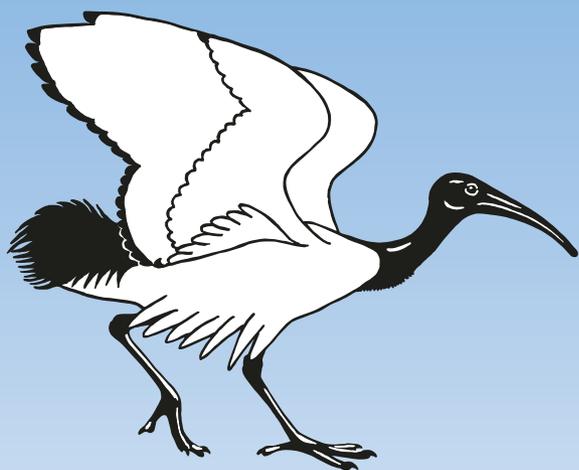


# Bulletin of the British Ornithologists' Club

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# Bulletin of the BRITISH ORNITHOLOGISTS' CLUB

Vol. 139 No. 2

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## CLUB ANNOUNCEMENTS

The 993rd meeting of the Club was held on Monday 18 March 2019 in the upstairs room at the Barley Mow, 104 Horseferry Road, London SW1P 2EE.

Twenty-nine people were present: Miss H. Baker, Miss A. H. Belman, Mr P. J. Belman, Mr R. Bray, Cdr. M. B. Casement, Mr S. Chapman, Dr J. Day (*Speaker*), Mr G. Davison, Mr G. de Silva, Mrs N. de Silva, Mr G. Hazlehurst, Mr R. Dickey, Miss J. James, Mr G. M. Kirwan, Mr R. W. Malin, Dr C. F. Mann, Mr D. J. Montier, Mr S. Portugal, Mr R. Price, Mr R. Pritchett, Mr D. Prŷs-Jones, Dr R. Prŷs-Jones, Mr R. Prytherch, Mr A. Reaney, Dr P. Rudge, Dr D. G. D. Russell, Mr S. A. H. Statham, Mr C. W. R. Storey (*Chairman*), Mr J. Verhelst.

Julia Day gave a talk entitled *Continental vs. island evolution of a 'great speciator': resolving the Zosterops taxonomic conundrum*. Different environments, such as islands and continents, have had profound effects on how biodiversity is shaped. While evolutionary processes are predicted to follow different patterns in island and mainland radiations, the extent to which these geographical contexts influence evolutionary trajectories remains poorly understood. This is in part because few studies have focused on species-rich groups of highly dispersive animals, which can colonise both continents and extensive archipelagos over comparable timeframes. In this talk Julia focused on how resolving the evolutionary relationships of white-eyes (*Zosterops*)—lauded as a 'great speciator'—in Africa, Arabia and associated islands, combined with morphological data, has allowed us to better understand evolutionary processes across these different geographic landscapes. Julia also discussed how museum collections and genetic data have aided in the task of deciphering the tricky and sometimes infuriating taxonomy of this highly cryptic group, leading to a likely substantial increase in mainland species.

The 994th meeting of the Club was held Monday 20 May 2019 in the upstairs room at the Barley Mow, 104 Horseferry Road, London SW1P 2EE.

Twenty-six people were present: Miss A. H. Belman, Mr P. J. Belman, Mr R. Bray, Cdr. M. B. Casement, Mr S. Chapman, Dr R. A. Cheke, Mr O. Crimmen, Mr G. de Silva, Miss J. Hatton, Dr J. Hume (*Speaker*), Mr R. Langley, Mr R. W. Malin, Dr C. F. Mann, Mr D. J. Montier, Mr E. Masotti-Black, Miss E. Nicholls, Miss B. Okamura, Mr A. Pittman, Dr S. Pringle, Mr R. Price, Mr D. Prŷs-Jones, Dr R. Prŷs-Jones, Mr R. Prytherch, Dr D. G. D. Russell, Mr S. A. H. Statham, Mr C. W. R. Storey (*Chairman*).

Dr Julian Hume gave a talk entitled *Birds of Lord Howe Island: past, present and future*. Lord Howe Island, situated 790 km north-east of Sydney in the Tasman Sea, was first observed on 17 February 1788, making it one of the last islands to be discovered by Europeans. It was found during the establishment of a penal colony on Norfolk Island, 896 km to the east, and was used as a ships' refurbishment station both to and from Norfolk. The birds were recorded and illustrated for the next two years, after which the island was used as a whaling station; the first ornithological survey did not take place until 1853. A settlement was established in 1834, by which time an endemic white, flightless gallinule had become extinct due to over-hunting (see *Bull. Brit. Orn. Cl.* 136: 172–198), followed by an endemic pigeon, known only from two illustrations, and a parakeet shortly afterwards. However, habitat alterations were minimal; therefore a diverse forest bird fauna remained intact.

The accidental introduction of Black Rats *Rattus rattus* in 1918 due to the grounding of the cargo ship *SS Makambo* resulted in a wave of native forest bird extinctions and Barn Owls *Tyto alba*, introduced in the 1920s to control rats, exterminated an endemic boobook by the 1940s. However, several endemics survived this disaster, including a flightless rail and a currawong, both of which were clearly able to tolerate rats. Seabird diversity remains high and they still breed in large numbers on the mainland or on offshore islands, although rat predation and plastic pollution is an ongoing problem. Due to its unique fauna and flora, Lord Howe Island was made a UNESCO World Heritage site in 1982.

