis*, including at times the oscillating lines on sonograms (Fig. 2), the difference in frequency is again striking. Fundamental frequency for *pusilla* ranges from 1.5 to 5.5 kHz, rendering it a very different sound to the ear that can be transcribed as a rather harsh *tchrr…tchrrr*. It is thus unsurprising that this apparent homology was not identified by Hayes *et al*. (2004), and we cannot exclude the possibility that this vocalisation type has an entirely different function in each taxon.

Pieplow (2017) provided a second, somewhat different sonogram of these rattles that depicts short monotone bursts of sharply overslurred notes (extracted from ML 14767). This

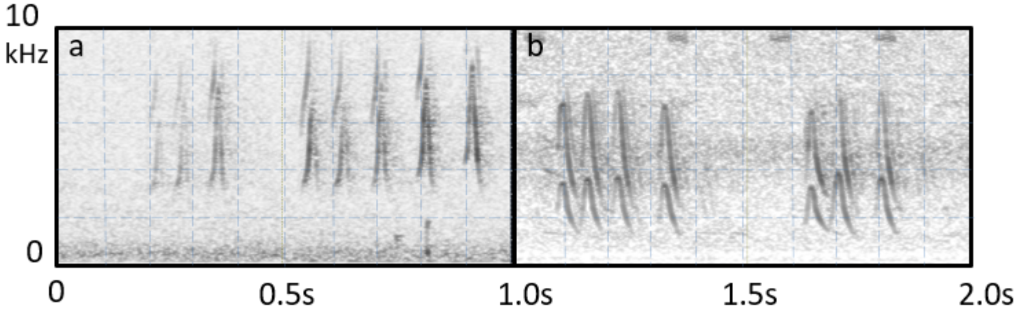

Figure 3. Sonogram of vocalisation 2. Short chittering bursts (a) Bahama Nuthatch *Sitta insularis* (M. Gardner); (b) Brown-headed Nuthatch *S. pusilla* (extract from ML 14767, South Carolina; C. Sutherland).

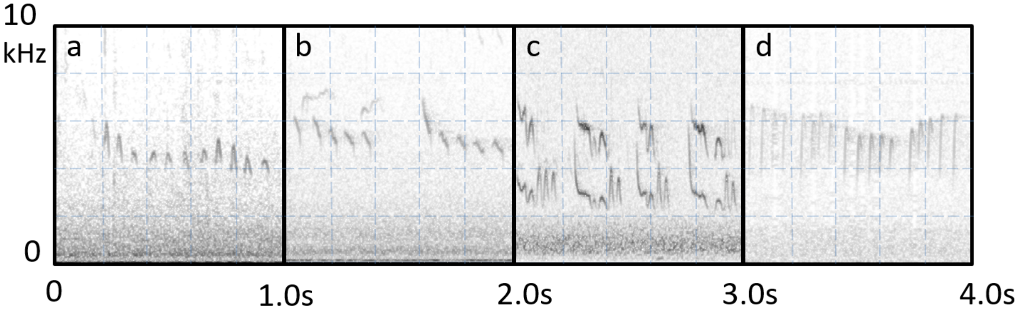

Figure 4. Sonogram of vocalisations 3 and 7, all of Bahama Nuthatch *Sitta insularis*. (a–b) Twitters (M. Oberle); (c) twitters (P. Merritt); (d) high-pitched trill (M. Gardner).

matches a variant found in Gardner's recordings of *insularis* surprisingly well, except again for frequency range: max. frequency is 3.3–4.0 kHz in *pusilla* but a striking 6.0–9.0 kHz in *insularis* (Fig. 3).

3. Twitters.—In *S. insularis* many mellow semi-nasal twitters were recorded around the nest site. Their structure was highly variable, with some examples reminiscent of, but mellower than, the long versions of the *skew-doo* call, whereas others simply represented random up-and-down twittering (Fig. 4a–c). Compared to the 'chitter/warble' call (vocalisation 2), twitters are less stereotypic and less emphatic, suggesting communication between a pair at close range rather than the louder chitter at group level. In general, sonograms of these calls look quite similar to the 'twitter' mentioned for *pusilla* by Pieplow (2017), who described them as 'soft, short, peeping'. Given the variability involved, we did not make pair-wise measurements to evaluate possible frequency differences between calls given by the two taxa, which seem to be less apparent than in the other vocalisations.

4. High-pitched *pit*.—In *S. insularis* the *pit* is a very short, soft, upslurred note that is probably homologous when compared on a sonogram to the *wink* call of *S. pusilla* (Pieplow 2017), which is also transcribed as *tip* or *pit* (Harrap 2008). The short *pic* notes mentioned by Hayes *et al*. (2004) for *insularis* most likely also involve this vocalisation. It can vary considerably in pitch, depending somewhat on the level of excitement of the bird, but the max. frequency in *insularis* reaches 5.0–7.5 kHz, whereas in *pusilla* it is *c*.2.5–5.0 kHz (*n* = 8), once again revealing a strikingly different frequency range in the two taxa (Fig. 5).

5. High-pitched *tink*.—In *S. insularis* this is another high-pitched, faint vocalisation, consisting of short notes over a narrow frequency range, given either singly or in pairs or triples, sounding like a pure *tink* or *ti-tink*. It is structurally very similar to, but again

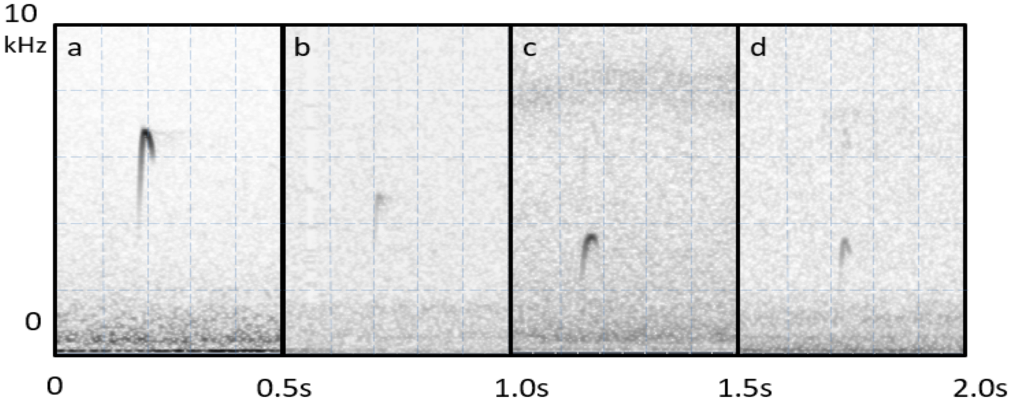

Figure 5. Sonogram of vocalisation 4. Single high-pitched *pit* note. Bahama Nuthatch *Sitta insularis* (a) high-pitched example (M. Oberle); (b) lower pitched example (M. Gardner); Brown-headed Nuthatch *S. pusilla* (c) extract from XC 130526 (Florida; M. Nelson); (d) extract from ML 87147361 (Florida; T. Auer).

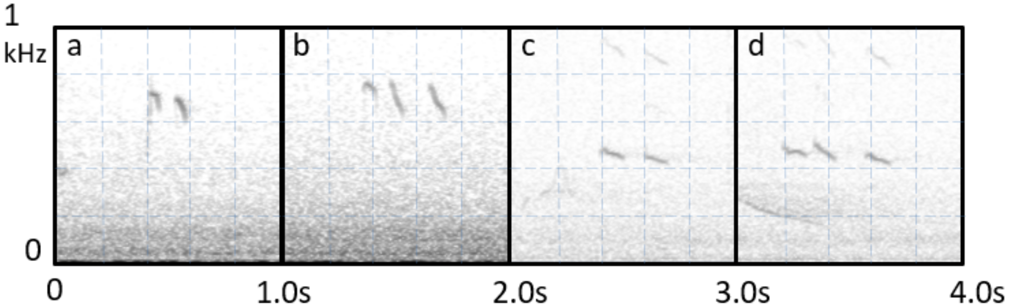

Figure 6. Sonogram of vocalisation 5. High-pitched *tink* calls: (a–b) Bahama Nuthatch *Sitta insularis* (M. Oberle); (c–d) Brown-headed Nuthatch *S. pusilla* extract from XC 112506 (Georgia; L. Wolff).

clearly higher pitched than, calls in a recording of *S. pusilla* made near a nest site in Georgia (XC 112506) (Fig. 6). The sonogram in Pieplow (2017) for the *seet* call in *S. pusilla* bears a superficial resemblance, but the original recording (ML 14767) on which that graphic was based reveals differences discernible both to the ear and on a sonogram in its rather polyphonic quality, with the lowest frequency around 3.7 kHz, slightly longer duration, and very faint hissing quality. Moreover, this call was uttered only singly.

6. Begging call.—In *S. insularis* this vocalisation, a high-pitched incessant *see..see.. see..* (Fig. 7), was only recorded at the nest site and undoubtedly uttered by the young inside. Remarkably, even for this vocalisation, the few available recordings of juvenile *pusilla* suggest a significant difference in frequency, the latter more than 3.0 kHz lower when comparing the fundamental frequency (e.g. XC 179671, ML 57525031, ML 164553561; Table 1). We do not know the age of the begging juveniles in every recording, however, so these findings should be treated cautiously.

7. High-pitched trill.—This vocalisation was found only a few times among the recordings of *S. insularis*, and it is probably therefore uncommon, perhaps representing only a variant of the twitters (vocalisation 3) or an excited version of the *pit* call (vocalisation 4). Different from the chittering (vocalisation 2), these rattling trills are long series of upstroke *pit* notes uttered at a very fast pace of *c*.20 notes per second (Fig. 4d). We have found no clear equivalent of this call in *S. pusilla*.

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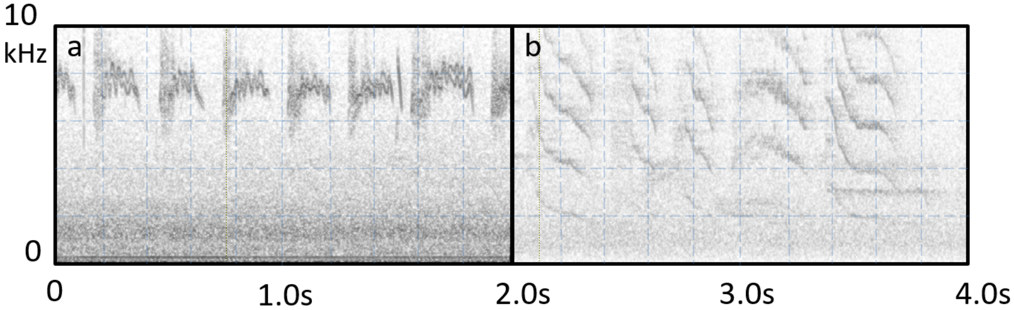

Figure 7. Sonograms of vocalisation 6. (a) Begging calls at the nest of Bahama Nuthatch *Sitta insularis* (M. Oberle); (b) Brown-headed Nuthatch *S. pusilla* 'juvenile begging calls', extract from ML 164553561 (North Carolina; L. Beegle).

8. *Schwee* / *seet* calls.—In *S. pusilla* the *schwee* call (Slater *et al*. 2013) and *seet* call (Pieplow 2017) are both linked to food begging by the presumed female from her mate, but they are not necessarily the same vocalisation, as Slater *et al*. (2013) gave a duration of 0.7 seconds for *schwee* whereas the sonogram in Pieplow (2017) suggests 0.175 seconds for *seet*. An equivalent in *S. insularis*, although not found on the recordings, is likely to exist, but possibly given only or mainly prior to breeding, and thus primarily in the first few months of the year.

Discussion

This overview of the vocalisations of *S. insularis* and *S. pusilla* clearly establishes that their vocabularies are comparable, and we can with reasonable confidence identify the homologous vocalisations. For almost all pairings of homologous calls, the different frequency range is remarkable, such that to the human ear most of the calls sound rather unrelated. The frequency difference of both taxa has only been alluded to qualitatively (Smith & Smith 1994), but it is now quantified and clarified per vocalisation type: *S. insularis* has almost its entire vocabulary *c*.2.0–3.0 kHz higher in frequency than *pusilla* (Table 1), which is an astonishing finding given that they are similarly sized and closely related taxa.

We were, however, unable to elucidate the degree of differentiation in particular vocalisations between males and females, or determine the degree to which a particular vocalisation is used exclusively or predominantly by one sex or the other. Such differences are poorly documented in the literature (none is mentioned in Harrap 2008 or Slater *et al.* 2013), but are sufficient to be used in playback lures in Florida to capture males or females, as needed (J. A. Cox *in litt*. 2020). Even so, our finding of a consistently much higher frequency in the calls of *S. insularis* is maintained across recordings.

The characters distinguishing *S. insularis*, and the scores given to them that led del Hoyo & Collar (2016) to recognise it as a species, were based mainly on evidence in Hayes *et al*. (2004): 'darker brown facial stripe (1); much longer bill (at least 2); considerably shorter wings (at least 1); and unique call, a rapid high "warble", which is apparently the principal vocalization (3)'. Given the resistance to that evidence (Banks *et al*. 2005, Slater *et al*. 2013) we reconsider these features here. The eyestripe difference is the most difficult to confirm: Bond (1931), on the basis of a tiny sample, treated it as one of two diagnostic characters; Smith & Smith (1994), using an equally small sample, reported that the two Bahamian birds they saw had 'noticeably more prominent brown eyelines and purer white underparts' than birds recently seen in Florida; and Slater *et al*. (2013) included the eyestripe as a genuine diagnostic trait. Hayes *et al*. (2004) further agreed with Smith & Smith (1994) that 'Grand

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Bahama forms exhibit more white and less gray on the throat and belly', but on the issue of the eyestripe they were silent: after examining 11 specimens of *insularis* and 99 mainland *pusilla* (but hampered by the poor condition of, evidently, *insularis*), they 'chose not to quantify plumage coloration because of substantial character overlap'. More detail on this problem would have been helpful, but after examining photographs on the internet and pending rigorous re-examination of museum material, we are inclined to agree that such overlap may exist and that, at present, this character (and the purer white underparts) should be treated as uncertain.

The much longer bill was, however, well established by Hayes *et al*. (2004), both in a photograph of three individuals of each taxon and in a boxplot based on all 11 *insularis* and 99 *pusilla* measured. This boxplot shows *insularis* and *pusilla* with median bill lengths (nares to tip) of 12.4 and 10.6 mm respectively, with very little overlap in range. A similar boxplot for wing length yielded medians of 60 and 63 mm, respectively, albeit with near-complete overlap. A single unsexed *insularis* and five random male *pusilla* in the American Museum of Natural History, New York (material not used by Hayes *et al*. 2004), yielded respective measurements (taken by NJC) of bill (skull to tip) 18.6 vs. mean 15.0 mm, wing (curved) 62.0 vs. mean 64.6 mm (no overlap) and tail 33.0 vs. mean 30.6 mm (no overlap), consistent with previous evidence on bill and wings. Although we cannot generate effect sizes from the data in Hayes *et al*. (2004), we are very confident that the bill length difference (2) and moderately confident that the wing length difference (1) were correctly scored in del Hoyo & Collar (2016).

This then leaves the new information on vocal divergence. Although Hayes *et al*. (2004) considered the 'warble' call unique to *insularis*, it apparently occurs in *pusilla* as the (lower pitched) 'rattle' (Pieplow 2017). However, in the dominant acoustic signal used by the two taxa, the *skew-doo* call, the differences in max. frequency (effect size 11.19, score 4) and duration plus frequency range (effect size 2.35, score 2) produce a score for voice of 6. Even discounting scores for eyestripe and wing length, this carries the Bahama Nuthatch to a total score (8) higher than that by which it earlier achieved species rank. That this large difference (which is also, as noted, reflected in the other vocalisations in its vocabulary) has biological significance has been increasingly apparent. In May 1993 Florida birds responded to a broadcast recording of *S. pusilla* but Grand Bahama birds, sounding 'briefer… weaker, faster and higher', did not (Smith & Smith 1994). In July–August 2004 Grand Bahama birds 'virtually ignored playback of the continental rubber ducky call' (Hayes *et al*. 2004). From October 2017 to March 2018 at St Marks National Wildlife Refuge, Florida, *S. pusilla* responded to recordings of their own 'rubber ducky' calls 72% of the time but only 30% to equivalent calls of Pygmy Nuthatch *S. pygmaea* and 27% to those of *S. insularis* (involving the Merritt recordings from May 2005), whereas in July 2012, on Grand Bahama Island, *S. insularis* responded 83% to their own calls and 25% to those of *S. pusilla* (Levy & Cox 2020; also Levy 2018). These consistent findings reflect recent work showing that significant vocal differences are highly correlated with degree of playback response in both suboscines and oscines (Freeman & Montgomery 2017).

While in New World avian taxonomy vocal characters have particularly been used for species delimitation in suboscine passerines, based on the finding that their songs are innate, there is a growing recognition that vocalisations are at least under partial genetic control in the voice-learning oscines, and are thus also useful for delimiting species (Remsen 2005, Cadena & Cuervo 2010). Even so, in some oscine passerine families local populations can be defined by dialects, so could the vocalisations of *Sitta insularis* simply be considered a dialect of those in *S. pusilla*? We argue not: there is no indication at all of local dialects in continental *Sitta pusilla*, in which on the contrary the stereotypic rendition of the *skew-doo*

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call over its entire range is striking, as reflected by the low standard deviations in Table 2, and we are unaware of any case where the term 'dialect' has been applied to an entire vocabulary that occupies a completely different frequency range to that of a conspecific.

The relatively recent proposed split of Bahama Warbler from Yellow-throated Warbler, based on genetic and phenotypic evidence (McKay *et al*. 2010), has been accepted by all four world lists (Dickinson & Christidis 2014, del Hoyo & Collar 2016, Clements *et al*. 2019, Gill *et al*. 2020); yet, as noted above, the genetic distance recorded between the two is smaller than that between *Sitta insularis* and *S. pusilla*. There are many similar instances of closely related taxa in the Caribbean which were once considered conspecific and are now not, notably including Bahama Yellowthroat *Geothlypis rostrata* and Common Yellowthroat *G. trichas*, whose mostly minor morphological differences have been supplemented by a Tobias score of 4 for their level of acoustic divergence (Boesman 2016b). *Sitta insularis* clearly merits the same taxonomic rank as these two other Bahamas species, and incidentally shares with them the considerably larger bill than their mainland counterparts (Kirwan *et al*. 2019). Smith & Smith (1994) assumed that, since it was unknown from the neighbouring island of Abaco, the nuthatch must have colonised Grand Bahama after the two islands separated some 2,500 years ago, which would of course generally be regarded as far too recent to have permitted a speciation event. However, the genetic evidence indicates that *S. insularis* and *S. pusilla* diverged from a common ancestor around 685,000 years ago (Metcalf *et al*. undated), and this finding has now been complemented by late Pleistocene fossil remains of *insularis* from Abaco (Steadman & Franklin 2015, Steadman *et al*. 2015) and Long Island (Steadman & Franklin 2020).

The phenotypic and genetic evidence, results of playback experiments, and parallel circumstance of the two parulid warblers combine to create a situation in which the burden of proof, in Gill's (2014) formulation, now lies with those who would wish to continue to treat *S. insularis* as a subspecies of *S. pusilla*. This is now almost certainly a matter of 'academic' interest, however, since *insularis*, clearly in serious trouble throughout this century, can surely not have survived the devastating impact on Grand Bahama of Hurricane Dorian over 2–3 September 2019 (295 km/h winds for >24 hours). For this reason in particular we recommend that any other sound-recordings, videos, photographs or records be deposited in secure archives such as the Macaulay Library and Xeno-canto in order to preserve for posterity as much as possible of our knowledge and experience of the Bahama Nuthatch.

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We warmly thank Matthew Gardner, Peter Merritt and Mark Oberle for permission to use their recordings; moreover, Messrs Merritt and Oberle went to very considerable trouble to recover, listen to, prepare and send their recordings to us, and we salute this generosity. Jim Cox (Tall Timbers Research Station and Land Conservancy) magnanimously helped our enquiries and provided the unrefereed version primarily focusing on playback experiments of Levy & Cox (2020) well in advance of publication. John Lloyd and Gary Slater were prompt and kindly correspondents. Paul Sweet (American Museum of Natural History, New York) permitted access to specimen material. The staff of the Macaulay Library of the Cornell Lab of Ornithology, Ithaca, NY, USA, and the Xeno-canto bird sound database, together with their large number of supporting sound-recordists, were indispensable sources. Two referees made helpful comments; in particular, Curtis Marantz provided a very thorough and rigorous review for which we are particularly grateful.

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Avifauna of the Ninigo, Hermit, Sae and Kaniet Islands, and adjacent seas, Papua New Guinea

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http://zoobank.org/urn:lsid:zoobank.org:pub:A6F3C925-4F03-48A9-941F-EA6384666DF6

Summary.—One of us (SMH) surveyed the Ninigo and Hermit Islands (27 January–13 February and 2–14 October 2019), providing the first observations of birds on these islands for *c.*50 years. KDB collated data from the unpublished diaries of W. F. Coultas, a member of the Whitney South Sea Expedition, including observations from the nearby Kaniet and Sae Islands. Four new landbirds, in addition to six new shorebirds and five new seabirds, were added to the list of birds for these poorly known islands, bringing the total list to 59 species. We also document significant extensions of the known breeding ranges of Brown Noddy *Anous stolidus*, Black Noddy *A. minutus* and Red-footed Booby *Sula sula*. The biological importance of the West Melanesian Trench is further emphasised by our seabird observations.

The birds of the small islands in the far north-west of Papua New Guinea are poorly documented. A list of the species recorded from the Ninigos, Hermits, Anchorites (= Kaniet Islands) and Wuvulu can be derived from Mayr & Diamond (2001), while a few notes on species of interest were made in Dutson (2011). Bell (1975) noted that 'the birds comprise a depauperate atoll avifauna, of strong affinities with the Bismarck Archipelago and not with mainland New Guinea, which is almost equidistant'. Published historical records are collated here alongside previously unpublished notes from W. F. Coultas' visits in 1934 and SMH's visits in 2019. Three subspecies are endemic to these islands (Mayr & Diamond 2001), a number dependent on taxonomy, and a significant proportion of the global population of the extremely range-restricted Atoll Starling *Aplonis feadensis* is found there. This paper presents new records of four landbird species, six shorebirds and five seabirds, and the first breeding of Red-footed Booby *Sula sula* in the region.

Geography of the region

The Ninigo Islands are a group of seven coralline atolls including some 48 islands and islets (www.Bing.com/maps/aerial), *c.*260 km north of mainland Papua New Guinea and *c.*265 km west of Manus. The largest atoll is approximately 18 × 33 km and includes 21 islands. None of the main Ninigo islands is higher than 2 m. The four most populated islands are Longan (50 ha) in the north-west, Amik (9 ha) and Pihun (70 ha) in the east, the latter which SMH did not visit but was visited by Coultas, and Mal (305 ha) in the south. Longan supports *c.*200 people that live in the eastern quarter of the island, while garden crops and brush cover the western part. The islanders keep pet cats and dogs, and occasionally wing-clipped Rainbow Lorikeets *Trichoglossus haematodus*. Mal has several family settlements, a clinic and a school, and is characterised by coconut palms *Cocos nucifera*, breadfruit *Artocarpus altilis*, Indian almond *Terminalia catappa* and ornamental plants. Menam (88 ha) now has a small population of farmers. As there is no longer a viable market for copra, the coconut plantations are being left to die, or are burned and cleared for food crops and housing. Many islands are characterised by a few large, old hardwood

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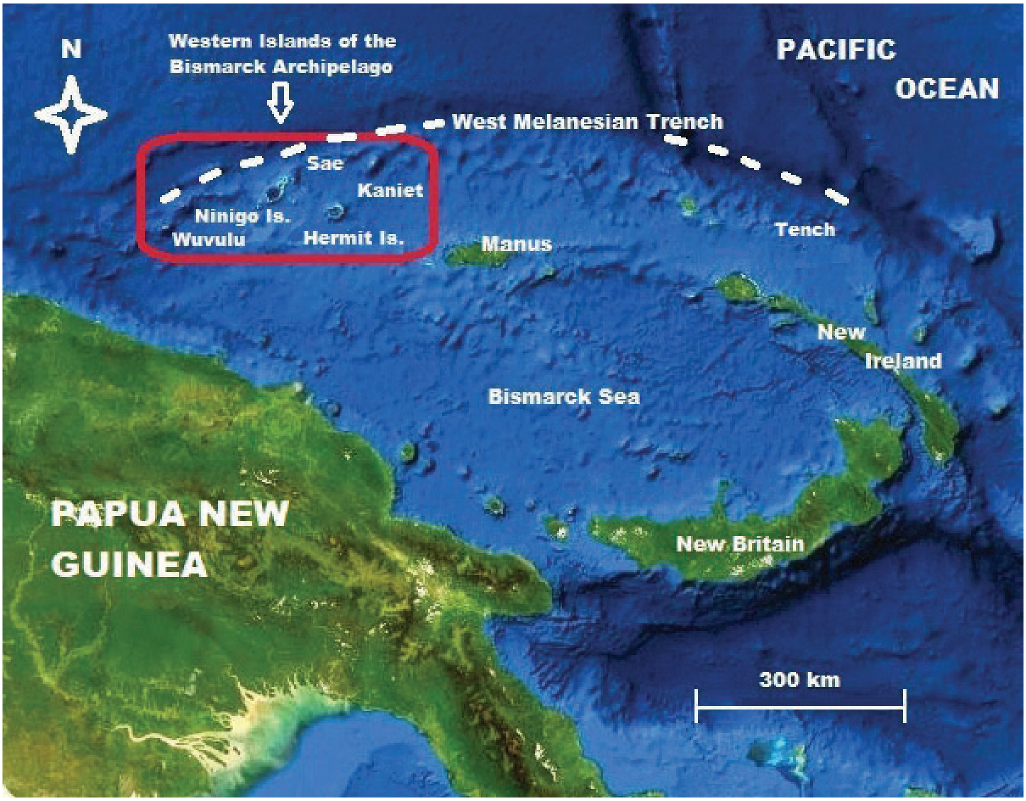

Figure 1. The western Admiralty Islands (inside the red rectangle), the West Melanesian Trench, and their geographical relationship to the Bismarck Archipelago and mainland New Guinea. Contextually important islands such as Wuvulu, Manus and Tench are also shown (based on https://www.arcgis.com/home/webmap/viewer.html?webmap=c1c2090ed8594e0193194b750d0d5f83).

trees (probably *Pisonia* sp.) along the beaches, in addition to the commoner Indian almond. Coasts are composed of white sand and coral, with extensive tidal flats and reefs.

Nahanu (1 ha), Bahanat (5 ha), Xaheihon (13 ha) and Nana (0.4 ha) are all uninhabited islands, typically covered in a very dense mosaic of *Cocos nucifera*, mangrove *Rhizophora* sp., *Pandanus* sp. and *Casuarina* sp. Nahanu is frequently visited by villagers to gather coconut crabs, pigs and introduced chickens. Xaheihon and Nana have prominent sand spits which host an assemblage of shorebirds and terns.

The four largest Hermit Islands (plus three tiny islets) form a single atoll (*c.*16 km across) with a rim of nine low sandy islands surrounding a lagoon. The atoll is *c.*260 km north of mainland Papua New Guinea and *c.*175 km west of Manus. Unlike the Ninigos, the interior islands are of volcanic origin, high and rocky. Luf (234 m, 600 ha) is the most populous, followed by Akib (109 m, 75 ha) (www.Bing.com/maps/aerial; www.gpsnauticalcharts.com/main/australia-nautical-charts-by-folio.html). Slopes on the north sides of Maron, Akib and Luf appear to retain a dense native vegetation dominated by *Ficus* sp., casuarinas and *Pandanus* sp. with a shoreline fringe of mangrove. In contrast, old coconut plantations still dominate the south slope of Akib. South-west Akib is currently being cleared for a school, and on Luf trees have been cleared in small plots high above villagers' homes to create gardens. SMH did not birdwatch on Luf and only briefly on Akib, but in view of the topography and dense vegetation these islands would probably be very productive areas to explore (as suggested by Bell 1975). Pemei (9 ha) is a low, uninhabited island densely

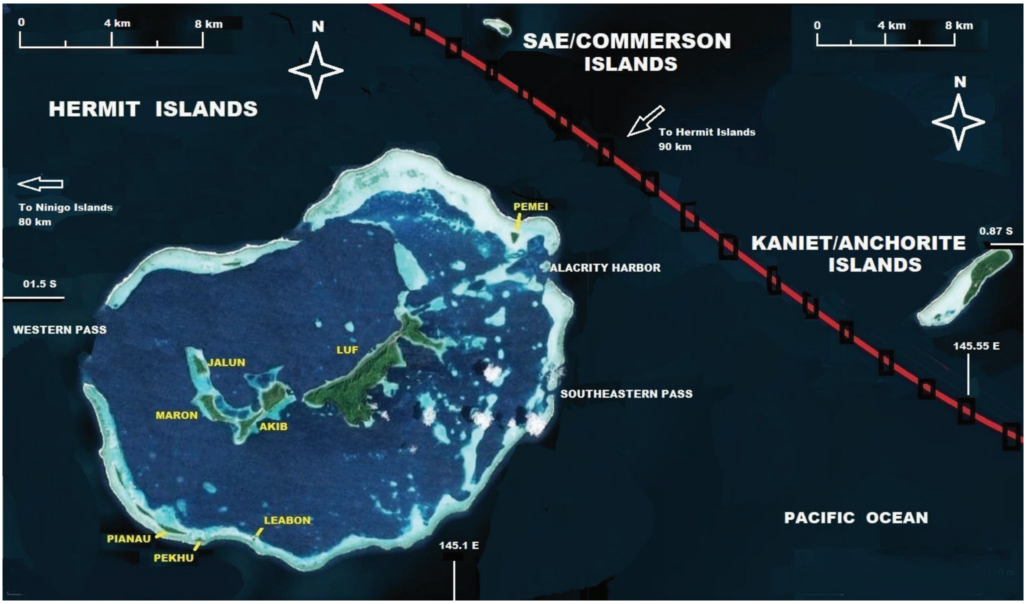

Figure 2. The Hermit Islands, showing all of the islets mentioned in the text; the Sae and Kaniet Islands are shown at a different scale (based on www.Bing.com/maps/aerial).

covered in coconut palms, *Casuarina*, mangrove, *Terminalia catappa* and *Pandanus* sp., which makes penetration of more than a few dozen metres into the interior near-impossible. The south-west coralline islands support similar vegetation with tall *Casuarina* predominating. Dense vegetation made casual access impossible. These islands are uninhabited except three families that reside on the eastern tip of Pianau (37 ha).

Coultas camped on Suf, the largest of the five Kaniet Islands and described it in 1934 as low-lying and covered in coconuts with no 'bush' remaining and populated by fewer than 50 people. Fresh water was scarce and birdlife almost non-existent, although formerly (according to a native informant) landbirds were present. He described Sae from aboard his ship as two 'flat sandy knobs connected at ebb tide by a reef.' The larger of the two was covered in shrubs and trees, while the smaller bore a single coconut palm. Coultas was informed that these islands were breeding grounds for turtles and seabirds including 'countless' terns and frigatebirds nesting there in November and December.

Historical knowledge of the avifauna

The first zoological exploration of these islands was by collectors on behalf of Johann Caesar Godeffroy (Hartlaub 1867) and the species he collected are marked (G) in the species accounts. Reichenow's (1899) treatise on the birds of the Bismarcks appears to merely repeat Hartlaub. Ernst Mayr made a small collection on Mal, in the Ninigos, on 10–11 November 1928, including specimens of Bismarck Black Myzomela *Myzomela pammelaena* and Singing Starling *Aplonis cantoroides* (Meise 1929a,b). During the Whitney South Sea Expedition, William Ferrell Coultas (hereafter WFC) collected on three of the four island groups in 1934: 10–14 May Hermits; 16–22 May Kaniets and Sae (but was unable to land on the latter); and 23 May–1 June Hermits, where he was based on Maron but visited Luf and other unspecified islands (Fig. 2). During 3–18 June WFC visited the Ninigos, where he camped for a week on Ahu, one day on Taulil and spent an unspecified amount of time on Pihun and other islands (Fig. 3). Information on the number of specimens and the locations

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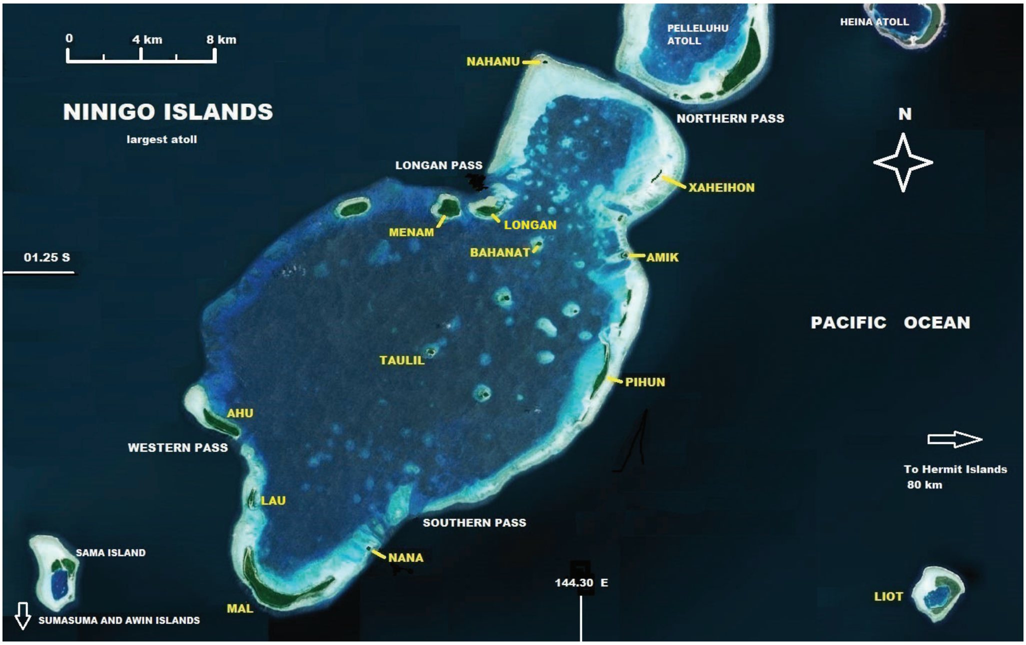

Figure 3. The main Ninigo Atoll, showing all of the islets mentioned in the text (based on www.Bing.com/maps/aerial).

where they were collected was initially taken from WFC's unpublished diary. This was subsequently amended following reference to the American Museum of Natural History, New York's (AMNH) online catalogue, which is based on WFC's specimen label data. To our knowledge, the Kaniets and Sae have not been surveyed ornithologically since WFC's visit, but in 1970, Lt.-Col. Harry Bell camped on Menam, in the Ninigos, on 10–12 August and visited Luf in the Hermits on 13–14 August (Bell 1975).

Although the seas of north-western Northern Melanesia are potentially very interesting in terms of seabird distributions, especially around the West Melanesian Trench, which is close to Sae and the Ninigos, there are very few data for this region (Cheshire 2010).

Methods

On 27 January–13 February 2019, SMH sailed from Indonesia to the Ninigos and Hermits and then further east, returning to the Ninigos and Hermits on 2–14 October 2019. During seven days at sea in a 14 m yacht moving at an average of six knots, SMH observed birds for *c*.12 hours per day and recorded all birds seen. During 18 of 23 days in the Ninigos and Hermits, SMH with, at times, one or two companions, Liz Crawford (LC) and Chris Herbert (CH), logged >35 hours of bird observations. Some observations were made from a 2.9 m inflatable dinghy off the coast of small islands if getting ashore was not feasible. Birds and times were recorded in field notes. A large proportion of these records has been submitted to eBird (https://ebird.org/home). Photographs of seabird flocks were used to confirm species identification and estimate numbers and composition of flocks. Seabird locations were determined by correlating photographic time stamps with track files recorded using navigational software. In the species accounts below, omission of an island group implies a lack of known records for that group. Species new for either the Ninigos or Hermits, but not both, are indicated by an asterisk next to the name of the group; those new for the entire region are similarly indicated next to the species name. Nomenclature and sequence follow Beehler & Pratt (2016) for all species included therein.

Annotated list of birds of the Ninigo, Hermit, Sae and Kaniet Islands, and adjacent waters

MELANESIAN SCRUBFOWL *Megapodius eremita*
Occurs on virtually every island in Northern Melanesia including several tiny islets (Mayr & Diamond 2001).
Ninigos WFC collected 22 specimens: two each on Ahu and Taulil, and 18 on Pihun (AMNH 336200–221), and received local reports from Liot. Bell (1975) noted that in 1970 imported labourers hunted the birds and took their eggs. He recorded one bird on Menam and found two disused nesting mounds. 6 October 2019: five were scratching leaf-strewn and coconut husk-covered ground on Bahanat. Local people sometimes consume scrubfowl eggs, but it is not a common practice (local informant).
Hermits WFC considered the species extinct in the Hermits, but Bell (1975) noted that villagers on Luf insisted that it still occurred in tiny patches of scrub on coral islands, but not on Luf. No sign of scrubfowl on any of the five islands visited in 2019.
Kaniets Capt. Mackenzie (pers. comm. to WFC) found scrubfowl common in 1921; however, in May 1934 WFC saw none.

WHITE-BIBBED GROUND DOVE *Alopecoenas jobiensis jobiensis*
Recorded in the Admiralties only on Tong (Dutson 2001, 2011, Mayr & Diamond 2001).
Hermits The only record is a specimen collected by WFC from Maron, 24 May 1934 (AMNH 336319).

NICOBAR PIGEON *Caloenas nicobarica*
Mayr & Diamond (2001) observed that this is one of the most widespread species in Northern Melanesia, but there appear to be very few records from the study area. Neither SMH nor Bell (1975) observed it on the Ninigos or Hermits. WFC noted that it is 'known to occur on Luf at times and at others absent. We did not encounter it on our visit', and that there were 'old native reports' for Sae. Coates & Swainson (1978) observed one on Wuvulu 160 km south-west of the Ninigos on 27 February 1975. Apparently local people report its presence on Wuvulu in small numbers, but have noted that its gizzard stones could not have been picked up there. WFC included it for the Hermits because he was told that the species visits Luf occasionally.

YELLOW-BIBBED FRUIT DOVE *Ptilinopus solomonensis johannis*
Widespread in Northern Melanesia (Mayr & Diamond 2001).
Ninigos WFC collected three on Pihun (AMNH 336246–248) but none on Taulil, and mentioned that local people reported the species from Liot. Bell (1975) recorded it on Menam. Two photographed by CH, one observed and many heard on Longan.
Hermits Collected by WFC on Luf where he considered it rare (however, AMNH 336318 is listed as having been collected on Maron, 25 May 1934). Heard on Pemei (SMH).
Kaniets WFC noted that it used to occur on these islands.

PACIFIC IMPERIAL PIGEON *Ducula pacifica sejuncta*
Scattered and local distribution off northern New Guinea, including on Wuvulu, but common to the south-east (Dutson 2011).

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Ninigos WFC secured a single specimen and noted the species to be 'very rare'. Bell (1975) found it common on Menam and Pihun. Five in breadfruit trees in the cultivated area of Longan, three on Bahanat and two on Mal (SMH).
Hermits WFC noted that a few remained on Luf where it was hunted. Bell (1975) found the species common. Heard on Pemei (SMH).
Kaniets Apparently extirpated long ago (WFC).

FLOURY (ISLAND) IMPERIAL PIGEON *Ducula pistrinaria*
Widespread throughout Northern Melanesia (Mayr & Diamond 2001).
***Ninigos** 13 October 2019: three seen and heard on Mal; photographs were not obtained but SMH clearly saw the white around the bill base, an impression of white around the eyes, and definite lack of a bill knob. The neck and hindneck were pale grey, offset by darker glossy green upperparts. Overall jizz was of a paler-necked bird than Pacific Imperial Pigeon, with a brighter green back and wings, and no knob. Furthermore, SMH is familiar with the call of this species from extensive experience in the Solomons and Bismarcks during the previous seven months. This would appear to be the first record of the species for the Ninigos, but it is known from the nearby Hermits, as well as Wuvulu and Manus (Mayr & Diamond 2001) and was thus perhaps to be expected.
Hermits WFC, who was only on Luf for a few hours, collected a single specimen that was not 'saved'. He was informed that both species of *Ducula* were occasionally taken by hunters but mainly *D. pacifica*. Bell (1975) saw a group of *Ducula* sp. that was probably this species.

***WHITE-TAILED TROPICBIRD** *Phaethon lepturus*
The nearest known breeding site appears to be Tench (*c.*705 km east of the Ninigos) (Coates 1985, Beehler & Pratt 2016).
Ninigos One photographed at sea 17 km east of the Ninigos and north of Liot. Previously recorded off Wuvulu (Coates & Swainson 1978).

MATSUDAIRA'S STORM PETREL *Oceanodroma matsudairae*
Ten seen 193–357 km north-east of Suf Atoll (Kaniet Islands) (Cheshire 2010).

WEDGE-TAILED SHEARWATER *Ardenna pacifica*
Widespread and recorded in most, if not all, months throughout northern Melanesia but does not breed (Coates 1985, Dutson 2011). Approximately150 reported 133 km north-west of Sae and *c.*60 354 km north-east of the Kaniets (Cheshire 2010).
Ninigos One south of the Ninigos (Bell 1975). 'Numerous' in 2019 with a large mixed feeding flock of seabirds 240 km west of the Ninigos; one inside the main lagoon, presumably in response to strong winds outside the atoll (SMH).

***STREAKED SHEARWATER** *Calonectris leucomelas*
During October–April (especially December–March) it is locally common in the seas north of New Guinea including around the Admiralties and Bismarcks (Coates 1985, Cheshire 2010, Dutson 2011, Beehler & Pratt 2016).
Ninigos 2019: at least 23 and then *c.*13 seen with mixed-species feeding flocks 240 km west of the atoll (SMH).
Hermits 2019: 20 seen with a feeding flock of seabirds 85 km east of the Hermits (SMH).

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YELLOW BITTERN *Ixobrychus sinensis*
Ninigos WFC collected two specimens at a swamp on Ahu, probably migrants from Asia (AMNH 336191–192).

BLACK BITTERN *Ixobrychus flavicollis australis*
Ninigos WFC collected six roosting in coconut trees on Ahu, with evidence of marine and terrestrial foraging (AMNH 336185–190). One near the centre of Menam (Bell 1975).
Hermits One at *c.*130 m in steep hillside jungle on Luf (Bell 1975).

NANKEEN NIGHT HERON *Nycticorax caledonicus australasiae*
Ninigos WFC collected seven (AMNH 336193–198, 336277) and noted that the species roosted on Ahu and other islands with swamp vegetation; he also heard it on Pihun. Bell (1975) observed two on Menam. Three seen on Longan (SMH).
Kaniets One collected in the swamp on the most northerly island (WFC).

EASTERN REEF EGRET *Egretta sacra*
Ninigos Recorded by WFC and Bell (1975) on Menam. Ones and twos of both grey and white morphs on Longan, near Nahanu, Amik, Xaheihon, Mal and Nana (SMH).
Hermits Scarce. Recorded by WFC and Bell (1975). Single black-splotched white morph seen off Pemei and near the western islands (SMH).
Kaniets and Sae Recorded by WFC.

GREAT FRIGATEBIRD *Fregata minor*
Small numbers of unidentified frigatebirds occasionally seen offshore.
Ninigos Recorded by Bell (1975). Approximately 20 with a large mixed feeding flock of seabirds 19 km offshore (SMH).
***Hermits** One seen amongst *Sula sula* on Pekhu (SMH).

LESSER FRIGATEBIRD *Fregata ariel*
Ninigos Recorded by Bell (1975). Small numbers (<5) seen offshore including *c.*20 with a large mixed feeding flock of seabirds 19 km west of the Ninigos, and two over the main lagoon (SMH).
Hermits Recorded by WFC and Bell (1975). Nine over Pemei and two roosting on Pekhu and Leabon (SMH).
Sae 'Observed in abundance about Commerson (*sic*). It roosts and nests there.' (WFC).

MASKED BOOBY *Sula dactylatra*
The status of this pantropical species is somewhat enigmatic in Northern Melanesia, with very few records, although this may, however, simply reflect the paucity of observers. King (1967) regarded it as a vagrant to the south-west Pacific.
***Ninigos** SMH photographed an immature in a large mixed seabird flock *c.*240 km west of the atoll on 27 January 2019.
Hermits Bell (1975) noted one over the western entrance to the lagoon.
Sae Numerous (WFC).

***RED-FOOTED BOOBY** *Sula sula*
Infrequently recorded in Northern Melanesia, except around small remote islets (Dutson 2011).
Ninigos One over the main lagoon at Mal (SMH).

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Figure 4. Nesting Red-footed Boobies *Sula sula*, Pianau, Hermit Islands, October 2019 (Sue Muller Hacking)

Hermits 3 October 2019: Pianau *c*.300, with 124 nests (17 with chicks) mostly high on open branches of *Casuarina* with a few in dense mangrove (Fig. 4); on Pekhu, *c*.200 birds and at least 40 active nests, a few with chicks (photographed); and on Leabon, the smallest island, with fewest *Casuarina*, *c*.100 with *c*.10 nests (2–3 with chicks) (SMH). These are the first observations of nesting in Northern Melanesia west of Tench, and also apparently the first of the species breeding in *Casuarina* trees (Schreiber *et al*. 2020).
Sae Numerous (WFC).

BROWN BOOBY *Sula leucogaster*
Although regularly observed within inshore waters, there are no known breeding sites in Northern Melanesia (Dutson 2011, Schreiber & Norton 2020).
Hermits Two at the western entrance of the lagoon (Bell 1975). Three in the eastern passage to the lagoon, and two near Pekhu and Leabon (SMH).
Sae Numerous (WFC).

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BUFF-BANDED RAIL *Hypotaenidia philippensis anchoretae*

Race *anchoretae* is endemic to the region, although birds breeding on Wuvulu (Coates & Swainson 1978) probably involve this subspecies.

Ninigos WFC collected 11 specimens on the smaller islands including Taulil (AMNH 336222–232) and reported this rail to be common on almost every island he visited in the Ninigos (Ahu, Mal, Longan, Taulil, Pihun, Ami, Lau and others), including at the edge of villages where it appeared quite tame. Bell (1975) revisited the same islands but failed to find the species. 2019: one observed by LC (*in litt*. to SMH) on Nahuna and one on Longan, where the species is apparently hunted.

Hermits WFC collected nine on Maron (AMNH 336305–313), but noted that it apparently did not occur on Luf.

Kaniets WFC collected ten (AMNH 336278–287) and noted that Buff-banded Rail was common in 'the olden days' but that there were only 'a few left in the islands and those, in all probability, will not survive many years.'

LONG-TAILED CUCKOO *Eudynamys taitensis*

Breeds almost exclusively in New Zealand during October–February (Higgins 1999) and would probably have been absent at the time of SMH and Bell's visits.

Ninigos WFC saw but failed to collect the species.

***SWIFTLET** *Collocalia* / *Aerodramus* sp.

Ninigos 12 October 2019: two swiftlets observed over Mal (SMH). They appeared larger than Glossy *Collocalia esculenta* or White-rumped Swiftlets *Aerodramus spodiopygius*, had a light grey mantle with a barely discernible paler rump, and a shallow but well-defined tail fork. They were perhaps Uniform Swiftlet *A. vanikorensis*, which is resident on Manus and mainland New Guinea, but other species could occur and field identification of swiftlets is not always possible.

PACIFIC GOLDEN PLOVER *Pluvialis fulva*

***Ninigos** 13 October 2019: one off the north-west tip of Mal (SMH).

Hermits WFC collected one, the only shorebird he recorded in the Hermits. 3 October 2019: two on Leabon (SMH).

***GREY PLOVER** *Pluvialis squatarola*

Ninigos 10 October 2019: at least ten on a sand spit off the north end of Xaheihon (SMH; photo).

***LESSER SAND PLOVER** *Charadrius mongolus*

Ninigos 10 October 2019: seven photographed in a mixed shorebird flock on a sand spit off northern Xaheihon; 13 October, one on a sand spit on Mal (SMH).

***BAR-TAILED GODWIT** *Limosa lapponica*

Ninigos 10 October 2019: six photographed in a mixed flock of shorebirds on a sand spit on Xaheihon (SMH). Previously recorded on Wuvulu (Coates & Swainson 1978).

WHIMBREL *Numenius phaeopus*

***Ninigos** In January, February and October 2019, small numbers seen daily on Longan including a roost of seven; in October, 20 in a mixed flock of shorebirds on Xaheihon (SMH).

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Figure 5. Eastern Curlew *Numenius madagascariensis* with Whimbrel *N. phaeopus*, Grey Plover *Pluvialis squatarola* and Lesser Sand Plover *Charadrius mongolus*, Xaheihon, Ninigo Islands, October 2019 (Sue Muller Hacking)

Hermits Bell (1975) recorded >20 on Luf in August. 9 February 2019: four in flight on Pemei; 10 February, one in flight on Pemei.

***EASTERN CURLEW** *Numenius madagascariensis*

Over the last 30 years this curlew's population has declined to such an extent that its conservation status has changed from Near Threatened to Endangered (van Gils *et al*. 2020). Dutson (2011) regarded it as a rare migrant with records from just a few islands in Northern Melanesia.

***Ninigos** 10 October 2019: SMH photographed one on a sand spit on Xaheihon in a mixed flock of shorebirds (Fig. 5).

WANDERING TATTLER *Tringa incana*

Ninigos Bell (1975) thought it common on Menam during August. 12 October 2019: SMH photographed one with a flock of terns and *Anous stolidus* at the eastern end of Nana.

Hermits One seen on Luf (Bell 1975).

COMMON SANDPIPER *Actitis hypoleucos*

***Ninigos** 2 February 2019: one on Longan; 7 October, one off Longan with a flock of noddies; singles also seen on Xaheihon and the north coast of Mal in October (SMH).

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Hermits Bell (1975) collected a specimen and observed *c*.20 on Luf. 9 February 2019: four flushed on the sandy coast of Pemei (SMH).

RUDDY TURNSTONE *Arenaria interpres*

Ninigos By far the commonest shorebird on the islands: 29 January 2019: eight near Longan; 31 January, a large flock flying off on Nahuna; 3 February, 14 in flight near Amik; 5 October, eight seen off Longan with four there on 10 October; 12 October, three in a mixed shorebird flock on Nana; 13 October, two in flight on Mal. McClure (1968) reported an adult, ringed 9 May 1968 at Ichikawa, Chiba, Japan, found dead on Amich (*sic*), Ninigo group, 16 January 1969.

Hermits Bell (1975) saw five in full breeding plumage in August on Luf. 3 October 2019: SMH photographed a flock of *c*.75 on Leabon.

***RUFF** *Philomachus pugnax*

Rare but regular visitor to eastern New Guinea (Beehler & Pratt 2016) and Northern Melanesia (Dutson 2011), but possibly only on passage (Coates 1985).

Ninigos 13 October 2019: SMH photographed a juvenile male on Mal.

***RED-NECKED PHALAROPE** *Phalaropus lobatus*

Ninigos 28 January 2019: a flock of 12 flushed from the sea, possibly associated with a large mixed seabird flock 19 km west of the Ninigos.

Hermits 5 February 2019: a tight flock of *c*.40 flushed from the sea 2 km west of the atoll.

BROWN NODDY *Anous stolidus*

The nearest known breeding sites are on Wuvulu (D. J. Ringer in www.birdsofmelanesia.net) and Tench (Coates 1985).

***Ninigos** 2019: common on and around Longan, *c*.20 on Nahanu,15 near Liot, 1–2 seen daily on Mal, and *c*.20 on Nana including some apparently on nests, but too deep in dense foliage to photograph (SMH). Numbers probably under-estimated as often impossible to distinguish from Black Noddy *A. minutus*.

Hermits One seen by Bell (1975). 2019: *c*.40 regularly seen in flight over, or roosting on, Pemei (SMH); could not be confirmed if the species was nesting.

Kaniets Observed (WFC).

Sae Abundant, flying to and from the island (WFC).

BLACK NODDY *Anous minutus*

Ninigos Bell (1975) considered this species abundant, but only a few were seen by WFC. 31 January 2019: at least six pairs nesting on Nahanu, in low tangled mangroves, 3–4 m above ground, plus *c*.100 in flight over the island; seen daily near Longan with roost counts of 23–103 birds, a feeding flock of *c*.200 off Bahanat, and smaller numbers off Liot and Mal (SMH). *A. minutus* was far commoner than *A. stolidus* (in a ratio of 4:1 to 7:1). Large counts of unidentified noddies included *c*.80 just outside the western entrance and *c*.200 in a feeding flock.

Hermits One collected by WFC and a few others seen. Bell (1975) observed a flock of 150 outside the lagoon and many groups (of 5–10) inside it. 2019: *c*.25 on Pemei (SMH). Nesting was not confirmed; however, the birds were roosting in *Casuarina* trees on the shore and were seen to frequently disappear into the interior. Large counts of unidentified noddies included *c*.300 near the western entrance and *c*.200 roosting and flying around Leabon.

Sae Abundant, flying to and from the island (WFC).

WHITE TERN *Gygis alba candida*
Ninigos WFC noted a few and collected two specimens on Maron (AMNH 336315–316). 2019: ten on Longan, <1 km from Menam where Bell (1975) found it almost certainly nesting; 22 off Mal and Nana (SMH).
Hermits Recorded by WFC but not by Bell (1975). 2019: *c*.200 on Pemei, some of which were aggressive, circling and swooping, suggestive of nesting (SMH).
Kaniets WFC observed three or four, and took one specimen.
Sae Nests on Sae (WFC).

CRESTED TERN *Thalasseus bergii*
Widespread throughout Northern Melanesia, but perhaps uncommon west of Manus, with no previously known breeding sites in the region (Dutson 2011).
Ninigos Bell (1975) recorded small numbers during August. In late January 2019, <5 with a large mixed feeding flock of seabirds *c*.240 km west of the Ninigos, and two seen with a large feeding flock 19 km offshore. Noted in small numbers on Longan on 1 February and again 5–10 October, including 2–10 at roosts.
Hermits Bell (1975) noted small numbers outside the reef and on Luf.
Kaniets Observed over the reefs (WFC).
Sae 'Nests on Sae' (WFC).

BRIDLED TERN *Onychoprion anaethetus*
Hermits Bell (1975) saw two inside the lagoon.

SOOTY TERN *Onychoprion fuscatus*
Typically more pelagic than most terns in the region (Coates 1985, Dutson 2011), and none was seen within the atolls.
Ninigos Bell (1975) noted four or five at the entrance to the main lagoon. 2019: approximately 32 with mixed-seabird feeding flocks 240 km west of the Ninigos (SMH).
Hermits 2019: *c*.30 just west of the atoll within a mixed feeding flock of 400 terns, and *c*.20 in a mixed feeding flock 85 km to the east.

ROSEATE TERN *Sterna dougallii*
***Ninigos** Three in breeding plumage photographed near Liot (SMH).
Hermits Bell (1975) noted two on Luf, both in breeding plumage.

***BLACK-NAPED TERN** *Sterna sumatrana*
Ninigos 2019: *c*.95 observed 19 km west of the Ninigos, >50 on Nahanu, *c*.20 on Nana, and 3–6 around Mal; 2–34 seen daily on Longan in February and October, many of them roosting (SMH).
Hermits 2019: five just west of the entrance into the Hermits and 47 on a sand spit on Leabon (SMH).

COMMON TERN *Sterna hirundo longipennis*
Ninigos Bell (1975) noted small groups in August. In January–February 2019, a max. 20 in the main lagoon and *c*.40 observed 19 km west of the Ninigos; in October singles were seen in the north of the atoll and on Nana (SMH).
Hermits Bell (1975) noted small flocks provisionally identified as this species. In February 2019, *c*.60 with a mixed flock of seabirds near the western entrance; one on Leabon in October (SMH).

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***LONG-TAILED JAEGER** *Stercorarius longicaudus*

Very rare in New Guinea waters (Beehler & Pratt 2016) with even fewer records in Northern Melanesia (Dutson 2011).

Ninigos 14 October 2019: a first-year with a flock of feeding seabirds 260 km west of the Ninigos, at the edge of the West Melanesian Trench (Fig. 6).

Figure 6. Juvenile Long-tailed Jaeger *Stercorarius longicaudus*, near the West Melanesian Trench, October 2019 (Sue Muller Hacking)

OSPREY *Pandion haliaetus cristatus* (G)

Ninigos 9 June 1934: WFC took a specimen (AMNH 336199) and noted a total of eight in flight near Longan. Bell saw two on Menam (Bell 1975). 2019: one seen on Longan (SMH).

BRAHMINY KITE *Haliastur indus*

Ninigos Not seen by Bell (1975) whereas WFC recorded it 'several times'. 2019: three flying over Longan on two consecutive dates (SMH).

RAINBOW BEE-EATER *Merops ornatus*

None recorded in 2019: this migrant is usually present in Northern Melanesia from early March to early October.

Ninigos Bell (1975) saw birds roosting on Menam.

Hermits Bell (1975) observed a flock of five on Luf.

Kaniets WFC reported a few.

BEACH KINGFISHER *Todiramphus saurophagus admiralitatis*

Those on the Ninigos, Hermits and Kaniets (plus Wuvulu) are usually treated as an endemic race *anachoreta*. Bell (1975) noted that this species 'has a white-headed (*admiralitatis* Sharpe, 1892) and a blue-headed (*anachoreta* Hartlaub, 1867) phase, originally described as separate species, but recognized as phases by Stresemann (1923) and Mayr (1949b [= 1950]). Specimens in the AMNH show that the phases are not linked to sex and that intermediates occur. The museum has no white-headed specimens from the Ninigos, but has almost the same number of specimens of both from the Hermits. WFC, under the impression that there were two species, thought that blue-headed birds were more common on the Ninigos and vice versa on the Hermits.'

Ninigos WFC found it more common in the Hermits. Bell (1975) reported this species to be abundant on Menam. White-crowned birds were seen on Bahanat, Xaheihon, Longan and Mal, and dark blue-crowned individuals on Bahanat, Longan and Mal (SMH).

Hermits WFC found it common and breeding. Bell (1975) collected one on Luf. A single white-crowned bird was seen on Pemei and a dark blue-crowned individual on Akib (SMH).

Kaniets WFC collected ten but did not believe the species to be common.

Sae Reported to WFC.

SACRED KINGFISHER *Todiramphus sanctus*

Ninigos Bell (1975) observed unidentified kingfishers, possibly this species, on Menam.

Hermits The only record is of one seen on Luf (Bell 1975).

RAINBOW LORIKEET *Trichoglossus haematodus* (G)
The Ninigo population is considered to be an endemic subspecies *nesophilus* and, although Mayr & Diamond (2001) treated birds in the Hermits as *flavicans* (otherwise found east to New Hanover), most if not all other recent commentators suggest these birds too belong with *nesophilus* (Dickinson & Remsen 2013, del Hoyo & Collar 2014, Collar *et al*. 2020).

Ninigos WFC noted it to be the commonest landbird in the group, with flocks of 2–10 everywhere. Bell (1975) found it 'abundant (2–5) in plantations, feeding on flowering coconuts; seen to fly to Longan, 800 m from Menam.' 2019: up to six on Longan, Bahanat, Xaheihon and Mal (SMH).

Hermits WFC reported it to be common. Bell (1975) also found the species common but only in coconuts fringing beaches on Luf. 2019: small flocks flying between Luf and Akib (SMH).

BISMARCK BLACK MYZOMELA *Myzomela pammelaena ernstmayri*
This subspecies is confined to small islands from Wuvulu east to the Admiralty group (Mayr & Diamond 2001).

Ninigos WFC collected ten (AMNH 336266–276) and found it 'moderately common', reporting that the species 'appears to go in flocks or waves through the plantation.' Mayr collected one in May 1928 (AMNH 294655). Bell (1975) collected two on Menam and found it abundant in coconuts and forest. 2019: common on Longan, Bahanat and Mal, where 2–14 recorded most days (SMH).

Hermits WFC collected five on the outer islands but did not find it on Luf. Bell (1975) remarked that one of his party reported a 'black sunbird' in coconut trees, which was probably this species. 2019: four seen in *c*.15 minutes of observation on Pemei within 10 m of the beach (SMH).

Kaniets 'A few' of which WFC collected four.

[***COMMON CICADABIRD** *Edolisoma tenuirostre*]
The nearest known population is on Manus, where the subspecies *admiralitatis* exhibits sexual dimorphism similar to that of birds observed in the Ninigos.

Ninigos 6 October 2019: on Bahanat, SMH observed two black and one russet-plumaged bird of similar size and structure on the small outer branches of a tree *c*.8 m overhead. They were seen through binoculars but flew off before photographs could be taken. The rufous individual had a grey crown, rufous breast and belly, and brown/rufous upperparts. The black birds had dark eyes and an unbarred belly. SMH is familiar with *E. tenuirostre* and related taxa from the Solomons and New Britain, and confirmed the sighting based on the illustration in Dutson (2011). Other grey-and-rufous birds were eliminated, such as Island Monarch (grey, not rufous neck and upperparts), as well as other dark birds like Shining Flycatcher *Myiagra alecto* (head too angular, different jizz), Singing Starling *Aplonis cantoroides* (tail too short), Atoll Starling *A. feadensis* (eyes yellow not black, tail too short) and Barred Cuckooshrike *Coracina lineata* (eyes yellow, black and white barring; far out of range). However, this population could represent an undescribed taxon and a considerable extension of range, meaning that much greater detail, preferably a photograph and / or specimen, will be necessary to confirm the presence of this species.

***WILLIE WAGTAIL** *Rhipidura leucophrys*
The nearest known population to the Ninigos is on Mussau (Mayr & Diamond 2001).

Ninigos 12 October 2019: SMH observed one on Mal; noting the black back, white breast and belly, white supercilium, and long wagged tail. Other potentially similar birds were

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eliminated: Manus Monarch (shorter tail and whiter body); Northern Fantail (white throat, and browner, not black-and-white plumage). SMH is very familiar with *R. leucophrys* from New Guinea and the Solomons where this species is common. This is a surprising record and ideally requires photographic or specimen confirmation. Nevertheless, SMH is confident of the identification.

ISLET MONARCH *Monarcha cinerascens fulviventris*

Ninigos WFC noted 'not too common but a few in small shrubs around plantations on Pihun.' He collected four (AMNH 336253–255). Bell (1975) collected an immature on Menam where it was 'extremely abundant'. 2019: singles or pairs on Longan and Bahanat, and 5–8 foraging in low bushes on Mal (SMH).

Hermits WFC collected eight on tiny outer islands of the atoll (AMNH 336347–354) but not on Luf. 2019: one on Pemei (SMH).

Kaniets WFC collected two, 16 May 1934 (AMNH 336298) and 21 May 1934 (AMNH 336299).

*MANUS MONARCH *Symposiachrus infelix*

Endemic to Manus, Rambutyo and Tong (Mayr & Diamond 2001, Dutson 2011).

Ninigos 1 February 2019: LC & CH saw a small, striking, black-and-white bird moving quickly through foliage in the south of Longan. Through binoculars, they were struck by its starkly contrasting black-and-white plumage, black-and-white head, black throat, black back and white belly. It was clearly a monarch but smaller than, albeit similarly proportioned to, Islet Monarch which they saw the same day. Later, on 1 February they identified the bird as a Manus Monarch using Dutson (2011). Other black-and-white birds were eliminated such as Willie Wagtail (less white, longer tail), a triller (*Lalage* sp.; different jizz, stance more upright, less black on face) and Northern Fantail *Rhipidura rufiventris* (grey and white with white not black throat, not black-and-white plumage). Manus Monarch is relatively uncommon and could have been overlooked by previous observers. Given that birds on Rambutyo and Tong are a separate subspecies, *S. i. coultasi*, it is likely that any population on the Ninigos represents an undescribed subspecies.

ARCTIC WARBLER *Phylloscopus borealis*

This northern Palearctic and Alaskan breeder winters largely in South-east Asia (Lowther & Sharbaugh 2020) including Indonesia as far east as the Moluccas (Coates & Bishop 1997).

Figure 7. Specimen of the Arctic Warbler *Phylloscopus borealis* complex (perhaps race *kennicotti*), collected by W. F. Coultas in the Kaniets, May 1934 (Paul Sweet, © American Museum of Natural History, New York)

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Kaniets An adult male collected by WFC on 21 May 1934 (Mayr 1955) is the sole record from the New Guinea region (Dutson 2011, Beehler & Pratt 2016), strangely though WFC made no mention in his diary of this specimen (AMNH 336300; wing 67.5 mm, tail 48.5 mm, bill to skull 14.46 mm, measured by P. R. Sweet). The coloration of the upperparts and its long bill agree best with race *kennicotti*, but the specimen is not certainly separable from *borealis* (P. R. Sweet *in litt*. 2020; Fig. 7). However, it bears mention that AMNH 336300 has not been critically re-examined in the light of the proposed splits of Kamchatka Leaf Warbler *P. examinandus* and Japanese Leaf Warbler *P. xanthodryas* from *P. borealis* (Alström *et al*. 2011); despite that their non-breeding distributions are poorly known, in the boreal winter both of these recently recognised species do occur well east into Wallacea (Eaton *et al*. 2016).

ORIENTAL REED WARBLER *Acrocephalus orientalis*
Kaniets A badly damaged specimen collected by WFC was probably this species (Coates 1990) but was not preserved (Bell 1975; P. R. Sweet *in litt*. 2020).

ATOLL STARLING *Aplonis feadensis heureka*
Range spread over many small islets, but probably encompasses no more than *c*.64 km^2 of land (Mayr & Diamond 2001).
Ninigos Bell (1975) collected a male on Menam and apparently found it quite common. 2019: 2–8 seen on Longan and Bahanat, and *c*.11 in open forest and near houses on Mal. A local informant stated that this species nests in holes of large broadleaf trees. SMH noted it as the most common starling on the atoll. Also recorded by WFC.
Hermits WFC found it to be the commonest landbird on these islands and collected 15. Found by Bell (1975) on Luf, the only island in the Hermits he visited. 2019: six adults and four juveniles recorded within a few minutes of being ashore on Pemei (SMH).

SINGING STARLING *Aplonis cantoroides*
Ninigos 11 May 1928: Mayr collected a single male (AMNH 294656) on Mal (Meise 1929b). The species was not found by Bell (1975) or WFC. 2019: two, six and four were seen on three dates on Longan. SMH found it more common on Longan in the indigenous gardens of the west of the island than on Bahanat or other uninhabited islands where the species was scarce. However, open agricultural areas are easier areas in which to see birds.
Hermits WFC found this to be one of the commonest species on these islands. Bell (1975) noted a flock of five unidentified starlings on Luf.

OLIVE-BACKED SUNBIRD *Cinnyris jugularis flavigastra*
Ninigos Bell (1975) observed one or two on Menam. 2019: four on Bahanat only permitted glimpses of their distinctive size, shape and bright yellow underparts (SMH).
Hermits WFC failed to find the species on Luf, but on Maron he noted it was 'not a common bird' and collected two. Bell (1975) found it 'very abundant' on Luf.

Discussion

We added four landbird species to the avifauna of the Ninigos and Hermits: a swiftlet sp., *Edolisoma tenuirostre*, *Rhipidura leucophrys* and *Symposiachrus infelix*. Whether these birds are recent colonists or vagrants is unclear, but three of these species are not typical migrants. The cicadabird, Willie Wagtail and monarch are all sedentary landbirds that are not known to migrate. Nevertheless, they probably travelled long over-water distances to reach these tiny atolls, although the possibility of ship-assisted travel is a possibility, albeit seemingly a remote one.

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The total list of birds for these islands and their adjacent seas is 59. Approximately 28 land and freshwater birds are now known from the Ninigos (24) and Hermits (18). Our observations added one resident species to the Ninigos' list: Island Imperial Pigeon. The Ninigos are richer than the Hermits in three presumed resident species: *Nycticorax caledonicus*, *Pandion haliaetus* and *Haliastur indus*. Although the Ninigos are considerably larger in area than the Hermits, they are 87 km further west of Manus, which is presumably the main source for most landbirds in these two island groups. However, the Hermits include two islands, Luf and Akib, which rise to 260 m and 100 m, respectively, and thus support a greater range of habitats.

Three austral migrants have been recorded on these atolls; *Eudynamys taitensis* from New Zealand, and *Todiramphus sanctus* and *Merops ornatus* from Australia and New Guinea. The low numbers and diversity of austral and Palearctic migrants is presumably a result of limited ornithological effort and the islands' locations at the extremity of these species' ranges.

Two Palearctic landbird migrants, *Ixobrychus sinensis* and *Phylloscopus borealis*, have been recorded in the region. *I. sinensis* is probably a regular Palearctic migrant to Northern Melanesia, given its status in New Guinea (Beehler & Pratt 2016). A third species, thought to be Oriental Reed Warbler *Acrocephalus orientalis*, was collected by WFC but the specimen was too badly damaged to identify with certainty (WFC; Coates 1990) and was not retained. Despite the paucity of non-shorebird Palearctic migrants recorded to date on the islands, the records mentioned in the Kaniets suggest that surveys of these islands during the southbound migration period (September–November) could produce additional species such as those recorded in northern Australia (see Menkhorst *et al*. 2017).

Migrant Palearctic-breeding shorebirds are moderately well represented, with 11 species now known from these atolls, albeit none in large numbers. We added six species to the list of Bell (1975). The presence of several flocks of *Phalaropus lobatus* further evidences that the seas of Northern Melanesia form part of the non-breeding range of this species.

In view of the avifaunal changes on these atolls between WFC's visit in 1934 and Bell's in 1970, it is relatively unsurprising that further changes should have occurred in the 50 years since they were last visited by an ornithologist (see Mayr 1942, Mayr & Diamond 2001). Unfortunately, however, the three surveys are not comparable in the islands visited or time involved, making it impossible to determine if such changes are genuine or a reflection of effort and / or seasonal differences. Nevertheless, the post-Bell colonisation of the Ninigos by *Aplonis cantoroides* (almost certainly from the Hermits) is a clear example of change. Our discovery of four previously unobserved landbirds indicates that a longer, well-timed and systematic survey of these islands may produce further additions. For example, SMH did not survey swamps where WFC found *Ixobrychus flavicollis* and *Nycticorax caledonicus*, and she did not visit Luf which supports tall hill forest and may harbour additional species.

Seabirds.—The seabirds of Northern Melanesia, in particular the north-west of the region, are very poorly known (Cheshire 2010, Dutson 2011). SMH's observations in the waters in and around the Ninigos and Hermits further evidence the importance of the West Melanesian Trench as a foraging area for pelagic birds, with feeding flocks of up to 900 *Anous* spp. and mixed-species feeding flocks of up to 500 individuals observed. Probably some species of seabirds were overlooked, in particular tubenoses such as *Oceanodroma matsudairae*, Bulwer's Petrel *Bulweria bulwerii*, Heinroth's Shearwater *Puffinus heinrothi* and others. This may reflect SMH's inexperience with this group, but it is also the case that her attention was often focused on sailing in at times challenging seas. Nevertheless, SMH's observations of *Phaethon lepturus*, *Ardenna pacifica*, *Calonectris leucomelas*, *Fregata* spp., *Stercorarius longicaudus*, three species of booby and nine of terns augments the steadily accumulating body of knowledge of seabirds in Northern Melanesia.

Conservation.—Bell (1975) suggested that the overall conservation status of these atolls had improved since WFC's visit there in 1934, and we broadly concur. However, without comparable observations from the same island(s) visited by WFC and Bell it is difficult to draw definite conclusions. Nevertheless, it is heartening that *Megapodius eremita* is extant and probably common on Bahanat. Conversely, its status in the rest of the Ninigos is unknown and the species may have been extirpated on the Hermits. However, the relatively rugged terrain and extensive wooded cover on some islands in the latter group could still harbour megapodes, but this needs confirming.

Arguably the species of greatest concern is *Hypotaenidia philippensis*, which WFC found to be common on both the Ninigos and Hermits, but was not seen by Bell or SMH. The only modern record for either atoll is that by LC (see above). Of the three pigeons apparently resident on the islands, *Ptilinopus solomonensis* is common on the Ninigos but may have been extirpated on the Hermits; *Ducula pacifica* is also numerous on the Ninigos but possibly extirpated on the Hermits where Bell (1975) reported it to be common *c*.50 years ago. The status of *D. pistrinaria* requires clarification. Atoll Starling remains common on both the Ninigos and Hermits.

The discovery of breeding colonies of *Anous minutus* on Nahanu (Ninigos), *A. stolidus* on Nana (Ninigos), *Gygis alba* on Pemei (Hermits) and *Sula sula* on Pekhu, Pianau and Leabon (in the Hermits) underlines the conservation importance of these little-known atolls.

Clearly, there is a need for a thorough survey of all of the islands comprising these four groups, but especially the remote islets such as Sama, Sumasuma and Awin in the southern Ninigos, and the two subsidiary atolls of Heina and Pelleluhu in the north, plus many of the small islands that form the Hermit Atoll. A survey of Sae in November–December should determine the status of its nesting seabirds.

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Origins of the upland avifauna of Yapen Island, New Guinea region

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Summary.—New Guinea's mountains consist today of the high Central Range, plus ten isolated lower outlying ranges. But during Pleistocene periods of low sea level, when New Guinea's current shallow continental shelf was exposed as dry land, the main island included further outliers that subsequently became cut off as land-bridge islands as rising sea levels submerged the shelf connecting them to New Guinea. We surveyed the upland avifauna of Yapen, the highest of those land-bridge islands. Yapen supports 26 upland species. That number is higher than on nearby oceanic islands of similar elevation, because Yapen in contrast to oceanic islands could acquire species overland during the Pleistocene. However, that number is much lower than on New Guinea's outliers of similar elevation, due to extinctions of many of Yapen's populations following its isolation as an island.

Of New Guinea's 193 upland species, some are much more widely distributed on the ten outliers than the rest. Yapen's upland species, and those of the other land-bridge islands, are a small subset of those successful colonists of mainland outliers. Part of the explanation for differential success is that only species whose elevational floors lie well below the summits of the outliers and of Yapen are likely to have survived on or colonised those mountains, all much lower than New Guinea's Central Range. For the remainder, we infer that more than half of Yapen's former upland populations have gone extinct since Yapen's isolation. For those species with poor ability to disperse overwater, abundance is a predictor of survival and continued presence on Yapen—as expected from the inverse relationship between extinction risk and population size.

We identify half-a-dozen mechanisms for colonisation by upland species: dispersal overwater when Yapen was an island; regular post-breeding descent to the lowlands; irregular straggling to the lowlands; dispersal through flat lowlands; dispersal over hill bridges; and dispersal during cool Pleistocene phases, when some current upland species had lowland populations. Relict sets of those mostly vanished Pleistocene lowland populations survive on three remnant fragments of southern New Guinea's former Arafura platform: on the Aru Islands, New Guinea's Fly River bulge, and the northern tip of Australia's Cape York Peninsula.

We report here four explorations and an analysis of the upland avifauna of Yapen Island, 21 km off the north coast of western New Guinea. (By upland avifauna, we mean species largely confined to sloping elevated terrain, and absent from the level-ground lowlands at or near sea level, as discussed below.) Yapen is one of the six large land-bridge islands on New Guinea's continental shelf (Fig. 1). That is, the ocean waters separating Yapen from New Guinea today are sufficiently shallow that they became dry land at Pleistocene times of low sea level, and Yapen then formed a northern extension of the New Guinea mainland (Beehler 2007). At that time, animal and plant species unable or reluctant to cross water, and that currently cannot reach Yapen overwater, were able to reach it overland. Those

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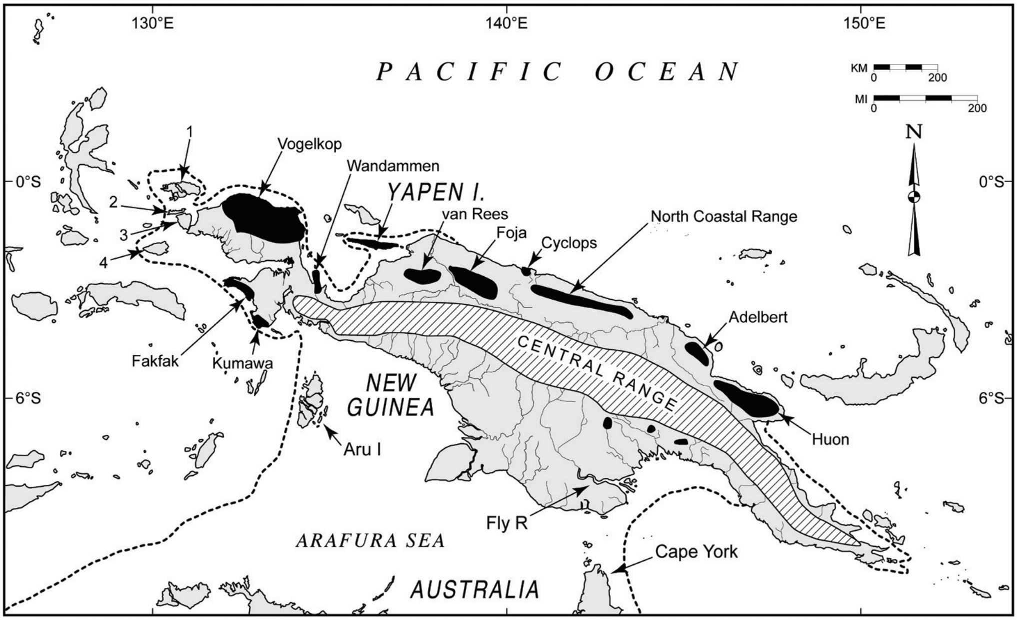

Figure 1. New Guinea (modified from Fig. 1 of Diamond & Bishop 2015), showing Yapen Island, the five other large land-bridge islands, and the main mountain ranges. The dashed line marks the limits of the New Guinea continental shelf. During Pleistocene times of low sea level, the shelf, which is now a shallow sea, was a dry-land extension of the New Guinea mainland, and Yapen and other large land-bridge islands formed part of the New Guinea mainland. The current Arafura Sea was then a large exposed lowland platform, of which the modern fragments are the Aru Islands, New Guinea's Fly River bulge, and the north tip of Australia's Cape York Peninsula. Islands: 1–4 = West Papuan Islands (1 = Waigeo, 2 = Batanta, 3 = Salawati, 4 = Misool). New Guinea's mountains are the Central Range (cross-hatched) and the ten outlying ranges on New Guinea's north and north-west coasts.

non-water-crossing species include the majority of New Guinea bird species, especially forest interior and upland species (Diamond 1972a), which avoid crossing water or forest clearings although perfectly capable of flight. When rising sea levels at the end of the Pleistocene flooded the land bridge and Yapen became an island, the Yapen populations of those non-water-crossing species became isolated, and many of those inferred former populations are now absent and presumed to have disappeared (Diamond 1972a).

As the highest of New Guinea's land-bridge islands (1,430 m), Yapen has the richest upland avifauna, currently known to comprise 26 species. That Yapen upland avifauna is interesting for at least four reasons. First, some of its inferred bird populations have survived, and many others evidently have not. What factors influenced that differential survival of bird populations in isolation?

Second, the mountains of the New Guinea mainland consist of the 5,000 m-high Central Range, extending 2,400 km west to east, plus ten isolated small ranges rising from the lowlands along the north and north-west coast (Fig. 1). Of the approximately 193 upland bird species or superspecies of the Central Range, some occur on all ten of the outliers, some on various but not all outliers, and some on none. What accounts for these great differences in mountain colonisation among New Guinea's upland species? Because five of the six large land-bridge islands (including Yapen) are high enough to support upland species and were formerly part of the New Guinea mainland, they add to the database for answering this question about mountain colonisation.

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Third, most of the mainland outliers are joined or nearly connected to the Central Range or to another outlier by low hills. But two of the outliers, the Fakfak Mts. and Kumawa Mts., are isolated from the nearest hilly terrain of the Central Range by 70–100 km of entirely level-ground lowlands almost at sea level. The Fakfak and Kumawa Mts. lack 15 upland species present on other outliers, and for which the Fakfak and the Kumawa Mts. lie within the elevational and geographic ranges of the species (Diamond & Bishop 2015). A possible explanation is that those upland species disperse overland through forest on low-elevation undulating terrain, but not through forest on flat terrain at sea level. When Yapen was part of the New Guinea mainland during Pleistocene periods of low sea level, the terrain that separated it from the nearest other New Guinea mountains was also level-ground terrain at sea level. Thus, Yapen's upland avifauna offers a test of the hypothesis that certain upland bird species do not disperse through flat lowland forest.

Finally, one can postulate at least six different mechanisms by which upland species might disperse between isolated blocks of suitable habitat. Yapen's upland avifauna may help to evaluate the relevant importance of those different mechanisms.

At the outset, we must dampen the expectations of readers hoping for unequivocal answers to those questions. We could obtain answers at high levels of statistical significance if the New Guinea region included hundreds each of ornithologically well-explored outlying mountain ranges, land-bridge islands, and oceanic islands of various areas and elevations, variously separated by hilly or flat terrain. But the New Guinea region offers only ten outliers and six large land-bridge islands, and only two of the outliers are isolated by level-ground terrain. Furthermore, Yapen is distinctive for two separate reasons, making it not straightforward to separate the contributions of those two factors: Yapen is currently a land-bridge island rather than a mainland outlier, and it was formerly isolated by flat rather than by hilly terrain. Furthermore, there is no fossil evidence to prove which bird species actually inhabited Yapen at Pleistocene times of low sea level; we are currently forced to rely on inference. Therefore, our tentative conclusions will require further testing, e.g., by fossil, molecular phylogenetic and population genetic evidence.

Natural environment

Yapen's area of 2,230 km^2 makes it the third largest of New Guinea's six large land-bridge islands, smaller than Aru or Waigeo, but larger than Misool, Salawati or Batanta. The island is long and narrow, 166 km from west to east, but only 26 km north to south at the widest point in the island's centre. Yapen's central mountain chain also runs west–east and comprises two sections: a slightly lower western section almost due north of the coastal town of Serui, and a slightly higher eastern part. Maps give the summit elevations as 1,435 and 1,496 m, respectively. However, the real elevations are slightly lower; in 1983 JD determined that of the highest western peak (Mt. Aror) as 1,340 m by ascending it with a Thommen altimeter, and that of the eastern peak as 1,430 m by flying past it in clear weather in a fixed-wing airplane with an aviation altimeter. The elevations of the western and eastern peaks that KDB measured using Google Earth are 1,374 m and 1,422 m, respectively. Elevations that I. Woxvold kindly measured by NASA's Shuttle Radar Topography Mission are 1,380 and 1,450 m, respectively.

Rainfall at various sites on Yapen, from Indonesian government records and Brookfield & Hart (1966), is 3.1–3.8 m p.a. in both the northern and southern watersheds. The wetter months are January–May in the northern watershed, and June–September in the southern watershed (including at the mountain village of Ambaidiru and coastal town of Serui). However, seasonal differences in rainfall are modest: at all sites, the driest month receives only 30–50% less rainfall than the wettest.

Yapen's mammals include many species unlikely to be able to cross water, thereby clearly demonstrating the legacy of the Pleistocene land bridge. Among them are at least three species of kangaroos and wallabies, three species each of *Echymipera* bandicoots and dasyurids (marsupial carnivores), six species of phalangers and pseudocheirids (mostly arboreal possums), and a giant rat (*Uromys* sp.), plus many species of bats and smaller rodents (Flannery 1990; K. Koopman pers. comm., T. Flannery pers. comm.).

Yapen harbours *c.*150 resident bird species, of which about 120 occur in the lowlands and 26 are upland. That avifauna includes some 13 endemic subspecies, of which the most distinctive are the Northern Variable Pitohui *Pitohui kirhocephalus jobiensis*, Tropical Scrubwren *Sericornis beccarii jobiensis*, and Lesser Bird of Paradise *Paradisaea minor jobiensis*. The avifauna reveals the legacy of Yapen's Pleistocene land bridge as clearly as does the mammal fauna, by including representatives of many New Guinea bird genera confined to the mainland and its land-bridge islands, but absent from all islands of the Papuan region not on New Guinea's continental shelf. Land-bridge relict genera present on Yapen include *Goura*, *Pseudeos*, *Probosciger*, *Melidora*, *Ptilorrhoa*, *Crateroscelis*, *Sericornis*, *Arses*, *Tregellasia*, *Peneothello*, *Pachycephalopsis*, *Pitohui*, *Toxorhamphus*, *Melilestes* and *Melanocharis*.

Tall forest, decreasing in height with increasing elevation, still covers much of Yapen. The dominant tree species that one encounters from the beach into the mountains, provisionally identified in 1983 by A. Kayoi, can be briefly summarised as follows. Along the beach one finds *Terminalia catappa*, *Barringtonia asiatica*, *Calophyllum inophyllum*, *Artocarpus* sp. and *Casuarina* sp., and immediately behind it is often a swamp of Nipa palms (*Nypa fruticans*). On coastal slopes dominant trees are *Palaquium amboinense*, *Octomeles sumatrana*, *Intsia bijuga*, *Ficus benjamina*, *Eugenia* sp. and *Artocarpus* sp. In lowland forest further inland dominant are *Palaquium amboinense*, *Octomeles sumatrana*, *Calophyllum* sp., *Terminalia* sp., *Manilkara* sp., *Pometia acuminata* and *P. pinnata*. In the mountains the main species are *Pometia acuminata*, *Cryptocarya* sp., *Tristania* sp., *Palaquium amboinense* and *Calophyllum* sp., whereas *Araucaria cunninghamii* and *Anisoptera polyandra* are patchily distributed in the uplands. At 1,340 m on the summit of Mt. Aror the forest is *c.*15 m tall, with many small ferns in the understorey, much dead leaf litter on the ground, and some moss on trunks and limbs. In second growth on sites of former gardens and landslides the dominant tree is *Albizia falcata*, which often forms almost monospecific stands. The export logging industry on Yapen used mainly *Campnosperma brevipetiolata*, *Cananga odorata*, *Palaquium amboinense* and *Intsia bijuga*, with lesser use of *Diospyros* sp., *Dracontomelon* sp. and *Artocarpus* sp. Trees felled by hand for local use consist mostly of *Intsia bijuga* and *Pometia acuminata*.

People and languages

Yapen's largest town is the government centre of Serui on the south coast, an hour's drive east of the airport linking Yapen by scheduled flights to Biak. Formerly, much of Yapen's population, now grown to 100,000 people, lived in the mountainous interior, to escape attacks by raiders from Biak. Once the risk of these attacks vanished, most people moved to the coast, attracted by stores, medical care, schools, government services, and access by ship and plane to the outside world. The only mountain villages still inhabited are Ambaidiru and nearby Mambo, inland of Serui on the southern slopes of Yapen's western peaks.

The language atlas *Ethnologue* (Lewis 2009) lists 13 native languages as spoken on Yapen. Of these, 11 belong to the widespread Austronesian language family, believed to have reached the New Guinea lowlands (mainly the north coast) from Taiwan via Indonesia around 3,500 years ago. Ten of these Austronesian languages are confined to Yapen and nearby islets; the 11th is a small population speaking the Biak language, presumably

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brought more recently by Biak raiders. Yawa and Saweru, the two other languages, are Yapen's only Papuan tongues, i.e. belonging to a language family spoken only on New Guinea and presumably representing the main island's earlier population pre-dating Austronesian arrival. Surprisingly, the only other languages thought to be related to Yawa and Saweru are six languages spoken in the far west of the Vogelkop Peninsula, 400 km west of Yapen. Yawa, Yapen's second largest language with 6,000 speakers, is the one that we encountered at Ambaidiru. Our species accounts provide Yawa language names that Ambaidiru informants volunteered for 13 of Yapen's upland bird species, which they and we encountered together at Ambaidiru.

Ornithological studies by others

In the 1800s six collectors or teams obtained bird specimens on Yapen. At the time the island was not controlled by the Dutch colonial government and was dangerous: for example, one of William Doherty's hunters was murdered, and two others attacked, during Doherty's visit of a few weeks in 1897. All of those early collectors were based on the south coast and may at most have obtained some specimens from hunters in the interior. The species that they recorded, including ten upland species, were found by us at elevations below 600 m. The material was reported by Salvadori (1880–82), by Rothschild & Hartert (1901–15), or by both. The six early collectors were H. Rosenberg in 1869; A. B. Meyer in 1873; A. A. Bruijn's hunters, sometimes with Léon Laglaize, in 1874–85; Odoardo Beccari in 1875; F. H. H. Guillemard, sometimes with Wilfred Powell, in 1883; and William Doherty in 1897.

The largest collection of Yapen birds, 106 species, was made in 1931 by Georg Stein, who was the only collector known to have reached the interior and higher elevations. He made his upper camp at an elevation of 950 m and thereby added six species to our knowledge of Yapen's upland avifauna. His collection was reported by Rothschild *et al*. (1932).

In 2019 Verhelst & Pottier (2020) camped at 1,310 m on Yapen's eastern peak, used camera traps as well as sound-recorders, observed 12 of the 23 upland species previously recorded, and added three further upland species.

Our studies

1983.—JD surveyed birds as member of a four-man team whose three other members were studying forests and environmental issues (Alexander Kayoi of the Indonesian Forestry Department, and Ardy Irwanto and Karel Rumboirusi of the Indonesian Environment Department = PPHA). JD & Irwanto arrived in Serui on 6 August. On 7–8 August JD surveyed forests, second growth, and gardens on the coast from Serui east to Kabuena village. On 9 August JD and the other three team members drove from Serui a short distance inland to Wontembu village, from where they and their porters climbed on foot all day to Ambaidiru village (640 m) by the eastern of the two tracks linking Wontembu to Ambaidiru. The latter remained the team's base until their return to Wontembu on foot on 18 August by the western trail fording the Wendanu River (680 m), then by vehicle to Serui. From Ambaidiru, JD ascended Mts. Aror (1,340 m), Muibini (1,245 m) and Mangkiniwai (915 m), and surveyed forests from those summits down to 530 m.

2016.—KDB arrived in Serui by plane on 2 December and departed on 7 December. Transport options were more extensive than in 1983: whereas in 1983 the only motor roads were on or near the coast, by 2016 a paved trans-island road had been completed from the south coast east of Serui, reaching a first crest at 720 m, dropping to a bridge over a river at 126 m, and rising to a second crest at 938 m before dropping again to the north coast.

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At an elevation of 655 m along the trans-island road between the first crest and the river, an unpaved road forks left, rises to a crest at 1,260 m, and then drops down to Ambaidiru (640 m). West of Serui on the south coast, another road was under construction towards Ambaidiru but stopped at an elevation of 146 m. From a base in Serui, KDB used a vehicle to survey birds along all of these roads during his six days on Yapen.

2017.—JD & KDB arrived in Serui by plane 13 October and departed on 20 October. From our base in Serui, we travelled by four-wheel-drive vehicle to survey sites along the trans-island road, the Ambaidiru road, and the north and south coastal roads. On three days we surveyed the Ambaidiru road from its crest at 1,260 m to its junction with the trans-island road at 655 m. We surveyed the trans-island road from its crest at 938 m to 760 m in the southern watershed on two days, and to 365 m in the northern watershed on two others. On seven days we surveyed the river crossing at 126 m on the trans-island road. On one day each we made observations on the north coast road east from its junction with the trans-island road, and the south coast road west from Serui to the airport.

Methods

Our methods were similar to those that we described for our work in the Fakfak and Kumawa Mts. (Diamond & Bishop 2015). Briefly, most of JD's observations in 1983 were on foot trails in the forest, while all of our observations in 2016–17 were on roads, of which all except the coastal roads are narrow and mostly lined and overhung by forest. We devoted much effort to recording vocalisations with Sony TCM 5000 EV tape recorders, playing back unidentified vocalisations in the field to attract and identify singers, and re-listening to recordings in camp each day because our directional microphones often captured calls that we had not noticed in the field. We stopped at fruiting and flowering trees where birds gathered. We began observations by 04.00 h to detect nocturnal birds. Elevations of all significant observations were measured using Thommen altimeters or a Garmin GPS. The only collecting consisted of three mist-nets operating for three days at 1,000–1,100 m near Ambaidiru in 1983. Of the 11 individuals captured, ten were weighed and released. The remaining bird (the type of Green-backed Robin *Pachycephalopsis hattamensis insularis*) was prepared as a specimen for the Museum Zoologicum Bogoriense, Bogor, Indonesia. A previous paper (Diamond 1985) described that subspecies and mentioned 12 other species records on Yapen. We also made observations in the Yapen lowlands during all three of our visits, but this paper reports only on upland species. Our nomenclature follows Beehler & Pratt (2016), with one exception suggested by further information (see *Sericornis beccarii* under Species accounts).

Results

This paper discusses a fraction of Yapen's avifauna: its upland species, defined as those species largely confined to sloping elevated terrain, and absent from the level-ground lowlands at or near sea level. The literature concerned with avian distributions on tropical mountains often refers to 'montane species', namely those largely confined to altitudes above some specified elevation, e.g., for New Guinea, 800 or 1,600 m (Stresemann 1923) or 1,700 m (Archbold & Rand 1935). That would be appropriate if there was a sharp break in distributions of many bird species at the specified elevation. In reality, elevational floors of New Guinea bird species are distributed continuously without concentration at any specific elevation (Diamond 1972b: 67–70). Consequently, a definition of species as montane if their elevational floor exceeds some specified value is completely arbitrary.

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We have instead found it useful to characterise species as absent in New Guinea's flat lowlands ('upland species') or else present there ('lowland species'). Of course, this definition also poses its own ambiguities and requires some arbitrary decisions, but those problems are much fewer than those in invoking an arbitrary elevational cut-off. The main ambiguities in New Guinea involve the following: species that breed at high elevation but descend post-breeding to the lowlands (e.g., Ornate Fruit Dove *Ptilinopus ornatus*); hill species of sloping terrain that descend to near sea level in such terrain but are absent from level-ground lowlands near sea level (e.g., Torrent Flycatcher *Monachella muelleriana*); borderline cases of species that occur mostly in sloping elevated terrain, but of which occasional individuals occur in the flat lowlands (how frequent must such 'occasional' encounters be to disqualify a taxon as an upland species?); borderline cases of species confined to mountains at most localities but with a few populations at sea level (e.g., Hooded Pitohui *Pitohui dichrous*); and 17 species confined to higher elevations in northern New Guinea but with sea level populations around southern New Guinea's Fly River mouth and / or on the Aru Islands (to be discussed in connection with Table 6). Diamond & Bishop (2015: 299–300) provided more examples of borderline cases.

Table 1 lists the 26 Yapen species that we regard as upland species under this definition. Characteristics tabulated for each species, and to be discussed in the text, are Yapen records, ability to disperse overwater, whether or not the Yapen population is regarded as an endemic subspecies, abundance and elevational floor on Yapen, and presence and abundance on the most nearly comparable outlying mountain ranges on the New Guinea mainland. Our concluding section of species accounts provides details.

Completeness of survey

How complete is that list of 26 upland species for Yapen likely to be? Knowledge of Yapen birds was obtained initially by six individuals or teams who visited Yapen between 1869 and 1897, evidently confined to the south coast and low elevations, and providing specimens but no field observations. Those specimens document ten upland species. Stein was the first collector to camp at higher elevation (950 m) in Yapen's interior. His specimens include four of the nine upland species recorded previously, plus six new records. However, Stein provided no field observations for Yapen birds, other than mentioning two conspicuous lowland species that he reported seeing on a brief second visit but did not collect (Rothschild *et al*. 1932: 216: Hooded Pitta *Pitta sordida* and Brown Oriole *Oriolus szalayi*). No previous or subsequent observer has recorded these two species on Yapen, so we suspect that Stein's comment refers to a different locality.

Our three visits recorded all but one (Meyer's Goshawk *Accipiter meyerianus*) of the 16 upland species previously collected on Yapen. We added seven new records. Advantages that we enjoyed over previous visitors included ascending the highest of Yapen's western peaks (1,340 m), familiarity with New Guinea bird vocalisations, extensive sound-recording with playback, and being able to devote most of our time to observing rather than collecting and preparing specimens.

Verhelst & Pottier (2020) added three more upland species in 2019, yielding a total of 26. Of this total, three are based on the observation or collection of a single individual by just one visitor or team (*Accipiter meyerianus*, Pygmy Eagle *Hieraaetus weiskei* and Yellow-legged Flyrobin *Kempiella griseoceps*). Two records (Dimorphic Jewel-babbler *Ptilorrhoa* cf. *geislerorum* and Black-eared Catbird *Ailuroedus melanotis*) are based on two observations of each species by Verhelst & Pottier (2020). Four (Chestnut-backed Jewel-babbler *Ptilorrhoa castanonota*, White-faced Robin *Tregellasia leucops*, White-rumped Robin *Peneothello bimaculata* and *Pachycephalopsis hattamensis*) were recorded on two visits, and two others

TABLE 1
Yapen's upland species.

Species	**Records**	**Water-crosser?**	**No. of outliers**	**Endemic subspecies**	**Abundance**	**Floor (m)**	**VFAK**	**Outlier abundance**
Wattled Brushturkey *Aepypodius arfakianus*	83, D, V	no	9	no/yes	2	?	VFK	1
Black-billed Cuckoo-Dove *Macropygia nigrirostris*	83, 17, S	yes	10	no/no	2	1,160, 0	VFAK	3
Pheasant Pigeon *Otidiphaps nobilis*	83, 17, D	yes	9	no/yes	1	580	VFAK	2
White-bibbed Fruit Dove *Ptilinopus rivoli*	83, 16, 17, S, Br, D, R, V	yes	10	no/yes	3	510	VFAK	3
Claret-breasted Fruit Dove *Ptilinopus viridis*	83, 17, S, Br, D, R	yes	8	no/yes	3	520	VFK	3
Papuan Mountain Pigeon *Gymnophaps albertisii*	83, S, D, G	yes	10	no/yes	1	450	VFAK	2
Mountain Swiftlet *Aerodramus hirundinaceus*	83, 17, S	yes	7	yes/yes	2	?	FAK	2
Pygmy Eagle *Hieraaetus weiskei*	16	yes	4	?/no	1	?	A	1
Meyer's Goshawk *Accipiter meyerianus*	M	yes	2	?/no	1	?	K	1
Black-eared Catbird *Ailuroedus melanotis*	V	no	9	?/yes	2	?	VFAK	2
Red Myzomela *Myzomela cruentata*	83, 16, 17, S, V	yes	8	no/yes	2	450	FAK	2
Mountain Meliphaga *Meliphaga orientalis*	83, 16, 17, V	no	8	?/yes	3	1,005	FAK	3
White-eared Meliphaga *Meliphaga montana*	83, 16, 17, S, V	no	9	yes/yes	3	795	VFAK	3
Tropical Scrubwren *Sericornis beccarii*	83, 16, 17, S, V	no	8	yes/yes	4	450	VFK	3
Dimorphic Jewel-babbler *Ptilorrhoa* cf. *geislerorum*	V	no	2	?/no	2	?	A	2.5
Chestnut-backed Jewel-babbler *Ptilorrhoa castanonota*	83, 17	no	9	?/yes	3	665	VFAK	2.5
Stout-billed Cuckooshrike *Coracina caeruleogrisea*	83, 17, M, R	no	10	no/no	2	855	VFAK	2
Papuan Cicadabird *Edolisoma incertum*	83, 17, Br, M, V	no	10	no/no	4	645	VFAK	3
Hooded Pitohui *Pitohui dichrous*	83, 17, S, V	no	10	no/no	4	450	VFAK	4
Green-backed Robin *Pachycephalopsis hattamensis*	83, 17	no	4	yes/yes	2	610?	V	3
Yellow-legged Flyrobin *Kempiella griseoceps*	V	no	5	?/no	1	?	VFAK	1
White-rumped Robin *Peneothello bimaculata*	83, 17	no	5	?/yes	1	900	VA	3
White-faced Robin *Tregellasia leucops*	83, V	no	9	?/yes	2	665	FAK	2.5
Magnificent Bird of Paradise *Cicinnurus magnificus*	83, 17, S, Be, D, G, M, R, V	no	10	no/yes	3	425	VFAK	4
Island Leaf Warbler *Seicercus poliocephalus*	83, 16, 17, V	yes	9	?/yes	4	675	FAK	4
Green-fronted White-eye *Zosterops minor*	83, 16, 17, S, D, M, V	no	10	no/yes	4	425	VFAK	3

Column 2. Records. Yapen records are coded as follows: 83, 16, 17 = our own observations in 1983, 2016 and 2017; S = Stein in 1931; 19th-century collections: Be = Beccari, Br = Bruijn, D = Doherty, G = Guillemard, M = Meyer, R = Rosenberg; V = Verhelst & Pottier in 2019.

Column 3. Water-crosser. Has the species demonstrated the ability to colonise overwater, as shown by its presence on oceanic islands near New Guinea but without a recent land bridge to the latter? See text for list of such islands.

Column 4. No. of outliers. Of the ten outlying mountain ranges of the New Guinea mainland, on how many does the species (or another allospecies of its superspecies in two cases) occur?

Column 5. Endemic subspecies. The first no/yes entry asks whether the Yapen population has been diagnosed as an endemic subspecies. (? = no specimen has been analysed to date). The second no/yes entry asks if subspecies of the species are recognised in the New Guinea region; if 'yes' but the answer to the first entry is 'no,' then the Yapen population has failed to subspeciate despite that the species has subspeciated elsewhere in the New Guinea region.

Column 6. Abundance on Yapen, as estimated on a scale from 1 (least abundant species) to 4 (most abundant species).

Column 7. Elevational floor on Yapen, in metres. ? = too few records at known elevations to assess the floor of that species. Double entry (1,160, 0) for *Macropygia nigrirostris* indicates calling individuals and presumed breeding occur down to 1,160 m, but silent, presumably non-breeding birds recorded to sea level.

Column 8. VFAK? Presence on four mainland outliers most similar in elevation to Yapen. V = Van Rees (authors' unpubl. obs.). FK = Fakfak and Kumawa (Diamond & Bishop 2015). A = Adelbert (Gilliard & LeCroy 1967, Pratt 1983, Beehler & Pratt 2016; pers. obs.).

Column 9. Abundance averaged over those four mainland outliers, as estimated on a four-point scale.

(Wattled Brushturkey *Aepypodius arfakianus* and Pheasant Pigeon *Otidiphaps nobilis*) on three. The other 15 species were recorded on multiple occasions during four or more visits.

These facts suggest that some local or rare upland populations await discovery on Yapen. Our guess is that particular attention is warranted for the following 11 currently unrecorded species, because they occur on multiple mainland New Guinea outliers, and because Yapen lies within their elevational range, but they are inconspicuous, uncommon, and / or local, so they may have been overlooked to date: Dwarf Cassowary *Casuarius bennetti*, White-eared Bronze Cuckoo *Chalcites meyerii*, Wallace's Owlet-nightjar *Aegotheles wallacii*, Red-breasted Pygmy Parrot *Micropsitta bruijnii*, Barred Cuckooshrike *Coracina lineata*, Spotted Honeyeater *Xanthotis polygrammus*, Obscure Honeyeater *Caligavis obscura*, Greater Melampitta *Megalampitta gigantea*, *Monachella muelleriana*, Russet-tailed Thrush *Zoothera heinei* and Blue-faced Parrotfinch *Erythrura trichroa*.

Upland species number

We now compare the number of upland species on Yapen (S_{up}) with those on three other sets of islands or mountains: oceanic islands of the Papuan region and northern Melanesia; the other land-bridge islands of the Papuan region besides Yapen; and the ten outlying mountain ranges of the New Guinea mainland.

Oceanic islands.—We first compare S_{up} on Yapen with that on specific mountainous oceanic islands of the Papuan region and northern Melanesia. Karkar in the Papuan region is higher than Yapen (1,831 vs. 1,430 m) but has less than one-third as many upland species (eight vs. 26: Diamond & LeCroy 1979: 486). Goodenough and Fergusson in the Papuan region are higher than Yapen (2,536 and 1,864 m, respectively) but also possess considerably fewer upland species (*c*.16 and 15, respectively: Beehler & Pratt 2016). Northern Melanesia has ten islands similar to Yapen in elevation (1,040–1,768 m, mean 1,288 m), but those islands have less than one-quarter as many upland species as Yapen (on average six, range 1–15; Mayr & Diamond 2001: 59–60). Even the three highest northern Melanesian islands (Bougainville, Guadalcanal and New Britain), with elevations almost double Yapen's (2,591, 2,448 and 2,439 m, respectively), support fewer upland species than Yapen (18, 23 and 16, respectively).

In addition to these comparisons with individual oceanic islands, we can make a more specific calculation for Yapen itself. If the latter was an oceanic island with no recent land connection to New Guinea, its expected number of upland species could be calculated as follows. For oceanic islands 8–500 km from New Guinea, the number of resident lowland land and freshwater bird species S is described by the equation $S = 12.3\ A^{0.22}$, where A = area in square kilometres (equation 1 of Diamond 1973); and the number of upland species S_{up} is described by the formula $0.089\ SL/1{,}000$ where L = elevation in metres. For Yapen (A

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TABLE 2

Populations of upland species on West Papuan Islands. Like Yapen, these are land-bridge islands that were formerly part of mainland New Guinea, but being geographically distant from Yapen they constitute 'natural experiments', independent of Yapen, in colonisation and survival of upland species on land-bridge islands. Nevertheless, while just 15 of New Guinea's 193 upland species occur on the West Papuan Islands, ten of them also occur on Yapen. This illustrates that certain upland species are disproportionately successful, and others disproportionately unsuccessful, in colonising and persisting on mountainous land-bridge islands. The summit elevation of each island appears below the island's name at the head of its column.

Species	**Water-crosser?**	**No. of outliers**	**Misool 509 m**	**Salawati 781 m**	**Waigeo 974 m**	**Batanta 1,172 m**	**on Yapen? 1,430 m**	**Arafura**
Wattled Brushturkey *Aepypodius arfakianus*	no	9	✓	--	[√]	--	✓	--
Claret-breasted Fruit Dove *Ptilinopus viridis*	yes	8	--		lowlands	✓	✓	--
Pheasant Pigeon *Otidiphaps nobilis*	yes	9	--	--	✓	✓	✓	✓
White-eared Bronze Cuckoo *Chalcites meyerii*	no	10	--	--	--	✓	--	--
Wallace's Owlet-nightjar *Aegotheles wallacii*	no	2	--	--	✓	--	--	✓
Black-eared Catbird *Ailuroedus melanotis*	no	9	lowlands	--	--	--	✓	✓
Spotted Honeyeater *Xanthotis polygrammus*	no	9	lowlands	lowlands	✓	--	--	
Mountain Meliphaga *Meliphaga orientalis*	no	8	--	--	✓	--	✓	--
White-eared Meliphaga *Meliphaga montana*	no	9	--	--	--		✓	--
Tropical Scrubwren *Sericornis beccarii*	no	8	--	--	✓	--	✓	✓
Chestnut-backed Jewel-babbler *Ptilorrhoa castanonota*	no	9	--	--	--	✓	✓	--
Barred Cuckooshrike *Coracina lineata*	yes	8	--	--	lowlands	--	--	
Papuan Cicadabird *Edolisoma incertum*	no	10	--	--	✓	✓	✓	--
Magnificent Bird of Paradise *Cicinnurus magnificus*	no	10	--	✓	[√]	[√]	✓	--
Banded Yellow Robin *Gennaeodryas placens*	no	4	--	--	--	✓	--	--
Total species			**1**	**2**	**8**	**8**		

Column 2 (water-crosser?) and Column 3 (# outliers) as columns 3–4 in Table 1.

Check mark = present on that land-bridge island as an upland population, in our field experience on the relevant island.

'lowlands' = the species is an upland taxon on New Guinea, and usually also on Yapen, but its population on the land-bridge island occurs in the flat lowlands, in our field experience on the relevant island.

[√] = present as an insular allospecies of a superspecies present on mainland New Guinea. Sources: Mayr (1941), Beehler & Pratt (2016), and pers. obs.

Column 8. √ = present as an upland population on Yapen.

Column 9. √ = present as a relict lowland population on the two extant fragments of the large Arafura platform exposed in the Pleistocene, but then mostly inundated at the end of that era (eee Table 6 and text for discussion).

= 2,230 km^2, L = 1,430 m) those formulas yield an expected S_{up} value of nine species: far less than Yapen's actual S_{up} value of 26 species.

Thus, Yapen possesses more upland species than the most nearly comparable mountainous islands near New Guinea but with no recent land connections to the latter, and more than calculated for an oceanic island of Yapen's area and elevation. The explanation is clear: Yapen received upland species overland from New Guinea's Central Range and other outliers whenever it was connected to the New Guinea mainland, as well as overwater at other times, whereas the oceanic islands have always received species only overwater. That conclusion for upland species also applies to lowland taxa: Yapen and the other large Papuan land-bridge islands all possess more lowland species than do similar-sized oceanic islands near New Guinea (Diamond 1972a).

Land-bridge islands.—The Papuan land-bridge islands most similar to Yapen are Batanta, Waigeo, Salawati and Misool (elevations 1,070, 970, 686 and 565 m, respectively), which resemble Yapen in lying on New Guinea's continental shelf and in having formed part of Pleistocene New Guinea. (It is unknown whether today's very narrow Sagewin Strait between Salawati and Batanta, which was an important geological feature and biogeographic boundary in the past, existed during the late Pleistocene.) Those four islands support eight, eight, two and one upland species, respectively (Table 2), i.e. many fewer than Yapen, because all of those islands are lower-lying. The remaining large Papuan land-bridge island, Aru, is so low (241 m) that it is not known to harbour any upland population.

New Guinea mountain outliers.—Of New Guinea's ten outlying ranges (elevations 1,262–4,121 m), all are considerably lower than the Central Range (4,884 m), but six are rather higher (1,886–4,121 m) than Yapen. The four outliers most nearly comparable to Yapen in elevation are Van Rees (1,262 m), Fakfak (1,400 m, closest to Yapen's elevation of 1,430 m), Adelbert (1,675 m) and Kumawa (1,654 m). Their S_{up} values of 34, 65, 67 and 72 species, respectively (Diamond & Bishop 2015; unpubl. obs.) are much higher than Yapen's 26 species. When Yapen was part of the New Guinea mainland until around 10,000 years ago, it was just another outlier, with a higher species total presumably similar to that of those four comparable outliers, and probably most similar to that of Fakfak (65 species). After the inundation of the land bridges turned Yapen, Batanta, Waigeo, Salawati and Misool into islands, preventing overland immigration, their populations of both lowland and upland species declined due to extinctions no longer being balanced by the overland immigration rates prevailing when they formed part of the mainland.

In short, Yapen has many fewer upland species (and also fewer lowland species: Diamond 1972a) than a piece of the New Guinea mainland of similar elevation and area. But, conversely, it has many more upland species (and also more lowland species: Diamond 1972a) than an oceanic island of similar elevation and area. That is, Yapen and the other large land-bridge islands are 'supersaturated' in species: they started out with the species richness of pieces of the New Guinea mainland when they were just part of that mainland during the Pleistocene; since the land bridges were severed around 10,000 years ago, they have been losing species by excess extinctions; but they still possess more species than comparable oceanic islands, although they already have fewer species than comparable areas of the New Guinea mainland (Diamond 1972a).

Upland species identities

Species differences in occurrence frequency.—Having compared Yapen's number of upland species with numbers on the most comparable mainland outliers, we now compare the identities of the upland species. The 34, 65, 67 and 72 upland species of Van Rees, Fakfak, Adelbert and Kumawa include most of Yapen's 26 upland species: 18, 21, 22 and 22 species, respectively. In turn, Yapen's upland species include most of those of the four lower land-bridge islands: six of Waigeo's eight, six of Batanta's eight, both of Salawati's two, and Misool's one. But the total of 193 upland species for New Guinea greatly exceeds any of the species totals shared between Yapen and the four most comparable mainland outliers, or between Yapen and the other four large land-bridge islands with upland species. Table 2 shows that the 19 upland populations on those other four land-bridge islands belong to only 15 different species, of which ten have upland populations on Yapen. This suggests that,

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TABLE 3

Upland species distributions on New Guinea's outliers. For each of New Guinea's 193 upland species, we tabulated how many of New Guinea's ten outliers the species occupies. That number (column 1) ranges from 0 (no outlier occupied) to 10 (all ten occupied). Column 2: the number of New Guinea upland species occupying that number of outliers. Column 3: the product of columns 1–2: i.e., the number of outlier populations attributable to species occupying that number of outliers. Column 4: the number of Yapen species attributable to species occupying that number of outliers. (For example, there are 20 New Guinea upland species which each occupy eight outliers; hence those 20 species account for 20 × 8 = 160 outlier populations; and four Yapen upland species belong to that group of 20.) See text for discussion. Sources: see Table 1 legend for four outliers; Beehler *et al*. (2012) for Foja; and Hartert (1930), Mayr (1931, 1941), Gyldenstolpe (1955), Freeman *et al*. (2013), Beehler & Pratt (2016) and LeCroy & Diamond (2017) for the five others.

No. of outliers occupied	**No. of species occupying that number of outliers**	**No. of outlier populations**	**No. of Yapen species**
0	35	0	0
1	29	29	0
2	19	38	1
3	17	51	2
4	14	56	1
5	13	65	1
6	10	60	0
7	10	70	2
8	20	160	4
9	17	153	7
10	9	90	8
Total	**193 species**	**772 populations**	**26 species**

of New Guinea's 193 upland species, only a small subset occurs repeatedly on mainland outliers, and an even smaller subset do likewise on the land-bridge islands.

Table 3 explores this suggestion systematically by tabulating, for each of New Guinea's 193 upland species, on how many of the ten mainland outliers that species occurs. It can be seen that 35 species occur on none of the outliers, and almost half of the 193 (83 species = 39%) are on just 0–2 outliers, but nine species occur on every outlier and 46 species on 8–10 of the ten outliers. Those 46 most widely distributed species represent only 24% of New Guinea's upland species but account for 52% of outlier populations. Evidently, some species are disproportionately successful colonists, others are disproportionately unsuccessful, and fewer are intermediate. Table 3 also demonstrates that 24% of the upland avifauna that accounts for half of the outlier upland populations also accounts for most—19 of 26, or 73%—of Yapen's upland populations.

That is, upland species successful at colonising mainland outliers have also been successful at colonising and persisting on Yapen. The explanation is presumably that Yapen *was* a mainland outlier until its land bridge to the New Guinea mainland was severed *c*.10,000 years ago. Thus part of the explanation for the composition of Yapen's upland avifauna consists of the same factors (whatever they may be) explaining the compositions of the upland avifaunas of the ten outliers. The other part of the explanation for the composition of Yapen's upland avifauna consists of factors explaining why Yapen has fewer upland species than comparable mainland outliers, i.e. why some of Yapen's upland populations that it inherited >10,000 years ago have subsequently become extinct, while others have not. We explore both sets of factors in the next sections.

Effects of elevation.—New Guinea's Central Range reaches its highest point at 4,884 m and large areas are above 2,000 m. As a result, the Central Range has a rich upland avifauna including many species whose elevational floors exceed 2,000 m, ranging up to a highest floor of 3,800 m (Snow Mountain Robin *Petroica archboldi*). In contrast, the highest outliers are 4,121 m (Huon) and 2,954 m (Vogelkop), and only three others just exceed 2,000 m (2,075–2,218 m). Nor is it the case that an outlier whose summit is at 2,218 m (Foja) can support populations of Central Range species with floors exceeding 2,000 m, because the area at high elevation of even the tallest outliers is small. The highest floors of any species population on an outlier are between 270 and 940 m below its summit, e.g. 500 m below the summit for Foja (Beehler *et al*. 2012), 265 m below the summit for Kumawa (Diamond & Bishop 2015) and almost 1,000 m below it for the Vogelkop.

Consequently, elevation explains more than half of the cases of the 35 New Guinea upland species present on no outlier. Of the 35, 20 are high-elevation species: 16 have floors ≥ 2,000 m, and six of those 16 have floors above 3,000 m. (The other 15 absentees that are not high-elevation species are absent from outliers for idiosyncratic reasons, such as there being no outlier within their geographic range.) Similarly, of the 29 species present on just one outlier, 28 are high-elevation species whose sole outlier population is on one of the two highest, Huon (4,121 m) or Vogelkop (2,954 m). It was thus inevitable that Yapen supports no population of these 64 species present on just one or no mainland outlier. Yapen's summit is only 1,430 m; the highest well-attested elevational floors on Yapen are 1,160 m for the breeding population of Black-billed Cuckoo-Dove *Macropygia nigrirostris*, 1,005 m for Mountain Meliphaga *Meliphaga orientalis* and 855 m for Stout-billed Cuckooshrike *Coracina caeruleogrisea*. Hence elevation explains a large fraction of absences of Central Range upland species on the mainland outliers and on Yapen.

Water-crossing ability.—Many tropical forest species are reluctant to cross clearings or fly above the canopy. Even among those species that do cross clearings or fly above the canopy over land, many have never been observed flying over water and have never been recorded on any island lacking a recent land connection to the source island. In New Guinea, for example, Papuan Spinetailed Swift *Mearnsia novaeguineae* feeds entirely by long flights in the open, and Dusky Lory *Pseudeos fuscata*, Black Lory *Chalcopsitta* [*atra*] and Blue-collared Parrot *Geoffroyus simplex* are regularly seen flying high and for long distances between roosts and feeding grounds, but none of these has ever been recorded from any New Guinea island lacking a recent land bridge. These and 300 other New Guinea species possess a behavioural refusal to cross water gaps, although their flight capabilities would easily permit it, and some have close relatives that do cross such gaps (Diamond 1972a).

We define water-crossing species as those of the New Guinea mainland recorded from any 'oceanic' island lacking a recent land connection. The oceanic islands with the most such records are Karkar, Biak, the D'Entrecasteaux Islands, and the Bismarck and Solomon Islands. By that definition, of New Guinea's 193 upland species, only 29 are water-crossers; the other 164 are strictly confined to New Guinea and its large land-bridge islands.

Table 4 tabulates water-crossers and non-water crossers among the upland species on Yapen and the four most comparable mainland outliers. It is apparent that Yapen has a considerably higher percentage of water-crossers than any of the mainland outliers (38% vs. 18–25%), mainly because Yapen has considerably fewer non-water-crossers (16 vs. 28–55 species), although a similar number of water-crossers (ten vs. 6–17 species). (Of course water-crossing populations of the mainland outliers reached there from the Central Range overland, not overwater; ability to disperse overwater does not preclude ability to disperse overland.) The straightforward explanation is that, once Yapen's land bridge to New Guinea was severed at the end of the Pleistocene making Yapen an island, populations now isolated

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TABLE 4

Water-crossing ability of upland species: total numbers, number of water-crossing species, and number of non-water-crossing species. Species are considered water-crossers if recorded from any 'oceanic' island lacking a recent land bridge to New Guinea (most records on Karkar, Biak, D'Entrecasteaux Islands, and the Bismarck and Solomon Islands). Non-water-crossers are species unrecorded on any oceanic island, but in many cases recorded on Yapen and other land-bridge islands reachable overland from New Guinea during the Pleistocene. The four mainland outlying ranges tabulated (VFAK) are those also tabulated in Table 1 due to their similar elevation to Yapen. Note: Yapen's number of water-crossing upland species is similar to comparable outliers, but Yapen has only one-third of the non-water-crossing species as comparable outliers (because post-Pleistocene population extinctions after Yapen became an island could not be reversed by overwater recolonisation). See text for discussion.

Mountain	**Total upland species**	**Water-crossing species**	**Non-water-crossing species**	**% water-crossers**
V = Van Rees	34	6	28	18%
F = Fakfak	65	15	50	23%
A = Adelbert	67	17	50	25%
K = Kumawa	72	17	55	24%
average, VFAK	58	14	46	23%
Yapen	26	10	16	38%

thereon during the Holocene began going extinct. Those extinctions could be reversed by overwater colonisation by water-crossing taxa, but not for non-water-crossing species.

Therefore, two main reasons explain why Yapen possesses fewer upland species than the ten mainland outliers, and many fewer upland species than the Central Range: lack of habitat for New Guinea's high-elevation upland species (Yapen is significantly lower than six of the ten outliers, and much lower than the Central Range); and post-Pleistocene extinctions of non-water-crossing populations incapable of reversal by recolonisation overwater. Below we explore further those inferred post-Pleistocene extinctions.

Inferred extinctions.—The comparisons in the section Upland species number, such as the large deficit of upland species on Yapen vs. the Fakfak mainland outlier most similar to the former in elevation (26 vs. 65 species, respectively), imply that many upland populations have become extinct since the severing of Yapen's Pleistocene land bridge to New Guinea. But that comparison alone does not answer the question: *which* upland populations were present on Yapen at the time of the Pleistocene land bridge, and have subsequently become extinct?

In the absence of proof from fossils, a reasonable guess is: species that are present on several of the most similar mainland outliers (Van Rees, Fakfak, Adelbert, Kumawa), and whose elevational floors are within the range for populations still present on Yapen, but are absent on the island today. Table 5 lists the 23 such species. On average, they occur on three of the four comparable outliers; all have floors on Van Rees, Fakfak and Kumawa below Yapen's highest floor (1,160 m), all but one have floors on those outliers below 915 m, and most are below 800 m. (However, three of the 23 have floors above 1,160 m on Adelbert, where floors average slightly higher.) Naturally, we do not claim that all 23 of the absent species did become extinct on Yapen: some of them might by chance have initially been absent, and the four outliers are not perfect matches for Yapen, as we shall discuss in Mechanisms for colonising Yapen. We can only reason that those species are particularly likely to have been among the dozens that did go extinct there.

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TABLE 5

Upland species whose populations may have disappeared on Yapen. Column 1: the 23 upland species that seem especially likely to have been formerly present, but have now disappeared, based on two criteria: presence on two or more of the four mainland outliers closest to Yapen in elevation; and elevational floors on those outliers well below 1,160 m (the highest floor of any Yapen population) and mostly below 800 m (most Yapen floors are below 800 m). On average, the 23 species are present on three of the four outliers; 17 of the 23 occur on either three or all four outliers. Column 2: water-crosser? Column 3: number of mainland outliers occupied (as columns 3–4 in Table 1). Columns 4–7: elevational floors on four outliers (from Diamond & Bishop 2015 for Fakfak and Kumawa, and our unpubl. obs. for Van Rees and Adelbert). Abbreviations F, V, K, A as Table 4. Column 8: average abundance on Fakfak and Kumawa, as assessed by Diamond & Bishop (2015) on a scale from 1 (least common) to 4 (most common). For the four species present only on Van Rees and Adelbert, where we did not estimate abundance, we use instead JD's estimates for Foja (in Beehler *et al*. 2012). See text for discussion.

Species	Water-crosser?	No. of outliers	Floor (m)				Outlier abundance
			V	F	K	A	
Dwarf Cassowary *Casuarius bennetti*	no	7	549	?	?	730	2
White-eared Bronze Cuckoo *Chalcites meyerii*	no	10	549	--	113	820	2.5
New Guinea Vulturine Parrot *Psittrichas fulgidus*	no	7	366	--	--	820	1.5
Red-fronted Lorikeet *Charmosyna rubronotata*	yes	3	915	?	?	730	1.8
Blue-collared Parrot *Geoffroyus simplex*	no	8	366	617	553	820	2.5
Red-breasted Pygmy Parrot *Micropsitta bruijnii*	yes	9	--	774	704	1,220	2.3
Spotted Honeyeater *Xanthotis polygrammus*	no	9	823	635	--	1,000	1
Brown-breasted Gerygone *Gerygone ruficollis*	no	5	--	787	742	1,575	2.8
Mountain Peltops *Peltops montanus*	no	9	518	684	604	700	2
Barred Cuckooshrike *Coracina lineata*	yes	8	854	--	728	975	1
Black-bellied Cicadabird *Edolisoma montanum*	no	9	--	863	786	1,100	2.5
Piping Bellbird *Ornorectes cristatus*	no	8	580	657	483	--	2.5
Sclater's Whistler *Pachycephala soror*	yes	5	--	690	375	1,525	3
Rusty Whistler *Pachycephala hyperythra*	no	8	580	690	671	850	1
Drongo Fantail *Chaetorhynchus papuensis*	no	9	610	690	622	567	3
Trumpet Manucode *Phonygammus keraudrenii*	yes	8	143	399	128	930	4
Greater Melampitta *Megalampitta gigantea*	no	4	--	835	680	--	2.5
Fantailed Monarch *Symposiachrus axillaris*	yes	9	915	774	652	850	2.3
Black-winged Monarch *Monarcha frater*	no	8	--	689	411	750	2.8
Torrent Flycatcher *Monachella muelleriana*	yes	5	518	--	--	567	1
Papuan Scrub Robin *Drymodes beccarii*	no	7	610	--	--	995	2
Banded Yellow Robin *Gennaeodryas placens*	no	4	--	457	104	1,000	2.7
Blue-faced Parrotfinch *Erythrura trichroa*	yes	8	--	546	1,025	820	3.5

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What distinguishes the 23 populations likely to have become extinct on Yapen from the populations that have persisted there? For species unable to cross water, there is the expected effect of population abundance on extinction probability, with abundance estimated on mainland outliers and tabulated in Tables 1 and 5. Expressing abundance on a four-point scale from 1 (the rarest) to 4 (most abundant species), abundance ± S.D. averages 2.65 ± 0.80 ($n = 16$) for species present on Yapen, vs. 2.22 ± 0.60 ($n = 15$) for those absent on Yapen. That difference has a probability of 0.058 by a one-tailed t-test, close to the conventional level of $p = 0.050$ for concluding statistical significance. (A one-tailed t-test is more appropriate than a two-tailed test, because the hypothesis is not that species present or absent merely differ in abundance in either direction, but that species present are more abundant.) However, for water-crossing species, there is no effect of abundance on inferred survival: 2.38 ± 0.91 ($n = 10$) for species present on Yapen, vs. 2.36 ± 1.03 (8) for those absent on Yapen.

The straightforward interpretation is as follows. Populations of non-water-crossing species have been isolated on Yapen since the land bridge was severed. More abundant species have been more successful at surviving, in agreement with the discovery that population size is the strongest predictor of extinctions among isolated populations (MacArthur & Wilson 1967). There is no effect of abundance for water-crossing species, because their populations on Yapen have not been isolated since the land bridge was severed; many population extinctions could have been reversed by post-Pleistocene overwater colonisation; and an increased likelihood of less abundant populations to go extinct was perhaps offset by higher dispersal rates expected for less abundant species.

Those inferred post-Pleistocene extinctions of non-water-crossing species on Yapen could explain what we consider to be the most puzzling feature of the Yapen upland avifauna. Four of Yapen's 16 non-water-crossing populations are species widespread on mainland outliers and moderately or very common there, of which three are vocal and easily detected: *Ailuroedus melanotis*, *Tregellasia leucops*, *Pachycephalopsis hattamensis* and *Peneothello bimaculata*. But all four are rare and / or very local on Yapen, having been found on just one or two visits. Human hunting could not explain their rarity; all are small and not colourful, and none is a beautiful singer or targeted by hunters. We wonder if the Yapen populations of these four species that are common on the New Guinea mainland are on the verge of disappearing on Yapen, as we infer so many other insular populations have already done since the end of the Pleistocene. Historical demographic inferences from population genetic studies may provide interesting avenues for addressing population declines in these non-water-crossing species, as well as recent exchanges of genes and individuals in the water-crossers (see, e.g., Pool *et al*. 2010).

Mechanisms for colonising Yapen

If many individuals of New Guinea upland species were fitted with satellite-transmitters, we could observe the routes via which colonists reached the outliers from the Central Range or from other outliers. In the absence of such data, we can suggest six colonisation paths and histories using indirect evidence.

1. *Overwater colonisation*.—Of Yapen's 26 upland species, ten (see Table 1) are inferred to be capable of having arrived overwater when Yapen was (or, as it is today) an island—because the ten occur on other islands without recent connection to New Guinea. (Of course, the fact that they *could* have arrived overwater does not mean that they did so; they could have arrived overland during the Pleistocene, as did Yapen's 16 non-water-crossing species.) Among the ten species, it is highly probable that *Hieraaetus weiskei* and *Accipiter meyerianus* did arrive recently overwater, because they are rare hawks with low population

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densities, and only one individual of each has been observed on Yapen, making it unlikely that they represent populations large enough to have survived on Yapen for 10,000 years of isolation.

Among Yapen's ten water-crossers, four regularly fly high above the canopy: both just-mentioned raptors, Papuan Mountain Pigeon *Gymnophaps albertisii* and Mountain Swiftlet *Aerodramus hirundinaceus*. Three other species often fly through the canopy: White-bibbed Fruit Dove *Ptilinopus rivoli*, Claret-breasted Fruit Dove *P. viridis* and *Macropygia nigrirostris*. Red Myzomela *Myzomela cruentata* makes frequent movements in search of flowering trees. The remaining two water-crossers, the terrestrial pigeon *Otidiphaps nobilis* and the arboreal Island Leaf Warbler *Seicercus poliocephalus*, appear to be territorial and have never been observed flying above the canopy. These two species may colonise only or mainly during juvenile dispersal.

2. *Regular post-breeding descent to the lowlands*.—Two of Yapen's upland species, the pigeons *Macropygia nigrirostris* and *Gymnophaps albertisii*, are among the species that breed in New Guinea at high elevation but descend to the lowlands at other times. Such behaviour is also suggested for the Yapen population of *Macropygia nigrirostris* given that we heard it calling only above 1,160 m, but we saw silent individuals in the lowlands. This would facilitate dispersal by these two pigeons overland between the Central Range and outliers, including Yapen when it was connected to the mainland. Alternatively, both species could have reached Yapen overwater, because both occur on oceanic islands that could only have been reached overwater (Goodenough and New Britain, plus *M. nigrirostris* on Karkar).

3. *Occasional lowland stragglers or populations*.—Several other New Guinea species occur as occasional immature individuals below the species' usual elevational range, perhaps during juvenile dispersal (Diamond 1972b: 30–31). This behaviour operates to an extreme degree in some bird of paradise and bowerbird species, for which females and immatures regularly occur as much as 1,000 m below the elevation of displaying adult males (Stein 1936, Pruett-Jones & Pruett-Jones 1986). We have observed this phenomenon in New Guinea for two Yapen upland species, Magnificent Bird of Paradise *Cicinnurus magnificus* and Papuan Cicadabird *Edolisoma incertum* (Diamond 1972b: 335). In most parts of New Guinea *Pitohui dichrous* occurs above an elevational floor of at least 600 m, often as high as 1,100 m, but has some local lowland populations. All of these phenomena of occasional lowland presences would facilitate dispersal through the lowlands to mountains by species that are predominantly upland species.

4. *Dispersal via hill bridges vs.* 5. *Dispersal via flat lowlands*.—Most of the New Guinea outliers are connected to each other and / or to the Central Range by 'bridges' of low hills, either as a continuous chain or punctuated by very narrow lowland corridors. This permits dispersal of upland species entirely or mostly within hilly terrain.

The striking exceptions among the outliers are Fakfak and Kumawa, which are entirely separated from each other, from other outliers, and from the Central Range by a broad expanse of 70–100 km of flat lowlands close to sea level, without any hills. For some New Guinea upland species, level-ground lowlands apparently constitute a strong barrier. Pesquet's Parrot *Psittrichas fulgidus* occurs in hilly terrain up to 1,500 m and down to the base of the hills, but not in flat lowlands distant from the hills. It is so noisy and conspicuous in flight above the canopy that we can be confident that is absent from expanses of flat lowlands. Three other species—Salvadori's Teal *Salvadorina waigiuensis*, *Monachella muelleriana* and Torrentlark *Grallina bruijnii*—occur throughout along mountain rivers but do not follow them far into the flat lowlands.

All four of these species are absent from both Fakfak and Kumawa. This suggests that their colonisation of outliers depends on hill bridges, and not only do they not occur in

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level-ground lowlands but they do not even disperse through these regions. Eleven other New Guinea upland species (listed in Diamond & Bishop 2015: 302, Table 2) are also absent from Fakfak and Kumawa, although they occupy 2–7 (on average, four) of the other eight outliers. None of those 11 other species has been reported from flat lowlands.

At the time that Yapen formed part of the New Guinea mainland, it, too, was separated from the nearest mountain (Van Rees) by 50 km of flat lowlands. Of the 15 species absent from Fakfak and Kumawa, 13—all of them except *Peneothello bimaculata* and *Pachycephalopsis hattamensis*—are also absent on Yapen. This suggests that, while the absence of those two species from Fakfak and Kumawa is unrelated to surrounding flat lowland terrain, many or most of the other 13 species really do depend on hill bridges for their dispersal.

6. *Pleistocene lowland relicts*.—During cold Pleistocene epochs, vegetation and climate zones on tropical mountains worldwide were depressed to elevations lower than currently. In New Guinea that lowering is supported by evidence such as glacial landforms being much more extensive and at much lower elevations than their current extent only at highest elevations. During those cold periods, some New Guinea upland species currently absent from the lowlands would have found suitable climate conditions in the lowlands. But those cold periods were also times of lower sea levels, which exposed as dry land an enormous platform connecting southern New Guinea to northern Australia, but now inundated as the shallow Arafura Sea (Fig. 1). As climate became warmer and sea level rose again at the end of the Pleistocene, most of the Arafura platform was drowned again, the Pleistocene lowland populations mostly disappeared, and their species again retreated upslope in New Guinea and became upland taxa.

But three legacies remained of the otherwise vanished lowland populations of upland species (Table 6), namely three sets of relict lowland populations of otherwise upland New Guinea birds, on the still-exposed parts of the platform furthest from the equator (hence in lowland areas climatically most similar to low elevations of New Guinea mountains). Those relicts are: 13 populations of upland species that the first and second Archbold Expeditions discovered at sea level on lowland New Guinea's southernmost bulge including the lower Fly River (Mayr & Rand 1937, Rand 1942); 11 populations on the Aru Islands, a fragment of the former platform surrounded by the Arafura Sea; and six of those species at the tip of Australia's Cape York Peninsula, even further from the equator (Fig. 1). Because the Aru Islands and Fly River bulge share lowland populations of seven upland species, but each has additional upland species not shared with the other, there is a total of 17 upland species with relict lowland populations still present on the Aru Islands and / or the Fly River bulge. Of the 17 species, seven have upland populations on Yapen, and six are represented on the Western Papuan Islands (Table 2).

We interpret these relict populations as evidence for one more mechanism whereby upland species colonised Yapen (and the Western Papuan Islands). Today, upland species are disjunctly distributed over New Guinea's outliers, the Central Range, and Yapen. But during cool eras in the Pleistocene, upland species shifted downslope, such that species with the lowest floors could have shifted into the lowlands and achieved continuous distributions. As climate warmed during the Holocene, these species shifted uphill again, abandoned the lowlands except relict populations in lowland areas furthest from the equator, and again became upland species with discontinuous distributions. Supporting this interpretation, Yapen's five upland species with relict lowland populations, and whose Yapen elevational ranges are best evidenced, have low elevational floors: on average, 600 m. Therefore it is plausible that they would have been species especially likely to shift downslope into the lowlands during the Pleistocene.

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TABLE 6
Relict lowland populations of New Guinea upland species on the Arafura platform. The shallow Arafura Sea, which presently separates Australia from New Guinea, was exposed as a large lowland platform at Pleistocene times of low sea level. The Aru Islands, south New Guinea's Fly River bulge, and the north tip of Australia's Cape York Peninsula survive as fragments of the former platform. Today, one, two or all three of those fragments support lowland populations of 17 species that elsewhere in New Guinea are upland birds, and that are probably relicts of Pleistocene populations formerly widespread on that lowland platform. Seven of those species now have upland populations on Yapen. See text for discussion.

Species	Fly River bulge	Aru Islands	Cape York tip	Yapen
Pheasant Pigeon *Otidiphaps nobilis*	--	✓	--	✓
Wallace's Owlet-nightjar *Aegotheles wallacii*	--	✓	--	--
Black-eared Catbird *Ailuroedus melanotis*	✓	✓	✓	✓
Flame Bowerbird *Sericulus ardens*	✓	--	--	--
Spotted Honeyeater *Xanthotis polygrammus*	✓	--	--	--
Tropical Scrubwren *Sericornis beccarii*	✓	✓	✓	✓
Painted Quail-thrush *Cinclosoma ajax*	✓	--	--	--
Stout-billed Cuckooshrike *Coracina caeruleogrisea*	✓	✓	--	✓
Barred Cuckooshrike *Coracina lineata*	--	✓	--	--
Piping Bellbird *Ornorectes cristatus*	✓	--	--	--
Black-headed Whistler *Pachycephala monacha*	--	✓	--	--
Hooded Pitohui *Pitohui dichrous*	✓	--	--	✓
Trumpet Manucode *Phonygammus keraudrenii*	✓	✓	✓	--
Yellow-legged Flyrobin *Kempiella griseoceps*	✓	✓	✓	✓
Papuan Scrub Robin *Drymodes beccarii*	✓	✓	✓	--
White-faced Robin *Tregellasia leucops*	✓	--	✓	✓
New Guinea White-eye *Zosterops novaeguineae*	✓	✓	--	--

Future studies

Many questions concerning Yapen's avifauna remain unanswered. We conclude by calling attention to six of them:

1. What further upland populations remain to be discovered on Yapen? Some surely await discovery, because five of the 26 known upland populations have been observed by just one visitor. On p. 431 we suggested 11 'missing' species especially deserving of searches.

2. Endemic subspecies are recognised for some nine of Yapen's lowland populations, and for four of its upland populations (Rothschild *et al*. 1932, Mayr 1941, Rand & Gilliard 1967, Beehler & Pratt 2016). As expected, subspeciation has been reported for proportionately more of Yapen's upland populations than its lowland populations (19% vs. 7% respectively), although two of the three most distinctive races are *Paradisaea minor jobiensis* and *Pitohui kirhocephalus jobiensis* in the lowlands. Recently discovered Yapen upland populations not yet collected or identified subspecifically are *Meliphaga orientalis* (distinctive in the field: p. 444), *Ptilorrhoa castanonota*, *P.* cf. *geislerorum*, *Seicercus poliocephalus*, *Tregellasia leucops*, *Peneothello bimaculata* and *Ailuroedus melanotis*.

3. Bird fossils are unknown for Yapen, and for almost all of New Guinea. Fossils could provide direct evidence of the former existence of Pleistocene populations that we infer

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existed but have vanished. Fossils could also provide evidence for when species arrived or disappeared.

4. Molecular phylogenetic and population genetic studies (e.g., Pool *et al*. 2010, Pedersen *et al*. 2018, Garg *et al*. 2020) could assess sources and relationships of Yapen's upland populations. The nearest upland sources are Van Rees, Wandammen, Vogelkop and the Central Range.

5. Molecular population genetic studies, as well as field observations, radio-tracking and banding, could provide tests of the dispersal mechanisms that we have postulated.

6. Yapen's lowland avifauna poses many of the same questions as its upland avifauna, but awaits a modern re-analysis to update that by Rothschild *et al*. (1932). The lowland avifauna comprises five times more species than in the uplands and offers rich material for analysis. Why does Yapen today harbour just 40% of New Guinea's lowland species? Yapen's lowlands were presumably much more species-rich when Yapen was still part of the mainland until 10,000 years ago: how can we explain why certain species of the New Guinea lowlands have been more successful than others at surviving on Yapen, and on five other large land-bridge islands?

Species accounts: Yapen's upland bird species

[**DWARF CASSOWARY** *Casuarius bennetti*
The sole cassowary species well evidenced on Yapen is the large lowland Northern Cassowary *C. unappendiculatus*, collected by Beccari and by Laglaize. But Rothschild (1914) described a new subspecies of the small montane species *C. bennetti*, from an individual brought alive to England by Walter Goodfellow from Yapen, presumably a captive, possibly bought as a chick. We saw no cassowaries of any species nor their droppings on our three visits, although Ambaidiru residents described cassowaries using the Yawa language name of 'apara'. Informants were equivocal as to whether they were familiar only with a large cassowary or also with a small one. New Guineans transport captive cassowaries widely, which is presumably how they became established on New Britain and Seram outside the Papuan region. Until *C. bennetti* is observed or collected in the wild on Yapen, its presence should be considered unproven.]

WATTLED BRUSHTURKEY *Aepypodius arfakianus*
JD observed one individual and saw a nest mound near the summit of Mt. Aror. The only specimen for Yapen is one that Doherty purchased on the coast, presumably brought from the mountains. Ambaidiru residents described this megapode and its mounds as 'ajinda', distinct from the other two Yapen megapodes, Red-legged Brushturkey *Talegalla jobiensis* = 'wayan' and New Guinea Scrubfowl *Megapodius decollatus* = 'mangkio'. Verhelst & Pottier (2020) obtained several photos from camera traps at different locations, suggesting that the species is common.

BLACK-BILLED CUCKOO-DOVE *Macropygia nigrirostris*
On Yapen, as elsewhere in the New Guinea region, the species called frequently and presumably was breeding only at high elevations (1,160 m), but was encountered silently (presumably non-breeding) at low elevations (700 m to sea level).

WHITE-BIBBED FRUIT DOVE *Ptilinopus rivoli*
By far the commonest *Ptilinopus* in the mountains of Yapen, from the summit to 510 m. There are two vocalisations, both similar to those of Mountain Fruit Dove *P. bellus* of mainland

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New Guinea (if that is considered a different species): a series of slightly upslurred *hoo* notes starting very slowly and at a constant pitch, then accelerating, and descending in pitch; and a single *hoo* initially slightly upslurred, then markedly downslurred, repeated *ad nauseam* every five seconds. Beehler & Pratt (2016: 80) suspected that identification of the Yapen population as the small-island allospecies *P. rivoli* might be mistakenly based on specimens collected on nearby small islands, and that the Yapen population might represent the New Guinea mainland allospecies *P. bellus*. While that suspicion was reasonable, the relevant specimens attributable with certainty to Yapen are two collected by Stein at his 450-m camp on two different dates, and are both *P. rivoli miquelii*, not *P. bellus* (Rothschild *et al*. 1932: 242). Yawa name: 'irán'.

CLARET-BREASTED FRUIT DOVE *Ptilinopus viridis*
From 1,100 m down regularly to 520 m, occasionally in the lowlands, and often heard but infrequently seen. The two distinct vocalisations on Yapen are similar to those in all of the outlying ranges on New Guinea's north coast from the Kumawa Mts. east to the North Coastal Range of Papua New Guinea. One vocalisation consists of a detached first note, followed by *c*.6 pairs of notes, the first note of each pair on a lower pitch, the second accented, higher pitched and upslurred. The other vocalisation is a repeated three-note phrase, the first short, the second a higher pitched downslur and the third note a lower pitched downslur. On Yapen but not elsewhere, that second vocalisation is sometimes reduced to a repeated two-note phrase. Yawa name: 'omande'.

PAPUAN MOUNTAIN PIGEON *Gymnophaps albertisii*
Observed only in 1983: a flock of 30 seen daily at 905–1,100 m, feeding on drupes of the tree *Haplolobus floribundus* (Burseraceae). Yawa name: 'mansauman'.

PHEASANT PIGEON *Otidiphaps nobilis*
Heard just once in 1983 at 580 m, and once in 2017 at 650 m, but familiar to Ambaidiru residents by the Yawa name: 'wanaum'. Previously recorded only by Doherty.

MOUNTAIN SWIFTLET *Aerodramus hirundinaceus*
Brown swiftlets were seen in 1983 in large numbers at and above Ambaidiru (640 m), and in 2017 uncommonly from the lowlands to 1,195 m. We assume that swiftlets at high elevation were predominantly *A. hirundinaceus* (collected by Stein), and that those at low elevation were Uniform Swiftlet *A. vanikorensis*. Yawa name: 'kamantiováni' (for all species of swiftlets).

PYGMY EAGLE *Hieraaetus weiskei*
The sole record is of one observed soaring at 600 m by KDB in 2016.

MEYER'S GOSHAWK *Accipiter meyerianus*
The only record is a specimen acquired from an unknown location by A. B. Meyer.

BLACK-EARED CATBIRD *Ailuroedus melanotis*
Observed and photographed at 1,080 and 1,300 m (Verhelst & Pottier 2020).

RED MYZOMELA *Myzomela cruentata*
In 1983 JD observed both sexes regularly in white-flowered *Eugenia* trees at 1,005–1,100 m, but nowhere else. In 2016 KDB observed one male in a flowering tree at 1,100 m. Our only

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sighting in 2017 was of a single male at 1,220 m. Verhelst and Pottier (2020) observed one at 950 m.

MOUNTAIN MELIPHAGA *Meliphaga orientalis*

First record for Yapen; the only other insular population is on Waigeo. Similar to Mimic Meliphaga *M. analoga* of Yapen's lower elevations, but distinguished with effort and practice both visually and by voice. Both species are large, yellow-eared, with long slender bills, and unspotted underparts. By sight, *M. orientalis* is best distinguished by the small size of its round yellow ear patch, vs. the larger and notably elongated yellow patch of *M. analoga*. Vocally, *M. orientalis* differs in its short snapped downslurred call note, whereas the analogous note of *M. analoga* is a disyllable (not a downslur) with the second note lower pitched. *M. orientalis* also has an upslurred call note, and a musical staccato call *tp* like other meliphagas, and quieter than the *tp* call of Yapen *M. analoga*. Compared to New Guinea mainland *orientalis* populations, that on Yapen differs in its large size (comparable to *M. analoga*, rather than noticeably smaller than *M. analoga* as on the mainland), and in its unspotted, pale grey underparts, unlike the ventral spotting of mainland birds. We found *M. orientalis* common from the summit down to flowering trees at 1,005 m, but replaced by *M. analoga* from around 855 m and below.

WHITE-EARED MELIPHAGA *Meliphaga montana*

Readily distinguished from three of the four other Yapen meliphaga species (*M. orientalis*, *M. analoga* and Puff-backed Meliphaga *M. aruensis*) by its ear patch being clean white rather than yellow; dull dark dorsal and ventral correlation; stout rather than long slender bill; loud wingbeats, unlike not only any other meliphaga but also all other small forest birds in New Guinea; stolid sluggish behaviour; and by not visiting flowering trees. We found it fairly common from the summit to 795 m, from the understorey to the canopy, and usually solitary but for occasionally joining mixed-species flocks. Yawa name: 'markugwá'. The remaining Yapen meliphaga species is Scrub Meliphaga *M. albonotata*, of which KDB saw one in sago swamp forest at sea level in 2016 (the first record for any New Guinea satellite island).

TROPICAL SCRUBWREN *Sericornis beccarii*

Moderately common at 665–1,250 m, being found 1–6 m above ground. Often in mixed flocks with *Gerygone* warblers and *Rhipidura* fantails. The song is a gerygone-like, light, fast, four-note, up-and-down pattern repeated without variation or pause, like a sine wave. Songs of Fairy Gerygone *Gerygone palpebrosa* are confusingly similar, but differ in their slight pauses and alternation of patterns within a song. *S. beccarii* occurs at low elevations (mostly below 1,400 m) on nine outlying mountain ranges (Kumawa, Fakfak, Arfak, Wandammen, Yapen, Van Rees, Foja, Cyclops and North Coastal Range), on north slopes of the Central Range above the Lakes Plains, and south slopes above the Kikori River. Plumage variation among these populations is considerable but geographically irregular, leading to divergent taxonomic treatments (e.g., Mayr 1941, Rand & Gilliard 1967, Diamond 1969, 1985, Beehler & Pratt 2016). Most recently, Beehler & Pratt (2016: 330–333) assigned some populations (including that on Yapen) to Tropical Scrubwren's high-elevation (above 1,400 m) relative Large Scrubwren *S. nouhuysi*. They interpreted the irregular geographic variation as due to variably massive hybridisation between *S. beccarii* and *S. nouhuysi*. We instead consider all low-elevation populations (we have field experience of all 11) to belong to *S. beccarii*, because: they all possess similar songs, distinct from that of *S. nouhuysi*; they all occur at similar elevations up to *c.*1,400 m; none is found above 1,400 m to which all unequivocal *S.*

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nouhuysi populations are confined; and five of them (Kumawa, Arfak, Foja and the north and south slopes of the Central Range) occur sympatrically with high-elevation *S. nouhuysi*, segregating by elevation with *S. beccarii* below and *S. nouhuysi* above 1,400 m. Yawa name: 'punti'?

CHESTNUT-BACKED JEWEL-BABBLER *Ptilorrhoa castanonota*
Observed many times between 665 and 1,110 m in 1983, and at 760–1,135 m in 2017. Our closest sighting was of an individual with blue underparts, wings and superciliary, chestnut upperparts from at least the crown to lower back, and a white throat edged black. Another glimpse was of an individual with chestnut upperparts including the tail. Vocalisations were ones we associate with *P. castanonota* elsewhere: a repeated high note, a duet, and a loud pair of *tsp-tsp* notes, with the second note especially loud. The first record for Yapen.

DIMORPHIC JEWEL-BABBLER *Ptilorrhoa* cf. *geislerorum*
Observed at 440 and 980 m by Verhelst & Pottier (2020).

STOUT-BILLED CUCKOOSHRIKE *Coracina caeruleogrisea*
Seen and heard nine times between 855 and 1,195 m, sometimes in mixed flocks with pitohuis. Yawa name: 'kowat'.

PAPUAN CICADABIRD *Edolisoma incertum*
Common (the most numerous of Yapen's five species of *Coracina* and *Edolisoma*), at 645–1,195 m. Because vocalisations of this species differ dramatically across New Guinea, we mention the three Yapen vocalisations, all shared with both the Foja and Van Rees populations: a series of several dozen buzzy notes repeated on constant pitch, but slightly decelerating; an otherwise similar series of several dozen musical notes repeated on the same pitch (heard only in 1983 but not in 2017); and a cheerful musical staccato call. Yawa name: 'nyukikas'.

HOODED PITOHUI *Pitohui dichrous*
Common from the summit down to 640 m (occasionally 570 m), and overlapping greatly in elevational range with Northern Variable Pitohui *P. kirhocephalus* (summit to sea level). Yapen has the sole insular population of this species. On the New Guinea mainland most populations are montane and largely at elevations above *P. kirhocephalus* or its southern counterpart Southern Variable Pitohui *P. uropygialis*, but *P. dichrous* also has some local populations at sea level. Incessantly before dawn on Yapen, *P. dichrous* repeated its lovely, slow, medium-pitched, signature call of a single note given several times at the same pitch, followed by a lower pitched downslur. Yawa name: 'popok'.

GREEN-BACKED ROBIN *Pachycephalopsis hattamensis*
Our only certain record, and still the only record for Yapen or any satellite island of New Guinea, was of an individual mist-netted at 1,070 m in 1983. Because that individual differs in colour and possibly size from New Guinea populations, it was taken as the type of *P. h. insularis* (Diamond 1985). In 2017 we heard two possible but uncertain calls at 610 and 925 m. The Yapen population must be rare or patchily distributed, because elsewhere the species is common and easily detected by its loud vocalisations.

YELLOW-LEGGED FLYROBIN *Kempiella griseoceps*
Verhelst & Pottier (2020) observed one at 440 m.

WHITE-RUMPED ROBIN *Peneothello bimaculata*
Our only records were of an individual seen at 900 m and 2–3 m above ground, in 1983, and of an unseen individual singing pre-dawn at 1,195 m in 2017. There were no previous Yapen records, nor on any other island except New Guinea itself.

WHITE-FACED ROBIN *Tregellasia leucops*
In 1983 JD observed six individuals at heights of 3–10 m above ground, and at elevations of 665–1,225 m. We did not encounter it in 2017, and there were no previous Yapen records. However, Verhelst & Pottier (2020) found it common on Yapen's eastern peak above 900 m.

MAGNIFICENT BIRD OF PARADISE *Cicinnurus magnificus*
Modestly common, from the summit down to 535 m, occasionally to 425 m. Females often join pitohuis in mixed-species flocks. Yawa names differ for the sexes, which are totally different in appearance: 'anauput' (male), 'chinchor' (female).

ISLAND LEAF WARBLER *Seicercus poliocephalus*
The commonest singer at 675–1,195 m, often heard in association with mixed-species flocks led by *Gerygone* warblers and *Rhipidura* fantails, but surprisingly infrequently seen. The small size, infrequency of sightings, high altitudinal floor, and the fact that no previous collector except Stein reached its elevational range explain why there were no previous records for Yapen, despite its abundance at high altitudes.

GREEN-FRONTED WHITE-EYE *Zosterops minor*
Common from the summit down to 425 m, in forest and even more numerous in second growth, forming monospecific flocks of up to 20, and occasionally joining mixed-species flocks. Differs from its southern watershed counterpart Black-fronted White-eye *Z. atrifrons* in its lack of a white-eye-ring and of a black forehead. Its song, given persistently before dawn, also differs from the descending 'wheel song' of *Z. atrifrons*: instead, a small but energetic series of notes on the same pitch, ending in 1–3 descending disyllables. Contact calls are weak, but the massed sound of many individuals calling simultaneously in a flock is loud. Yawa name: 'ainami'.

Mixed-species flocks

As elsewhere in New Guinea (Diamond 1987), on Yapen at elevations above 700 m we encountered two types of mixed-species foraging flocks: a 'brown-black' flock of mid-sized omnivores, most with brown and / or black plumage; and a flock of small insectivores. The noisiest, most numerous, and apparently leader species of brown-black flocks were *Pitohui kirhocephalus* and *P. dichrous*. Other regular members were Spangled Drongo *Dicrurus bracteatus*, female-plumaged birds of paradise (*Paradisaea minor*, King Bird of Paradise *C. regius* and Jobi Manucode *Manucodia jobiensis*) and cuckooshrikes (*Coracina caeruleogrisea*, Black Cicadabird *Edolisoma melas*, and *E. incertum*). In small insectivore flocks, the noisiest species were Chestnut-bellied Fantail *Rhipidura hyperythra*, Ochre-collared Monarch *Arses insularis* and Fairy Gerygone *Gerygone palpebrosa*. Other regular members were Northern Fantail *Rhipidura rufiventris*, Rufous-backed Fantail *R. rufidorsa*, Yellow-bellied Gerygone *Gerygone chrysogaster*, *Sericornis beccarii*, *Seicercus poliocephalus*, Grey Whistler *Pachycephala simplex*, Pygmy Longbill *Oedistoma pygmaeum* and Tawny-breasted Honeyeater *Xanthotis flaviventer*.

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A survey of the eastern uplands of Yapen Island, New Guinea, reveals three new species records

by Brecht Verhelst & Jonas Pottier

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Summary.—Compared to the outlying mountain ranges of New Guinea and surrounding islands, the known avifauna of Yapen Island numbers fewer upland species than expected, perhaps reflecting reduced coverage by ornithologists. In particular, the eastern portion of Yapen's uplands remained ornithologically unexplored until September 2019, when a seven-day expedition reached an elevation of 1,315 m, and documented three new species for the island. Two (Black-eared Catbird *Ailuroedus melanotis* and Yellow-legged Flyrobin *Kempiella griseoceps*) are widespread across the other outlying ranges and were therefore expected to occur on Yapen, whereas the third (Dimorphic Jewel-babbler *Ptilorrhoa geislerorum*) concerns a presumably isolated population of a species otherwise known from south-east New Guinea.

Survey

The avifauna of Yapen's uplands is of special interest in the study of dispersal and colonisation patterns between New Guinea's Central and outlying mountain ranges (Diamond 1985, Diamond & Bishop 2020). However, it remains poorly studied, and prior to 2019 only four ornithological expeditions had reached the higher elevations: G. Stein in 1931, J. Diamond in 1983, K. D. Bishop in 2016, and Diamond and Bishop in 2017 (Diamond & Bishop 2020). All four expeditions targeted the western uplands, which lie almost due north of the island's main town Serui, reach an elevation of 1,340 m, and have an area above 1,000 m of *c.*28 km^2 (measured using Google Earth). The eastern section is slightly higher, with a max. elevation of 1,430 m and an area above 1,000 m of *c.*31 km^2. The two upland areas are separated by hilly country over a distance of 22 km between the two highest points.

To document the avifauna of the eastern upland section, we undertook a ten-day survey in September 2019. We started from the village of Jobi on Yapen's north coast on 5 September, and reached a max. elevation of 1,315 m on 7 September. Attempts to reach higher were unsuccessful due to the extremely rugged karstic terrain. From there, we gradually descended the same trail, establishing camps at 1,315 m, 989 m, 470 m and 50 m. We divided our transect into five segments. The upper plateau (PH, above 1,250 m) is strewn with huge boulders and covered in stunted forest. From here, a very steep slope leads to segment R (600–1,250 m), where an existing trail to the village starts. It runs along a horizontal ridge through tall, mature forest before descending towards the river through extensive bamboo. Segment L (200–600 m) descends along a stream until reaching a rather level plateau (segment PL, 150–200 m) with numerous hunting trails but no evidence of recent logging. Finally, the trail runs through degraded forest intersected by small agricultural clearings, along a second river (segment D, 0–150 m). On average, we moved every second day between camps and spent the remaining time surveying birds along the trail. Where possible, we documented interesting observations with a Nikon D7200 camera and 300 mm lens, and recorded vocalisations with an Olympus LS11. In addition, we

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surveyed the higher parts (above 900 m) with the aid of nine camera traps of various types, which we retrieved on the final day of the survey. Throughout, the weather was dry, with only a little rain on the last day.

Observations

We observed a total of 76 bird species (Table 1), including three species new to the avifauna of Yapen: Black-eared Catbird *Ailuroedus melanotis*, Dimorphic Jewel-babbler *Ptilorrhoa* cf. *geislerorum* and Yellow-legged Flyrobin *Kempiella griseoceps*.

TABLE 1
Species observed by the authors in the uplands of eastern Yapen Island in September 2019. Columns D, PL, L, R and PH refer to different parts of the transect covered (see main text). Order and nomenclature follow Beehler & Pratt (2016).

		D	**PL**	**L**	**R**	**PH**
Wattled Brushturkey	*Aepypodius arfakianus*				X	X
Red-legged Brushturkey	*Talegalla jobiensis*		X	X		
New Guinea Scrubfowl	*Megapodius decollatus*	X				
Brown Cuckoo-Dove	*Macropygia amboinensis*			X	X	
Cinnamon Ground Dove	*Gallicolumba rufigula*				X	
Victoria Crowned Pigeon	*Goura victoria*		X			
Wompoo Fruit Dove	*Megaloprepia magnifica*		X	X		
White-bibbed Fruit Dove	*Ptilinopus rivoli*				X	X
Orange-bellied Fruit Dove	*Ptilinopus iozonus*	X				
Purple-tailed Imperial Pigeon	*Ducula rufigaster*		X			
Zoe's Imperial Pigeon	*Ducula zoeae*		X	X		
Greater Black Coucal	*Centropus menbeki*	X				
Chestnut-breasted Cuckoo	*Cacomantis castaneiventris*				X	
Marbled Frogmouth	*Podargus ocellatus*				X	X
Glossy Swiftlet	*Collocalia esculenta*	X				
Long-tailed Buzzard	*Henicopernis longicauda*	X		X	X	
Gurney's Eagle	*Aquila gurneyi*				X	X
Brahminy Kite	*Haliastur indus*	X				
Grey-headed Goshawk	*Accipiter poliocephalus*	X				
Papuan Boobook	*Ninox theomacha*				X	X
Blyth's Hornbill	*Rhyticeros plicatus*	X	X	X	X	X
Hook-billed Kingfisher	*Melidora macrorrhina*		X	X	X	X
Rufous-bellied Kookaburra	*Dacelo gaudichaud*	X		X		X
Yellow-billed Kingfisher	*Syma torotoro*	X	X	X		
Palm Cockatoo	*Probosciger aterrimus*	X			X	
Sulphur-crested Cockatoo	*Cacatua galerita*	X	X	X		
Black-capped Lory	*Lorius lory*		X	X	X	X
Rainbow Lorikeet	*Trichoglossus haematodus*	X		X		
Eclectus Parrot	*Eclectus roratus*	X				

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		D	**PL**	**L**	**R**	**PH**
Red-bellied Pitta	*Erythropitta erythrogaster*	X			X	
Black-eared Catbird	*Ailuroedus melanotis*				X	X
Red Myzomela	*Myzomela cruentata*			X		
Papuan Black Myzomela	*Myzomela nigrita*	X		X		
Tawny-breasted Honeyeater	*Xanthotis flaviventer*	X		X	X	
Helmeted Friarbird	*Philemon buceroides*			X	X	
Long-billed Honeyeater	*Melilestes megarhynchus*				X	
Mimic Meliphaga	*Meliphaga analoga*			X		
Mountain Meliphaga	*Meliphaga orientalis*				X	X
White-eared Meliphaga	*Meliphaga montana*				X	X
Rusty Mouse-Warbler	*Crateroscelis murina*		X	X	X	X
Pale-billed Scrubwren	*Sericornis spilodera*				X	X
Tropical Scrubwren	*Sericornis beccarii*			X	X	X
Yellow-bellied Gerygone	*Gerygone chrysogaster*		X	X	X	
Fairy Gerygone	*Gerygone palpebrosa*			X	X	X
Black Berrypecker	*Melanocharis nigra*		X	X		
Spectacled Longbill	*Oedistoma iliolophus*	X		X	X	
Yellow-bellied Longbill	*Toxorhamphus novaeguineae*		X	X	X	X
Dimorphic Jewel-babbler	*Ptilorrhoa* cf. *geislerorum*			X	X	
Hooded Butcherbird	*Cracticus cassicus*	X				
Boyer's Cuckooshrike	*Coracina boyeri*			X		
Papuan Cicadabird	*Edolisoma incertum*				X	
Black Cicadabird	*Edolisoma melas*				X	
Little Shrikethrush	*Colluricincla megarhyncha*			X	X	X
Rusty Shrikethrush	*Pseudorectes ferrugineus*			X	X	
Grey Whistler	*Pachycephala simplex*			X		
Northern Variable Pitohui	*Pitohui kirhocephalus*	X	X	X	X	
Hooded Pitohui	*Pitohui dichrous*				X	X
Rufous-backed Fantail	*Rhipidura rufidorsa*		X	X		X
Chestnut-bellied Fantail	*Rhipidura hyperythra*				X	
Northern Fantail	*Rhipidura rufiventris*	X	X	X	X	
Spangled Drongo	*Dicrurus bracteatus*				X	
King Bird of Paradise	*Cicinnurus regius*		X			
Magnificent Bird of Paradise	*Cicinnurus magnificus*			X	X	X
Lesser Bird of Paradise	*Paradisaea minor*	X	X	X	X	X
Ochre-collared Monarch	*Arses insularis*		X	X	X	X
Shining Flycatcher	*Myiagra alecto*			X		
Spot-winged Monarch	*Symposiachrus guttula*		X			
Grey Crow	*Corvus tristis*	X			X	
Yellow-legged Flyrobin	*Kempiella griseoceps*			X		

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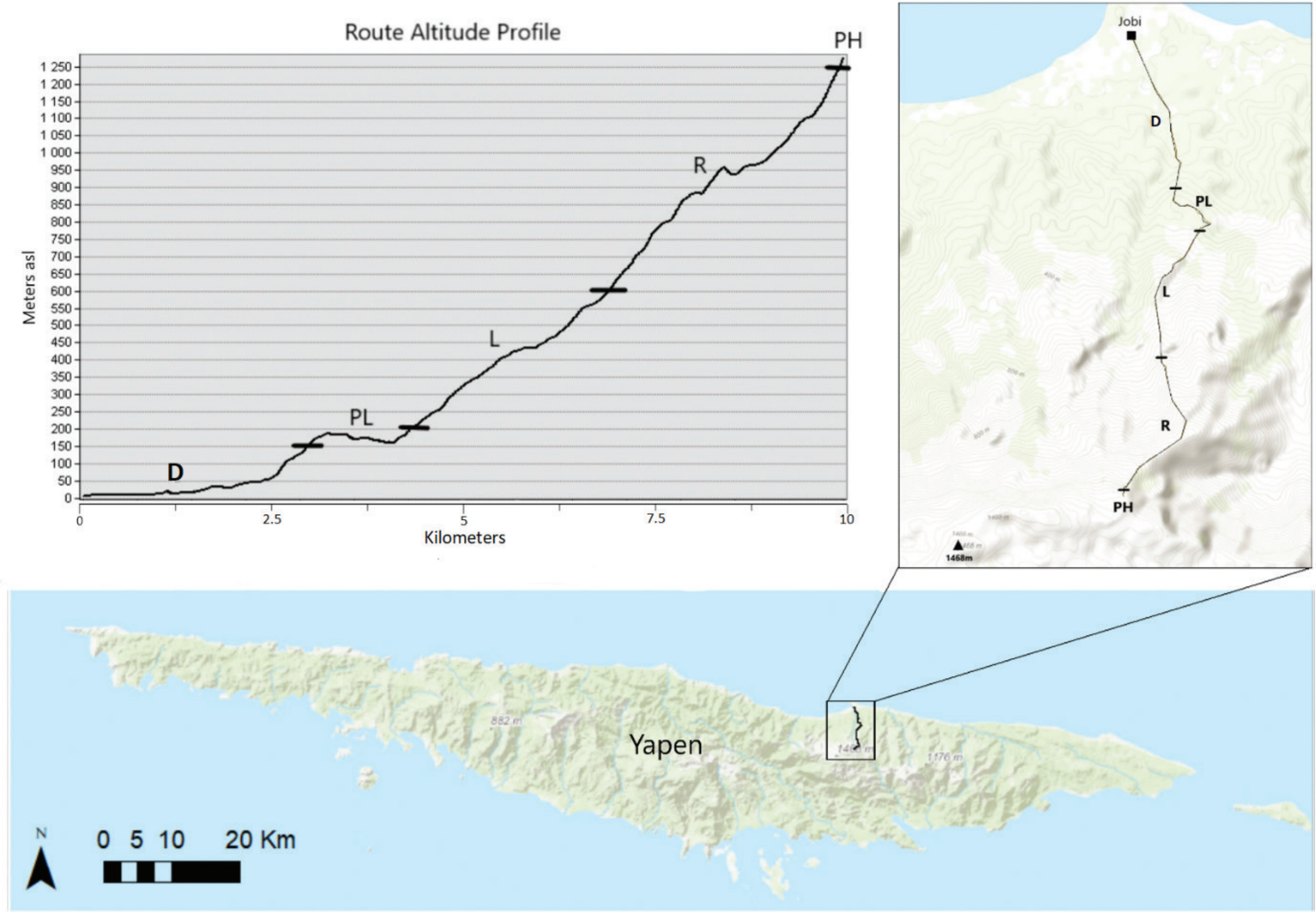

Figure 1. Survey transect of eastern Yapen Island, from the village of Jobi to the upper camp at 1,315 m.

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Figure 2. Black-eared Catbird *Ailuroedus melanotis*, Yapen Island, New Guinea, 8 September 2020 (Brecht Verhelst)

		D	PL	L	R	PH
Olive Flyrobin	*Kempiella flavovirescens*		X			
Black-chinned Robin	*Heteromyias brachyurus*			X		
White-faced Robin	*Tregellasia leucops*				X	X
Island Leaf Warbler	*Seicercus poliocephalus*					X
Green-fronted White-eye	*Zosterops minor*			X	X	
Metallic Starling	*Aplonis metallica*	X				
Red-capped Flowerpecker	*Dicaeum geelvinkianum*				X	
Number of species observed		**24**	**22**	**39**	44	25

Species accounts

BLACK-EARED CATBIRD *Ailuroedus melanotis*

We observed small groups of 5–10 individuals twice, on 8 and 9 September, at 980 and 1,300 m, and photographed two individuals. The dark throat with small pale spots, rufous-cinnamon breast with sharply contrasting dark crescents and black ear patch are suggestive of the subspecies *jobiensis*, which is also present in the Foja Mts., *c.*200 km further east in mainland New Guinea.

DIMORPHIC JEWEL-BABBLER *Ptilorrhoa* cf. *geislerorum*

A presumed male and female were observed at 980 m on 9 September by BV & JP, and a presumed male and two females on 10 September by BV at 440 m. One (presumed) male was photographed and its song sound-recorded (https://www.xeno-canto.org/566068).

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Figure 3. Presumed male Dimorphic Jewel-babbler *Ptilorrhoa* cf. *geislerorum*, Yapen Island, New Guinea, 9 September 2020 (Brecht Verhelst)

Although these observations were made at dawn and dusk, in poor light, the colour patterns could be reliably discerned. All individuals had a white throat bordered by a narrow black band that extended as a broad black mask. The three (presumed) females agreed with female *P. geislerorum* in being all dark chestnut-brown dorsally and ventrally, except the throat and mask. The (presumed) males agreed with male *P. geislerorum* in being entirely dark blue except the throat and mask, with a dull brown crown and pale superciliary. Both sexes differed greatly from Chestnut-backed Jewel-babbler *P. castanonota*, which in both sexes is blue ventrally, but dorsally largely or all chestnut-brown. Call was a loud *CHEW*, similar to that of *P. castanonota.* The song bout recorded was a repeated series of 13 accelerating, disyllabic whistles, rising in pitch. The observed colour pattern matches *P. geislerorum*, which is known from the Adelbert Mts. and north slopes of the Central Range in south-east Papua New Guinea. However, the song is very different from available recordings of *P. geislerorum* from the Adelbert Mts. and Kokoda Track in south-east Papua New Guinea, by its slower rhythm and higher max. frequency. Further study of the Yapen population is required to understand if any other differences exist vs. *P. geislerorum* and to define its taxonomic status. Collections and observations in the ranges between Yapen and the Adelberts—North Coastal Range, Cyclops, Foja and Van Rees—found only *castanonota* and Blue Jewel-babbler *P. caerulescens*, but not *geislerorum* (Beehler & Pratt 2016). If the birds on Yapen are confirmed as *geislerorum*, then the disjunct range might be explained by local extinctions in the intervening ranges. Interestingly, Diamond & Bishop (2020) found only *castanonota* during their surveys of the western uplands of Yapen, which species we did not observe. This may indicate a difference in species composition between the eastern and western uplands. Conversely, the co-occurrence of *P. geislerorum* and *P. castanonota* on the same island is not unusual. In the Herzog Mts. and Adelbert Mts., *P. geislerorum* and *P. castanonota* have been collected at nearby localities (Greenway 1935, Gilliard & LeCroy

1967), and in the Adelberts they have even been observed in the same forest (Coates 1990; J. Diamond & K. D. Bishop unpubl. obs.).

YELLOW-LEGGED FLYROBIN *Kempiella griseoceps*
One observed by BV and JP on 7 September at 440 m for several minutes, but no photo or sound-recording could be obtained. A medium-sized flycatcher with an upright posture, yellow legs and mandible, pale olive upperparts and pale yellow underparts, grey head with white throat and rather conspicuous eye-ring.

WHITE-FACED ROBIN *Tregellasia leucops*
Frequently seen above 900 m, with several individuals photographed. Apparently common at the upper elevations of our survey area. Previously, this species had been observed only in 1983 in the western uplands of Yapen (Diamond 1985), where it seems to be rare. The observed difference in abundance between the eastern and western upland sections of the island may suggest a process of ongoing local extinction.

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Description of the nest, eggs and nestling development of Maranhão Hermit *Phaethornis maranhaoensis*

by Surama Pereira, Beatriz Bacelar Barbosa & Flávio Kulaif Ubaid

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http://zoobank.org/urn:lsid:zoobank.org:pub:5520E9E2-AFEE-453E-BE22-EB5BB9458F9A

Summary.—Maranhão Hermit *Phaethornis maranhaoensis* is endemic to Brazil, where it occurs in the states of Piauí, Maranhão, Tocantins, Pará, Mato Grosso and Goiás. Nothing has been published concerning its breeding biology. We present the first descriptions of the nest, eggs and nestlings of *P. maranhaoensis*, with data on nestling development. We found four nests in the understorey of closed-canopy forest in eastern Maranhão. All four nests were attached to the undersides of babaçu palm fronds (*Attalea speciosa*), and were constructed of plant material and moss, bound together with spider webs. Nests are similar to those of other *Phaethornis*, conical and attached to the tip of the frond. They were sited at a mean height of 71.5 ± 21.3 cm above ground, and were 23.6 ± 1.8 cm in height, with an external diameter of 41.7 ± 2.7 mm, internal diameter 18.4 ± 3.7 mm, and the incubation chamber was 24.5 ± 3.1 mm deep ($n = 4$). Eggs are white and elliptical, measuring 11.9 ± 0.2 × 7.8 ± 0.1 mm, with a mean mass of 0.4 ± 0.05 g ($n = 4$). Our observations indicate that the species' breeding season occupies November–April.

Reproduction is a fundamental process in the natural history of all living organisms, but there are surprisingly large gaps in our knowledge of this process, even in relatively well-studied groups such as birds (Heming *et al*. 2013). Birds possess several different reproductive strategies and exploit a wide variety of nesting sites, which often hinder their identification and monitoring. Xiao *et al*. (2017) estimated that few or no breeding data are available for *c*.40% of the world's bird species. The lack of data on parameters such as the timing and duration of the breeding season, nest structure, and egg and clutch size, is especially apparent for Neotropical species. In fact, many taxa are known only from a few localities, with few or no data whatsoever on any aspect of their natural history (e.g. Alteff *et al*. 2019, Cleere & Sharpe 2020).

Phaethornis is a hummingbird genus endemic to the Neotropics, where it occurs from Mexico to southern Brazil and northern Argentina (Schuchmann 1999). It is the second most speciose trochilid genus, with between 25 and 29 species currently recognised (Dickinson & Remsen 2013, del Hoyo & Collar 2014, Clements *et al*. 2019, Winkler *et al*. 2020). In Brazil, as many as 18 species occur, making it the genus with the largest number of species nationally (Piacentini *et al*. 2015). Maranhão Hermit *P. maranhaoensis* is often considered a synonym of Cinnamon-throated Hermit *P. nattereri*, but the two possess apparently allopatric distributions (Mallet-Rodrigues 2006), and here we follow Piacentini *et al*. (2015) and treat *P. maranhaoensis* as a species. *P. maranhaoensis* is endemic to Brazil, found in the states of Piauí, Maranhão, Tocantins, Pará, Mato Grosso, and Goiás. The core of its geographic range lies within the Cerrado domain, although it also occurs in adjacent parts of Amazonia and the Caatinga (http://www.wikiaves.com.br). Few data are available on the natural history of *P. maranhaoensis* and its breeding biology is practically unknown (Piacentini & Ribenboim 2017, Hinkelmann & Boesman 2020a). Here, we provide the first description of the nest,

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eggs and nestlings of *P. maranhaoensis* from the Cerrado of Maranhão, with information on the growth of the nestlings.

Methods

Our observations were made in the Inhamum Environmental Protection Area (APA do Inhamum; 04°53′30″S, 43°24′53″W), municipality of Caxias, eastern Maranhão, Brazil. The APA do Inhamum covers 3,500 ha, dominated by *cerrado sensu stricto*, with some tracts of closed-canopy savanna woodland (*cerradão*) and gallery forest. In some forested areas, trees reach heights in excess of 25 m, with a dense and shady understorey, whereas in other parts the vegetation comprises shorter, more widely spaced trees that do not form a continuous canopy. The region's climate is tropical with dry winters, type *Aw* in the Köppen-Geiger classification system (Peel *et al*. 2007), with two well-defined seasons—a dry season in July–November, and a wet season in December–May, with mean annual precipitation of 1,600 mm and mean temperature 27.8°C. The study area lies in the central Itapecuru basin, an area where natural vegetation is being converted rapidly into farmland to produce cash crops, and impacted by illegal fires during the dry season.

The nests described here were encountered opportunistically during general avifaunal surveys in the APA do Inhamum. Once identified, each nest was monitored at intervals of 48 hours. Nests, eggs and nestlings were measured using a metal ruler (accurate to 1.0 mm) and callipers (0.05 mm), while the eggs and nestlings were weighed with a digital scale (0.01 g). Nest architecture was classified according to Simon & Pacheco (2005).

Results

We identified four active nests during the 2019/20 breeding season. The first was found on 18 November 2019, in an advanced stage of construction. The second was discovered on 8 December 2019, in the initial stage of building, and the third was found on 17 March 2020, when it was almost completed. The fourth nest was identified on 4 April 2020, when it contained two eggs. These observations indicate that the breeding season of *P. maranhaoensis* is from November to April, possibly until early May. Nests were of the high-cup/pensile type, and all were attached to the underside of still-growing leaves of babaçu palms *Attalea speciosa* in the understorey of *cerradão*. Nestbuilding starts with small leaves and dry twigs, which are attached to the babaçu frond with spider web (Fig. 1A). We observed the exuviae of spiders (Araneae) and grasshoppers (Proscopiidae) in the material used to construct two nests, although it was impossible to confirm if this material was brought to the nest by the birds. Nests were conical in shape, with a long 'tail-like' appendage of leaves that serves as a counterweight (Fig. 1B). The outer layer of the nest was covered with plant material and moss, attached with spider web. The internal cavity that forms the egg chamber was lined with fine whitish plant fibres. Construction of the second nest, which was encountered in the early stage of construction, took 20 additional days to be completed. None of the nests was successful. The first nest was abandoned with two eggs, one of them broken and covered in ants, while the eggs at the second nest were predated, as were the nestlings in the fourth nest. One of the nestlings in the third nest died on the 13th day of life and the other on the 17th day, both possibly victims of an infestation of *Philornis* larvae.

The nests averaged 23.6 ± 1.8 cm in height (Table 1; *n* = 4 for all parameters), with a mean outer diameter of 41.7 ± 2.7 mm, inner diameter of 18.4 ± 3.7 mm and depth of 24.5 ± 3.1 mm. Nests were sited 71.5 ± 21.3 cm above ground. When incubating the eggs, the female faces the leaf to which the nest is attached, with its head pointing upwards (Fig. 2A). All of the clutches we observed were of two eggs and the incubation period was *c*.16 days

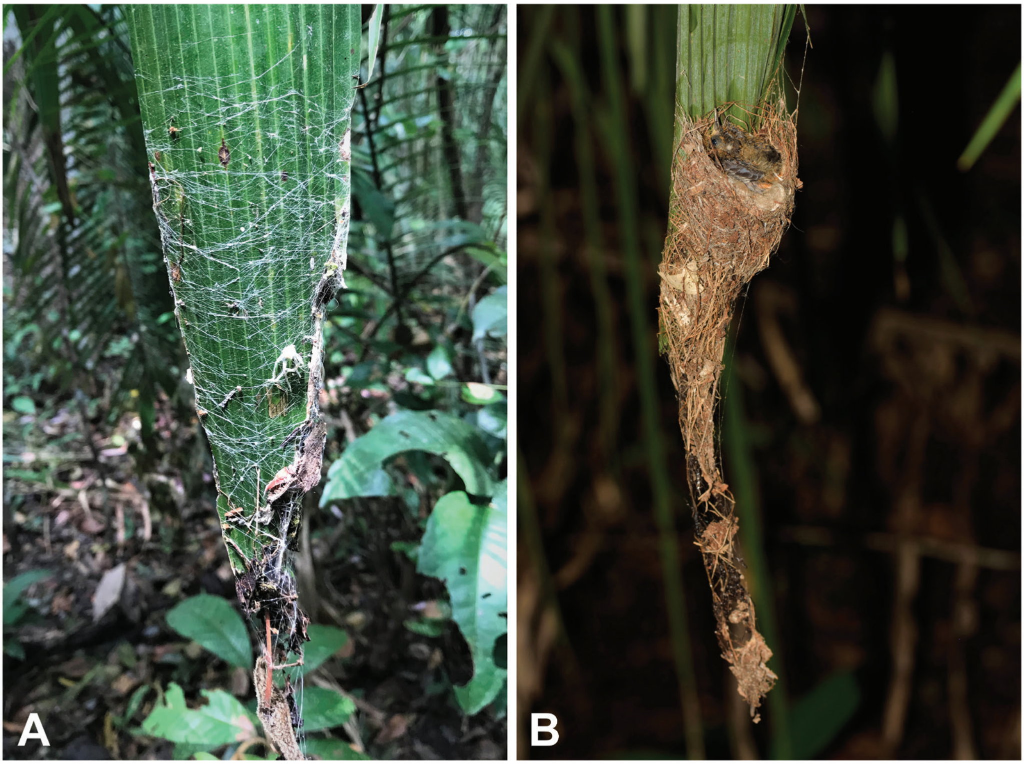

Figure 1. Architecture of a Maranhão Hermit *Phaethornis maranhaoensis* nest attached to the underside of an *Attalea speciosa* palm frond: (A) view of the upper surface of the frond, showing the spider web used to attach the nest; (B) completed nest containing two nestlings (A: Surama Pereira; B: Flávio Kulaif Ubaid).

(*n* = 1). Eggs were white and elliptical (Fig. 2B), with a mean mass of 0.4 ± 0.05 g (*n* = 4) and measured 11.9 ± 0.2 × 7.8 ± 0.1 mm (*n* = 4). Whenever the chicks at nest 4 were observed, they were invariably facing the leaf (Fig. 2C).

TABLE 1

Measurements of four Maranhão Hermit *Phaethornis maranhaoensis* nests in the Inhamum Environmental Protection Area, municipality of Caxias, Maranhão, Brazil, in 2019/20.

	N1	N2	N3	N4	$\overline{X}$	S.D.
Outer diameter (mm)	45.0	40.9	38.6	42.2	41.7	2.7
Inner diameter (mm)	21.5	15.6	21.7	14.9	18.4	3.7
Depth of the chamber (mm)	25.0	27.0	26.0	20.0	24.5	3.1
Height of the nest (mm)	24.0	26.0	22.5	22.0	23.6	1.8
Height above ground (cm)	94.0	50.0	85.0	57.0	71.5	21.3

Nestlings hatch with their eyes closed, and are almost completely naked, with 11 paired neossoptiles on the spinal tract (*pteryla dorsalis*). When they hatched, the nestlings weighed 0.43 ± 0.06 g (*n* = 3) and were 18 ± 0.3 mm in length (*n* = 2). Their skin was pinkish flesh, with a darker dorsum, yellowish bill and tarsi, well-defined whitish labial commissure, and black around the eyes. On the 17th day of life, the body of the nestling was completely feathered, yellowish on the ventral surface and greyish on the dorsal. By this age, the characteristic

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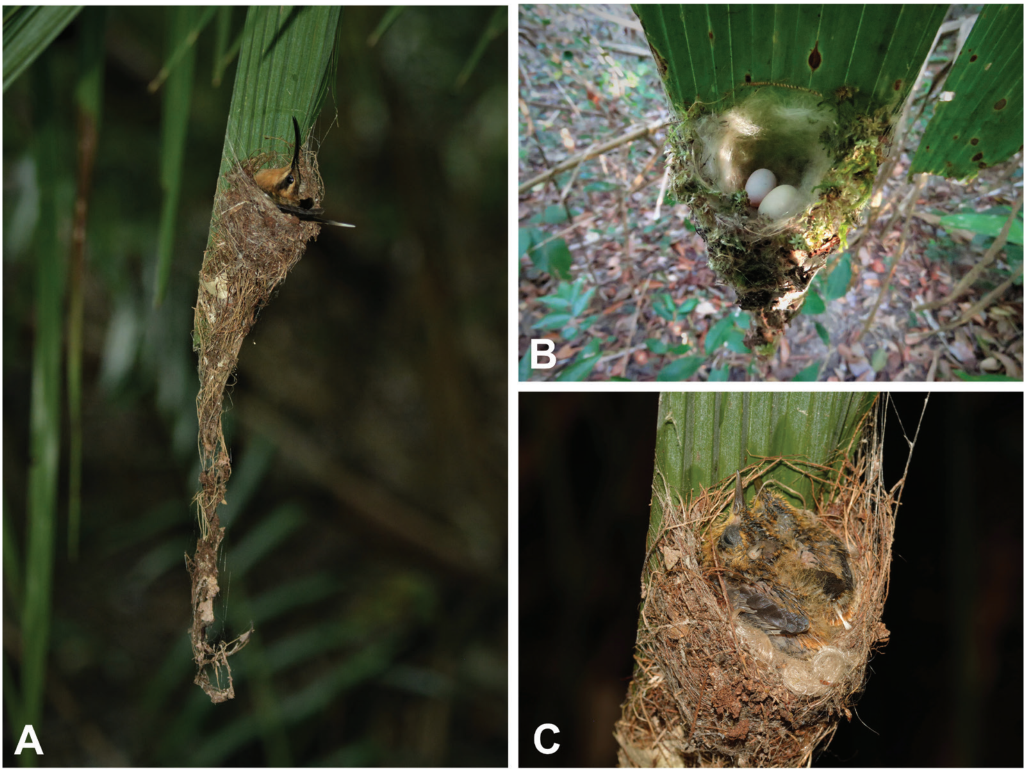

Figure 2A. Adult female Maranhão Hermit *Phaethornis maranhaoensis* incubating eggs; (B) clutch of two white, elliptical eggs; (C) detail of the nestlings when nearly two weeks old (A–C: Flávio Kulaif Ubaid; B: Surama Pereira)

white tips to the central rectrices were well defined, as were the black feathers on the wings, and the dark bill and nails. Growth of the two nestlings monitored from hatching is shown in Table 2. One nest was collected and deposited in the ornithological collection of the University of Brasília, UnB (COMB-N0735), and the others in the collection of the ornithology laboratory of the Maranhão State University (Caxias campus).

TABLE 2

Morphometric data for Maranhão Hermit *Phaethornis maranhaoensis* nestlings in the Inhamum Environmental Protection Area, municipality of Caxias, Maranhão, Brazil, 2019/20. *mean values (*n* = 2).

	Days of life													
	1	2	3	4	5	6	7	8	10	11	13	14	15	17
Mass (g)	0.4*	0.6*	0.7*	1.0*	1.0	1.4	1.7	2.2	2.5	2.8	3.2	3.3	3.3	2.9
Tarsus (mm)	-	-	2.1*	3.0	4.1	5.3	4.8	5.6	4.9	5.7	5.0	5.6	5.6	5.6
Cranium length (mm)	-	-	7.2	8.8	10.5	11.6	11.4	12.4	15.4	14.8	15.9	17.4	17.6	17.8
Culmen (mm)	-	-	3.0	3.1	3.3	3.4	5.6	6.0	5.7	6.2	6.0	6.3	7.3	7.4
Total length (mm)	18.0*	21.4*	22.4*	23.1	-	-	33.2	33.8	35.6	37.1	43.4	46.9	48	58.2

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Discussion

The present study provides the first data on nest architecture and morphology of the eggs and nestlings of *P. maranhaoensis*. The description of the nest of Cinnamon-throated Hermit *P. nattereri* (Grantsau 1989) appears to be purely speculative (Piacentini & Ribenboim 2017), and requires clarification. Nests attached to the tip of the underside of pendent leaves, or palm fronds, is typical of *Phaethornis*, and has been observed in White-bearded Hermit *P. hispidus* (Melo & Greeney 2019), White-whiskered Hermit *P. yaruqui* (Hinkelmann & Boesman 2020c), Green Hermit *P. guy* (Snow 1974), Tawny-bellied Hermit *P. syrmatophorus* (Hinkelmann & Boesman 2020b), Koepcke's Hermit *P. koepckeae* (Weske & Terborgh 1977), Needle-billed Hermit *P. philippii* (E. Endrigo; http://www.wikiaves.com.br/334168), Straight-billed Hermit *P. bourcieri* (Oniki & Willis 1982, Grantsau 1989), Long-billed Hermit *P. longirostris* (del Hoyo *et al*. 2020), Long-tailed Hermit *P. superciliosus* (Oniki & Willis 1982, 1983, Hudson 1984, Grantsau 1989), Great-billed Hermit *P. malaris* (Greeney *et al*. 2018, C. Veronese; http://www.wikiaves.com.br/1741825), Pale-billed Hermit *P. anthophilus* (Hinkelmann *et al*. 2020a), Dusky-throated Hermit *P. squalidus* (V. E. Florencio; http://www.wikiaves.com.br/1939289), Streak-throated Hermit *P. rupurumii* (R. Cavalcante; http://www.wikiaves.com.br/3035401), Little Hermit *P. longuemareus* (Skutch 1951), Minute Hermit *P. idaliae* (L. Freire; http://www.wikiaves.com.br/496871), Stripe-throated Hermit *P. striigularis* (Hinkelmann *et al*. 2020b), Grey-chinned Hermit *P. griseogularis* (Greeney *et al*. 2013), Reddish Hermit *P. ruber* (Oniki 1970, Oniki & Willis 1983, Muscat *et al*. 2014) and Scale-throated Hermit *P. eurynome* (D. Meyer; http://www.wikiaves.com.br/211551).

Like nest substrate, the architecture of the nest of *P. maranhaoensis* is similar to that of most of its congeners (e.g., Oniki 1970, Muscat *et al*. 2014, Greeney *et al*. 2013, 2018). Nests are constructed typically of plant fibres, with thick walls that shield the eggs and nestlings in lateral view. Nests of other species in the subfamily Phaethornithinae, such as *Glaucis* spp. and Saw-billed Hermit *Ramphodon naevius*, possess a simpler structure, with thinner walls, leaving the contents more visible from outside (Muscat *et al*. 2014, Lima *et al*. 2018).

Two-egg clutches are also typical of *Phaethornis* (Davis 1958, Skutch 1951, Schuchmann 1986, Muscat *et al*. 2014, Verea 2016), although Lima *et al*. (2007) reported a Planalto Hermit *P. pretrei* nest with four eggs. Morphometrics of the eggs of *P. maranhaoensis* are also consistent with those of congenerics of similar body size (Oniki 1970, Muscat *et al*. 2014), as was the nests height above ground in the understorey (Muscat *et al*. 2014, Greeney *et al*. 2018, Melo & Greeney 2019). The incubation period of *P. maranhaoensis* (16 days) is identical to that of *P. pretrei* (Lima *et al*. 2007), a slightly larger species, and similar to congeners such as *P. longuemareus* (14–15 days; Skutch 1951), *P. superciliosus* (17–18 days; Skutch 1964) and Sooty-capped Hermit *P. augusti* (20 days; Verea 2016).

Greeney *et al*. (2013) recorded 11 pairs of neossoptiles on the dorsum of recently hatched *P. griseogularis*, which is also similar to *P. maranhaoensis*. In nestlings of *P. augusti*, the pterylae is darker than the skin, with feathers emerging from the fifth day onwards (Verea 2016), while *P. pretrei* hatches entirely naked (Lima 2007). Unfortunately, few detailed descriptions of pterolysis and feather development in hummingbirds are available (Greeney *et al*. 2008), despite their potential for understanding phylogenetic relationships among species.

In general, the nest architecture and the eggs of *P. maranhaoensis* are similar to those of other *Phaethornis*. Our findings substantially advance our understanding of the species' natural history, which is still very poorly known. We encourage other researchers to focus on collecting such basic data for Neotropical birds, especially those that are still poorly known, to guarantee their effective, long-term conservation.

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Speckled Rail *Coturnicops notatus* recorded for the first time in coastal south-east Brazil

by Marcelo Bokermann, Emerson Luís Costa & Fabio Schunck

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Speckled Rail *Coturnicops notatus* is widely distributed in South America, with records in south-east Colombia, western Venezuela, Guyana, northern Argentina, north Bolivia, Paraguay, Uruguay, and south and south-east Brazil. It inhabits grassy savanna, dense marshy vegetation, rice and alfalfa fields, but has also been reported in crop stubble, humid woodland edges and urban areas; in lowlands to 1,500 m (Sick 1997, Bodrati 2005, Dias *et al*. 2016, Berbare *et al*. 2017, Taylor 2020). In Brazil, the species has been recorded in the states of São Paulo and Rio Grande do Sul (Sick 1997). Records in São Paulo (in the south-east of the country) are concentrated in the east, in the municipalities of São Paulo (São Paulo plateau) and Pindamonhangaba, Tremembé and Taubaté (Paraíba do Sul Valley). It was first noted in the municipality of São Paulo, in Ipiranga in September 1924 (Pinto 1938), but was not recorded again until May 2019 in Itaim Paulista (in the east of the city), when one was found in a house and subsequently released near Tremembé (A. Magalhães pers. comm.). The species has been known in the Vale do Paraíba since the 1930s, always in flooded rice fields between April and August, and this part of São Paulo has the most records of the species (Pinto 1938, Teixeira & Puga 1984, Sick 1997, Willis & Oniki 2003, Taylor 2020). Although there is some evidence of even long-distance displacement or dispersal, seasonal migration is not definitely known (Blake 1977, Taylor 2020). As it is one of the least known members of the Rallidae, all available information is important to better understand the species' range and natural history.

On 23 May 2020, at *c*.10.00 h, an adult *C. notatus* was photographed by G. L. Cunha & T. Novaes de Senne within the SESC Bertioga (23°49'36.49"S, 46°06'40.44"W; 10 m), in the urban area of Bertioga, on the coast of São Paulo state (Fig. 1). The SESC is surrounded by 3–4 m-high walls, and the bird was 1 km from the sea in an area with many plants, a small vegetable garden, and an artificial water source, forming an environment akin to a natural flooded area. The bird was catching small insects and only hid in the vegetation when the observers approached to within less than 2 m. On 22–23 May, eastern São Paulo, including the coast, experienced very strong winds of *c*.30–40 km/h, associated with the arrival of a cold front from the south.

The bird was seen again on 24 May in the same place, again feeding on insects (Fig. 2). At about 10.00 h, it entered a house. As domestic cats were present, the bird was captured to prevent its predation. Biometrics were taken, and blood collected for subsequent sexing, now deposited at the Laboratory of Genetics and Molecular Evolution of Birds (LGEMA), University of São Paulo. It was marked with a category G metallic band from the Centro Nacional de Pesquisas e Conservação de Aves Silvestres (CEMAVE) of ICMBio. At around 15.00 h, we released the bird in an area owned by SESC Bertioga, *c*.1.3 km from where it was captured. This area possesses different types of flooded environments, open areas with low vegetation and an extensive forest bordering the Itapanhaú River (Fig. 1). During the period the bird was held it fed on mealworm larvae (*Tenebrio molitor*) and exhibited no obvious stress.

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Figure 1. Eastern São Paulo state, south-east Brazil, with records of Speckled Rail *Coturnicops notatus*. São Paulo municipality (city of São Paulo): (1) Ipiranga, (2) Itaim Paulista; Paraíba do Sul Valley: (3) Taubaté, (4) Tremembé, (5) Pindamonhangaba; and coastal São Paulo: (6) Bertioga, A: main SESC Bertioga (public use); B: SESC Bertioga Reserve (restricted use) (© Google Earth, Landsat / Copernicus 2015)

Figure 2. Speckled Rail *Coturnicops notatus* in the environment where it was initially found (Emerson Luís Costa)

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Figure 3. The Speckled Rail *Coturnicops notatus* after banding (Fabio Schunck)

Figure 4. Details of the wing of the Speckled Rail *Coturnicops notatus* (Fabio Schunck)

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Figure 5. Sequence of images (left to right, top to bottom) showing the release of the Speckled Rail *Coturnicops notatus* (Fabio Schunck)

The *C. notatus* was an adult (25 g) with no apparent injury (Fig. 3). Mensural data: wing 73 mm, tail 33 mm, tarsus length 21.6 mm, tarsus diameter 3.1 mm, exposed culmen 18.5 mm and nostril to tip of bill 6.4 mm. It had no ectoparasites, active moult or incubation patch, but it had recently completed a moult (Fig. 4). The bird also lacked subcutaneous fat and had partially reduced chest muscles (category 2). The bird made three short sequential calls when captured, and twice emitted a low, hoarse call while being banded, but the vocalisations were not recorded. Playback was made before handling, release, and post-release, using several recordings (including those made by Dias *et al.* 2016), but the bird did not respond. On release, it walked calmly out of the cage where it was held and disappeared into the low vegetation within a few seconds (Fig. 5).

The SESC Bertioga is 48 km from Itaim Paulista in the city of São Paulo (at 735 m), where a *C. notatus* was found in 2019, and *c.*100 km from Tremembé (also on the plateau, in the high part of the Paraíba do Sul Valley, 560 m). This rail has also been recorded in Rio Grande do Sul, including the coast (Maurício & Dias 1996, Dias *et al.* 2016, Berbare *et al.* 2017), but until now there were no records in coastal São Paulo (e.g. Olmos & Silva e Silva 2003, Willis & Oniki 2003, Silva e Silva & Olmos 2007, 2020, Simpson *et al.* 2012; https://ebird.org; http://www.wikiaves.com.br, http://www.xeno-canto.org). The municipality of Bertioga possesses many natural wet areas, including around SESC Bertioga where ten species of Rallidae had been recorded previously (Bokermann & Pivelli 2019). However, in June 2018, a small, dark rail with some characters similar to *C. notatus* was observed by E. Gonçalves de Santana beside the Jaguareguava River, on the right bank of the Itapanhaú (23°49′50.09″S, 46°10′7.84″W; 10 m), *c.*6 km from SESC Bertioga.

The record at SESC Bertioga represents the third locality for the species in São Paulo, the first for coastal south-east Brazil, and the second anywhere on the country's coastal plain (after that in Rio Grande do Sul). It is the first individual in Brazil to be marked with a CEMAVE band. We consider that two principal hypotheses could explain this record: (1) the individual was forced into the SESC by the strong winds at the time, either from the São Paulo plateau, the Vale do Paraíba or elsewhere; or (2) the species is present somewhere in the Bertioga region but had previously been overlooked.

This record of *C. notatus* made by local people highlights the importance of a community environmental education programme ('Projeto Avifauna'), operated by SESC Bertioga since 1992. Bird observations are made by the Clube de Observação de Aves de Bertioga and there

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is a replanting initiative using native species to attract local fauna. It also installs feeders and, via courses, informs people about the importance of birds and protecting nature. This work has already provided other important records for the Bertioga region, such as a Uniform Crake *Amaurolimnas concolor* found dead in the SESC in August 2018, also during the coldest period of the year. It appears that coastal south-east Brazil should be included in the search area for Speckled Rail, one of the least known bird species in Brazil.

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Nest design and parental care of Striped Woodhaunter *Automolus subulatus*

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Summary.—The western and trans-Andean populations of Striped Woodhaunter *Automolus subulatus* are sometimes considered separate species. We discuss previously published data on the nesting of Striped Woodhaunter and present novel information concerning the nest, eggs, nestlings and parental care of western *A. s virgatus* and trans-Andean *A. s. subulatus*. Nest placement and architecture of the two populations are similar to each other and to other *Automolus* species. However, Striped Woodhaunter build shorter nest tunnels than other related species and genera. All similarities in nest design, nestbuilding behaviour and parental care presented herein support the genetic clade including *Automolus*, *Thripadectes* and *Clibanornis*, but do not differentiate between the subspecies of Striped Woodhaunter. More studies are required about adult attendance and nest design within this clade, taking into account more samples across the species' range.

The systematics of the non-monophyletic genus *Automolus* (Furnariidae: Philydorini) are still under scrutiny (Claramunt *et al*. 2013, Schultz *et al*. 2017). The most recent changes that have gained acceptance are the subsuming of *Hyloctistes* within *Automolus* (Claramunt *et al*. 2013) and the splits of Pará Foliage-gleaner *A. paraensis* from Olive-blacked Foliage-gleaner *A. infuscatus* (Claramunt *et al*. 2013, Clements *et al*. 2019) and Chiriquí Foliage-gleaner *A. exsertus* from Buff-throated Foliage-gleaner *A ochrolaemus* (Freeman & Montgomery 2017, Chesser *et al*. 2018). Like other furnariids (Irestedt *et al*. 2006), nesting behaviour and nest architecture of *Automolus* spp. may prove useful for testing DNA-based taxonomic arrangements. However, the nesting biology of *Automolus* species is well known only for Chiriquí Foliage-gleaner (Skutch 1952, 1969) and White-eyed Foliage-gleaner *A. leucophthalmus* (Euler 1900, J. C. R. Magalhães *in* Remsen 2003a, Marini *et al*. 2007, Cockle & Bodrati 2017) but poorly known or unpublished for the other seven species (Remsen 2003a).

Striped Woodhaunter *A. subulatus* is distributed from eastern Nicaragua south to western Ecuador and, east of the Andes, from southern Venezuela and south-east Colombia to northern Bolivia and western Amazonian Brazil (Stiles & Skutch 1995, Remsen 2003a). Some authors treat western and trans-Andean populations as separate species, Western Woodhaunter *A. virgatus* and Amazonian Woodhaunter *A. subulatus* (Ridgely & Greenfield 2001, Hilty 2003, del Hoyo & Collar 2016) based largely on vocal differences (Ridgely & Tudor 1994, Freeman & Montgomery 2017). This split is considered premature by other authorities (see Remsen 2003b) and herein we follow Clements *et al*. (2019). Here we discuss and clarify published data on the nesting of Striped Woodhaunter and present novel information concerning the nests, eggs, nestlings and parental care for two subspecies, *A. s. virgatus* and *A. s. subulatus*.

Historical data for A. s. subulatus and A. s. assimilis.—The first published nest description attributed to Striped Woodhaunter was presented by Sclater & Salvin (1873). They quoted the notes of E. Bartlett, which accompanied a specimen of *A. subulatus* collected at Chamicuros, Loreto, eastern Peru (05°30′S, 75°30′W, *sensu* Stephens & Traylor

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TABLE 1

Monitoring dates, localities, nest contents and main observations of Striped Woodhaunter *Automolus subulatus* nests found in western Colombia (nest 1; Zyskowski & Prum 1999, Hilty 2003; K. J. Zyskowski *in litt*. 2018), in central-west Costa Rica (nest 2) and in eastern Ecuador (nests 3–7).

Nest	**Date found**	**Days monitored**	**Location/elevation**	**Coordinates**	**Nest contents**	**Observations**
1	15 Feb 1976		San Isidro, Buenaventura, dpto. Valle del Cauca, Colombia	03°27′0″N 77°10′0″W	2 nestlings	Nestlings more than half-grown
2	19 Dec 2002		Finca Rafiki Safari Lounge, Santo Domingo, Perez Zeledón, prov. San José, Costa Rica; 130 m	09°27′41″N 83°59′39″W	1 egg	Egg: 28.1 × 21.0 mm
3	15 May 2004	15–20 May 2004 and 25 Jun 2004	Near La Selva Jungle Lodge, *c*.75 km north-east of Coca, adjacent to Lake Garzacocha, prov. Sucumbíos, Ecuador; 250 m	00°29′53″S 76°22′23″W	2 fresh eggs	Eggs: 24.2 × 17.2 and 22.8 × 17.1 mm. Adult behaviour documented on video.
4	17 Feb 2012	17, 20, 25 Feb 2012	Cabañas Yankuam, south of río Pastaza, south (right) bank of río Nangaritza, prov. Zamora-Chinchipe, Ecuador; 1,100 m	04°15′0″S 78°39′30″W	empty	Burrow excavation.
5	26 Sep 2012	26 Sep 2012	Boanamo, near the prov. Pastaza/Orellana border, Ecuador; 230 m	01°15′45″S 76°22′54″W	2 eggs (1 inviable*)	Eggs: 24.2 × 17.8 and 23.7 × 17.9* mm; mass: 3.8 and 3.5 g.
6	5 Mar 2013	5, 7, 8, 10 Mar 2013	Gareno Lodge, south of río Napo, prov. Napo, Ecuador; 400 m	01°01′59″S 77°23′42″W	empty	Nest cup construction. Adult behaviour documented on video.
7	6 Mar 2013	7, 10 Mar 2013	Gareno Lodge, south of río Napo, prov. Napo, Ecuador; 400 m	01°02′01″S 77°23′15″W	2 eggs, 1 hatched	Eggs: 25.4 × 18.5 and 25.4 × 18.5 mm; mass: 4.2 and 4.3 g. Nestling mass: 4.7 g. Adult behaviour documented on video.

1983). However, the description, of a cup nest built 2–3 m above ground among dead palm fronds and holding two spotted eggs, is clearly in error, as first noted by Zyskowski & Prum (1999). The last-named authors provided the only other published information on the nest architecture of Striped Woodhaunter, including a photograph, based on a nest collected by N. Wheelwright in western Colombia (nest 1; Table 1). This nest was described as a platform-like cup of loosely interlaced leaf petioles placed at the end of an earth tunnel, and the photograph revealed two nestlings probably less than half-grown at the time of discovery (Zyskowski & Prum 1999). K. Zyskowski (*in litt*. 2018) kindly provided additional details (Table 1) on this nest which, based on its locality, is attributable to *A. s. assimilis*.

***Nest and egg of A. s. virgatus*.**—We examined a nest of *A. s. virgatus* collected by J. E. Sánchez & E. M. Carman at Finca Rafiki Safari Lounge, Costa Rica (nest 2; Table 1), and deposited at the Museo Nacional de Costa Rica, San José (MNCR-ONH772). Sánchez *et al*. (2004) provided a habitat description for the locality. Nest 2 was collected from a burrow excavated in a dirt bank adjacent to a forest trail (cavity with tunnel, *sensu* Simon & Pacheco 2005), with an expanded inner chamber at the end of a tunnel. The nest itself was a shallow, platform-like cup composed entirely of loosely interwoven leaf rachises (Fig. 1A). We detected both leaflet scars and extra-floral nectaries on most of the rachises, suggesting that they were probably from a plant in the family Fabaceae. No additional details concerning the burrow are provided on the specimen label, but we were able to measure the nest platform (Table 2; on Fig. 2, see measurements 10–15). A single, unmarked white egg

Figure 1. (A) Nest of Striped Woodhaunter *Automolus subulatus virgatus*, collected at Finca Rafiki, Santo Domingo, Perez Zeledón, San José Province, Costa Rica (nest 2) (© Alberto Pérez). (B) Immaculate white egg found in the nest (Karla Conejo-Barboza)

accompanied the nest (MZUCR-H205; Table 1; Fig. 1B) but the specimen label provides no details regarding clutch size or egg development. The size of the hole opened in the egg, however, suggested that it may have contained a well-developed embryo when collected.

Nests of A. s. subulatus.—HFG studied five nests of *A. s. subulatus* found between 2004 and 2013 at four localities in eastern Ecuador (Table 1): near La Selva Jungle Lodge (nest 3; Fig. 3A), Cabañas Yankuam (nest 4), Boanamo (nest 5; Fig. 3B–C) and Gareno Lodge (nests 6–7; Fig. 3D). Habitat was similar at all four localities, all representing mosaics typical of relatively undisturbed western Amazonian forest (see Greeney 2017, Greeney *et al*. 2018 for detailed descriptions). HFG visited the nests periodically to ascertain their status and contents. He checked nest contents either directly or using a small lighted mirror, and made direct observations of adult behaviours. When possible to document nest attendance by adults, he filmed nest activity at nests 3, 6 and 7 (Table 1) by placing a video camera on a tripod 1.5 m tall, 3 m from the nest entrance. Due to its position the video camera could not film activity within the inner chamber. Behaviour of the adults appeared to be unaffected by the presence of the camera.

All Ecuadorian nests were sited in earth burrows (cavity with tunnel, *sensu* Simon & Pacheco 2005) as described for *assimilis* and *virgatus* with entrances at a mean height of 124 cm (range = 60–230 cm; SD = 63.5 cm; Table 2) above ground (Fig. 2, measure 1). Nest 3 was in the root mass of an overturned *Cecropia* tree (Urticaceae), nest 4 was in a 1.5 m-tall bank with a 60 cm overhang along a road-cut, nest 5 was in streamside bank below an overhang of dirt and roots, and the other two nests were in the large (*c*.3 m tall) root masses of trees felled by wind action. The burrows' entrances led to tunnels that varied in slope from downward at a *c*.30º angle (nest 3) to sloping slightly upward, and opened into enlarged chambers containing the nest (nests 6 and 7). Nest cups of *A. s. subulatus* were platform-like structures of loosely arranged, stiff, unbranched leaf rachises that were barely sufficiently cohesive to remain intact when removed from the burrow. In the case of nest 5 (Fig. 3B), all rachises appeared to be from the same species of plant, but the taxonomic affinities of the nest materials were not examined closely at the other nests.

Measurements of *A. s. subulatus* burrows (Table 2; Fig. 2, measurements 2–9) were: entrance height = 7.1 cm (6.0–8.5 cm; SD = 1.1 cm; *n* = 4) and entrance max. diameter = 9.1 cm (8–11 cm; SD = 1.3 cm; *n* = 4); min. tunnel height = 5 cm (*n* = 1); tunnel width = 8.5 cm (7–10 cm; SD = 2.1 cm; *n* = 2); tunnel length (from entrance lip to start of inner chamber) =

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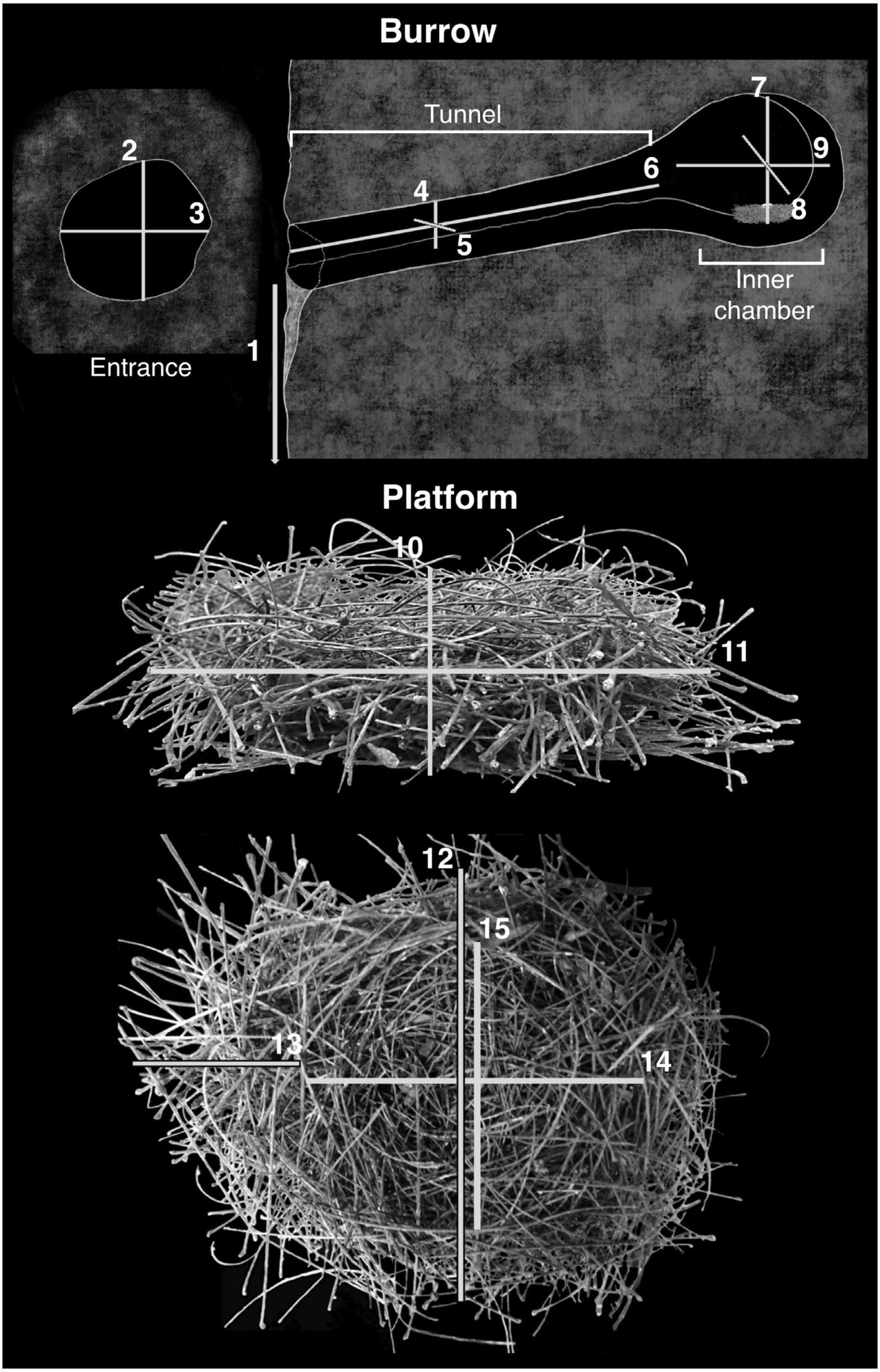

Figure 2. From top to bottom: schematic internal view of the burrow of a nest of Striped Woodhaunter *Automolus s. subulatus*, based on those found in eastern Ecuador (nests 3 and 5) and, a lateral and superior view of the platform nest of *A. s. virgatus* collected in central-west Costa Rica (nest 2). As in Table 2, numbers correspond to burrow height (1), entrance height (2), entrance max. diameter (3), tunnel height (4), tunnel max. diameter (5), tunnel length (6), inner chamber height (7), inner chamber max. diameter (8), inner chamber min. diameter (9), platform height (10), external max. diameter (11), external min. diameter (12), wall thickness (13), internal max. diameter (14), internal min. diameter (15) (Karla Conejo-Barboza)

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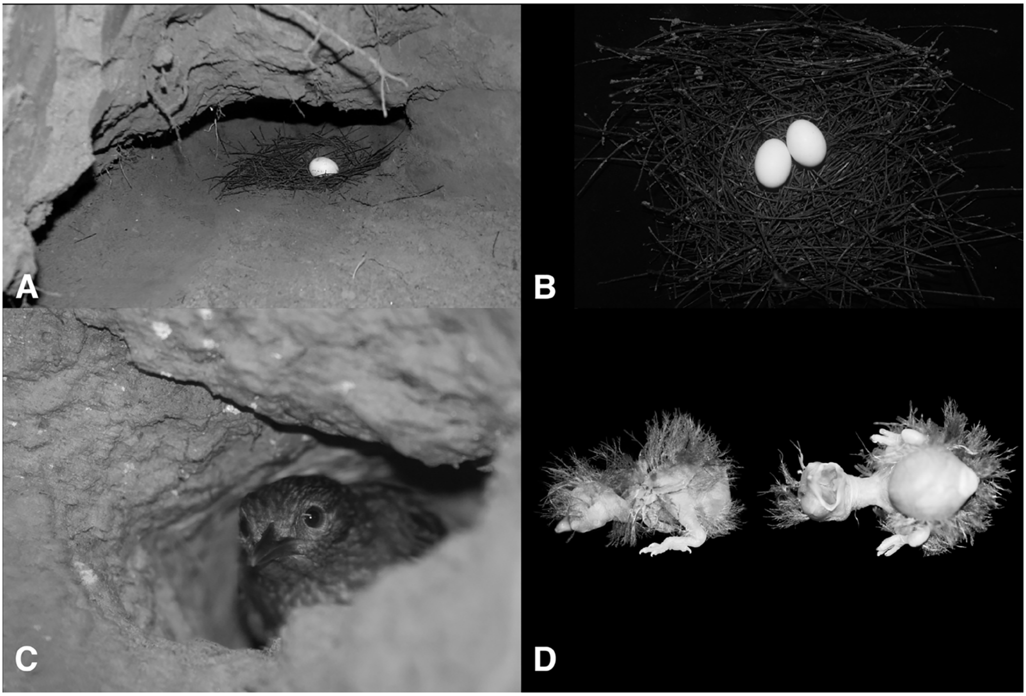

Figure 3. (A) Inner chamber and nest platform of Striped Woodhaunter *Automolus s. subulatus*, found near La Selva Jungle Lodge, *c.*75 km north-east of Coca, adjacent to Lake Garzacocha, Sucumbíos province, Ecuador (nest 3). (B) Nest platform, eggs and (C) an adult Striped Woodhaunter *A. s. subulatus*, found at Boanamo, near the Pastaza and Orellana province border, Ecuador (nest 5). (D) Chicks of Striped Woodhaunter *A. s. subulatus*, found in a nest at Gareno Lodge, south of the río Napo, Napo province, Ecuador (nest 7) (Harold F. Greeney)

26.3 cm (20–31 cm; SD = 5.2 cm; *n* = 4). Inner chamber height = 11 cm (10–12 cm; SD = 1.4 cm; *n* = 2); inner chamber max. diameter = 18 cm (13–23 cm; SD = 7.1 cm; *n* = 2); inner chamber min. diameter = 14 cm (12–16 cm; SD = 2.8 cm; *n* = 2). The inner chamber max. and min. diameter were measured perpendicular to each other on the horizontal plane (Fig. 2). HFG measured only the platform of nest 5 (Fig. 2).

***Eggs and nestlings of A. s. subulatus*.**—The complete clutch at three of the five *A. s. subulatus* nests comprised two immaculate white eggs, although some were slightly stained pale brown, probably from the surrounding earth of the inner chamber (Fig. 3A–B).When the adults were not at the nests, HFG measured and photographed the eggs (nests 3, 5 and 7; Table 1; Fig. 3A–B) and one newly hatched nestling (nest 7; Table 1; Fig. 3D). Mean measurements of six eggs were 24.3 mm (22.8–25.4 mm, SD = 1.0 mm; Table 1) × 17.8 mm (17.1–18.5 mm, SD = 0.6 cm; Table 1). The masses of three eggs with advanced embryonic development were 4.1 g (3.8–4.3 g; SD = 0.3 g; Table 1). An undeveloped and slightly damaged egg weighed during the latter half of incubation had a mass of 3.5 g (nest 5). On HFG's final visit to nest 7 (Table 1), at 16.30 h, it contained a single nestling that probably hatched on the morning of the same day based on its physical appearance and mass. The second egg was lightly pipped, suggesting that the eggs' hatching would occur *c.*24 hours apart. The nestling weighed 4.7 g. It had long, densely plumose, grey natal down on its capital, spinal dorsal, spinal pelvic, alar, ventral sternal, femoral and crural regions (*sensu* Proctor & Lynch 1993). The skin was pinkish, including the tarsi and toes, with the cloaca and surrounding skin noticeably more whitish. Its nails were dusky white, as was the bill,

TABLE 2

Measurements (cm) of all Striped Woodhaunter *Automolus subulatus* nests that we found, in central-west Costa Rica (nest 2) and eastern Ecuador (nests 3–7). Ent. = entrance, max. = maximum, diam. = diameter, I. cham. = Inner chamber, min. = minimum, Ext. = external, Int. = internal. Numbers in parentheses correspond to the measurement's numbers in Fig. 2.

Measurements	**Nest 2 (cm)**	**Nest 3 (cm)**	**Nest 4 (cm)**	**Nest 5 (cm)**	**Nest 6 (cm)**	**Nest 7 (cm)**
Burrow height (1)		110	120	230	60	100
Ent. height (2)		7.5		8.5	6	6.5
Ent. max. diam. (3)		11		9	8	8.5
Tunnel height (4)		5				
Tunnel max. diam. (5)		10		7		
Tunnel length (6)		31		20	24	30
I. cham. height (7)		12		10		
I. cham. max. diam. (8)		23		13		
I. cham. min. diam. (9)		16		12		
Platform height (10)	4.2					
Ext. max. diam. (11)	14.9			14		
Ext. min. diam. (12)	12.4					
Wall thickness (13)	3.4					
Int. max. diam. (14)	6.2			5.5		
Int. min. diam. (15)	6.0					
Depth (16)	1.9			1.5		

except the dusky-grey tip. The prominent egg tooth, tomia and inflated rictal flanges were bright white and the mouth lining was pale pink, similar to the skin colour (Fig. 3D).

Behaviour of A. s. subulatus adults.—At two nests (4 and 6) HFG observed nest construction over the course of 3–4 days. Nest 4 was visited three times during burrow excavation and, when first found, was *c*.10 cm deep. Three days later the tunnel was *c*.1.5 cm deeper, and eight days after discovery it was *c*.15 cm deep. A single adult was flushed from the nest on both the first (09.30 h) and final (14.30 h) visits. On both occasions the adult emerged with soil on its bill, flew directly into dense vegetation 3–5 m from the nest, and vocalised continually for the 4–5 minutes that HFG remained at the nest. The vocalisation, presumably an alarm call, was nearly identical to that recorded at a nearby locality by B. M. Whitney, given by an adult in response to playback of the same vocalisation (www.xeno-canto.org/86344). HFG was unable to determine if both sexes participated in excavation. The burrow of nest 6, when discovered, contained an empty but apparently fully formed nest. HFG visited the nest six times over the course of five days, between 06.15 h and 17.00 h, without observing an adult. Three days after discovery, during one hour of video observation (08.30–09.30 h), HFG recorded a single adult visit. The adult, of unknown sex, arrived with a single leaf petiole in its bill and remained in the burrow for *c*.3 minutes before flying away.

When first encountered, nest 3 contained a single egg showing no signs of development and a second with a tiny (>1 mm) embryo. Based on the experience of HFG with the embryonic development of numerous tropical suboscine passerines, we estimate that the clutch was completed 2–4 days prior and suspect that the undeveloped egg was inviable. HFG recorded adult incubation rhythms (on/off-bouts), between 06.00 h and 18.00 h (sunrise to sunset) on the five consecutive days following discovery of nest 3. As he was able to record only entrances and exits at the nest burrow, he inferred that the eggs were covered during the entire period an adult was inside. Both adults incubated the eggs, as evidenced by the observation of adults replacing each other at the nest, but HFG could not distinguish the sexes. During the entire observation period, adults spent 63.5% of daylight hours warming the eggs. Daily percentage attendance for the five days was 64.5, 43.4, 37.2, 79.2 and 80.0%, respectively. On HFG's final visit to nest 7 (Table 1), direct observations of adults at the nest revealed that both brooded the nestling and delivered single, very small (1–3 mm) prey items.

Discussion

The nest placement and architecture of the three Striped Woodhaunter subspecies reported here are similar to those reported for other *Automolus* (*A. leucophthalmus*: Euler 1900, J. C. R. Magalhães *in* Remsen 2003a, Marini *et al*. 2007, Cockle & Bodrati 2017; *A. ochrolaemus*: Van Tyne 1926; *A. paraensis*: Snethlage 1935, Pinto 1953; *A. exsertus*: Skutch 1952, 1969). In particular, the exclusive use of leaf rachises in nest construction appears to be ubiquitous in *Automolus*, but their nests are otherwise similar in form and placement to the nests of related genera (*Thripadectes*, *Clibanornis* and Buff-fronted Foliage-gleaner *Philydor rufum*: Derryberry *et al*. 2011) being platforms of loosely woven material placed at the end of upward-angled earth burrows (Skutch 1969, Kiff *et al*. 1989, Strewe 2001, Remsen 2003a, Maillard *et al*. 2006, Faria *et al*. 2008, Botero-Delgadillo & Guayara 2009, Zyskowski & Greeney 2010, Miller *et al*. 2012, Smith & Londoño 2013, Cockle & Bodrati 2017). The nest descriptions reported here demonstrate that general nest placement and design support the strong relationship within genera of the *Automolus-Thripadectes-Clibanornis* clade (see Cockle & Bodrati 2017), and do not appear to vary between currently recognised subspecies or populations of Striped Woodhaunter (Remsen 2003a, Clements *et al*. 2019).

Perhaps of significance, we found that tunnel length of Striped Woodhaunter burrows is generally shorter (26.3 cm; 20–31 cm; SD = 5.2 cm) than reported for related genera (81.4 cm; 38–200 cm; SD = 47.5 cm; Van Tyne 1926, Remsen 2003a, Marini *et al*. 2007, Faria *et al*. 2008, Botero-Delgadillo & Guayara 2009, Zyskowski & Greeney 2010, Miller *et al*. 2012, Cockle & Bodrati 2017). We know from other burrow nesters that habitat and nest design (e. g., entrance size and orientation, and tunnel length) may be important for the regulation of appropriate nest microclimates (Ellis 1982, Haggerty 1995, Ke & Lu 2009). The single nest of *A. s subulatus* that we observed with a downward-sloping entrance tunnel (nest 3), may reflect regional variation in architecture based on local microclimate or, alternatively, may have been an error by the adults or one forced by roots, rocks, or other obstructions within the substrate.

At present, we are unable to confirm that both sexes of Striped Woodhaunter participate in burrow excavation and nest construction, as is known for some species in the *Automolus-Thripadectes-Clibanornis* clade (see Cockle & Bodrati 2017). We can confirm, however, that both parents participate in incubation and chick provisioning. This behaviour is shared among most furnariids including all members of the *Automolus-Thripadectes-Clibanornis* clade studied to date (Remsen 2003a, Cockle & Bodrati 2017) but differs vs. other relatives in the Philydorini (*sensu* Derryberry *et al*. 2011), e.g., Ochre-breasted Foliage-gleaner *Anabacerthia lichtensteini* and Sharp-billed Treehunter *Heliobletus contaminatus*, which have uniparental care (Cockle & Bodrati 2017). Although based on relatively small sample sizes, it appears that parental attendance during incubation may be higher in Striped Woodhaunter (63.5%) than has been reported for Chiriquí Foliage-gleaner (58.0%: Skutch 1952). A preliminary interpretation of these data might be that the shorter entrance tunnels of Striped Woodhaunter burrows, which may promote more rapid loss of heat within the nest (Ke & Lu 2009), may promote improved attendance. We suggest that further

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information on adult attendance and nest design within this group may uncover interesting correlations. Furthermore, the seemingly rare occurrence of downward-inclined burrows in Striped Woodhaunter merits further investigation.

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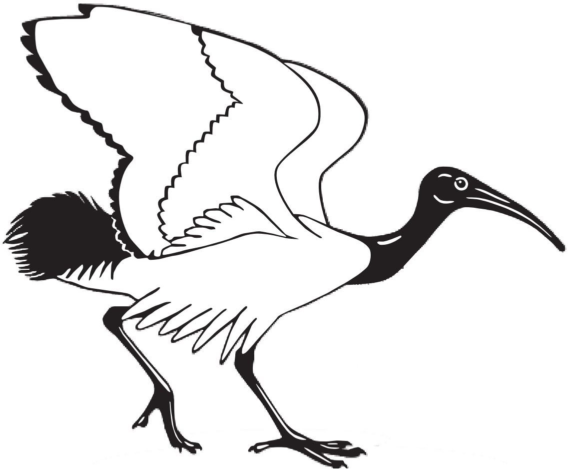

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