A palaeontological survey of Lord Howe Island in November 2018 by the author and others resulted in the discovery of a wealth of fossil material, including the first subfossil remains of the gallinule, pigeon and parakeet. These will help determine morphological similarities and differences between Lord Howe taxa and related forms elsewhere, which in turn will support the possibility of rewilding the island with taxa closely related to those that have gone extinct.

Despite evoking some resentment from some human inhabitants, efforts to finally rid Lord Howe Island of rats using poison bait (PestOff Rodent Bait 20R) will take place in summer 2019. This constitutes

the largest, permanently populated island on which the eradication of rodents will have been attempted anywhere. If successful, Lord Howe Island will become a flagship case, evidencing the logistical approach necessary to reverse the negative impact of humans over the last 200 years of habitation.

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### 2018 Annual Review Meeting

The 994th meeting of the Club was preceded by the Annual Review Meeting which was attended by: Miss A. H. Belman, Mr P. J. Belman, Cdr. M. B. Casement, Mr S. Chapman, Mr G. de Silva Wijeyeratne, Mr R. Langley, Mr R. W. Malin, Dr C. F. Mann, Mr D. J. Montier, Mr A. Pittman, Dr R. Prÿs-Jones, Mr R. Prytherch, Dr D. G. D. Russell, Mr S. A. H. Statham, Mr C. W. R. Storey (*Chairman*).

The Review and the Trustees Report and Accounts for 2018 may be accessed at: <http://boc-online.org/wp-content/uploads/BOC-Report-and-Accounts-2018.pdf>. Chris Storey reported that the administrative year had included implementing the requirements of the new General Data Protection Regulations; integrating the Herbert Stevens Trust deeds into the BOC CIO; finalizing the BOC CIO's banking arrangements and managing the development of the website and the flow of Newsletters and other information.

Richard Malin, Hon. Treasurer, introducing the Accounts for 2018, highlighted the 9% rise in income compared to 2017, a substantial reduction in annual expenditure and the 3% reduction in the Club's assets as a consequence of market conditions during 2018. He added that expenditure in 2019 would inevitably be higher owing partly to a full year of BioOne charges and anticipated publishing costs. The purchase of £100,000 investment units is expected to produce a higher income than current deposit rates. In answer to a question he explained that the Charity Commission did not require the Club's accounts to be formally examined (as the Club's turnover was less than £25,000 p.a.): however, prior to publication and subsequent submission to the Commission the accounts had been independently scrutinised by a fellow Trustee, Tony Statham.

Dr Robert Prÿs-Jones outlined the 2018 talks programme and the rewarding joint conference with the Society for the History of Natural History held in the World Museum, Liverpool. He reported that the year had been very successful with increasing numbers attending the talks at the Barley Mow, augmented by those who watched the talks on YouTube.

In his concluding remarks the Chairman drew attention to the Hon. Editor Guy Kirwan's report on the Bulletin and in particular to the welcome increase in received manuscripts which he suggested might be owing to 'the extra visibility the Bulletin potentially enjoys in its new online home at BioOne'.

Finally Chris Storey noted that the process that began in 2016 was at the end of 2018 coming to fruition: the Club had had its first year of trading as an open-access online journal and the BOC CIO was fully established. However as the Report indicates the Trustees are very much aware of the new territory in which the Club exists. It is a very long way from its beginnings as a gentlemen's dining club. BOC operates in a very crowded market place and it is essential that the Club's activities are distinct, valuable and consistent with its charitable objectives. He said that the Hon. Editor's positive report as to the rise in potential authors plus the increasing numbers attending the Barley Mow talks programme and our joint conferences suggested that the Club was making a success of the transition. But it is a very uncertain world and, encouraged by Douglas Russell, the Trustees are looking at what the BOC's vision, mission and inclusivity statements might be. Is the BOC an exclusive, closed Club or an open inclusive society, active on the web and in its regular meetings with an engaged, broad-based and committed following? Chris ended by stating that the views of all would be very welcome.

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### REVIEW

Abe, N. 2019. *'Cherry' Ingram: the man who saved Japan's blossoms*. Chatto & Windus, London. 380 pp, colour and black-and-white photographs. ISBN: 978-1-78474202-7. Hardback, £18.99.

This may at first sight not seem an obvious title for review in the *Bulletin*, being predominantly focused on the conservation of species and varieties of cherries *Prunus* spp. However, the main protagonist, Collingwood Ingram (1880–1981), was not only also passionately interested in birds, but undoubtedly the longest-serving member of the British Ornithologist's Club. He joined in 1901, in which year he published his first short note in the *Bulletin* (Ingram 1901), and remained a member until his death on 19 May 1981, having submitted his last short *Bulletin* paper, a lament for the decline of English songbirds, in March (Ingram 1981). The then Hon. Secretary of the Club, R. E. F. Peal, wrote his obituary in the *Ibis* (124: 214, 1982).

An independently wealthy man, who never needed to earn a living and travelled widely, notably to Japan in 1902, 1907 and 1926, his early years were dominated by his interest in and study of birds. However, this all began to change around 1919, when he acquired The Grange, in Benenden, Kent, the large house set in extensive land that would be home for him and his wife for the rest of their long lives. In conjunction with a feeling of disillusionment with ornithology, which he decided had become 'a somewhat tired and exhausted science', this triggered a switch of focus to plants, and in particular the acquisition of the horticultural knowledge necessary to create a major new garden. Central to this was his fascination with two mature Japanese cherry trees, a rarity in Britain at the time, which were already growing next to his house. As Naoko

Abe, a Japanese writer who has lived in Britain for more than 15 years, observes: 'Within months Ingram's goals began to crystallise: to collect as many cherry-tree varieties for his garden as he could find, and to become a globally recognised cherry-blossom expert'.

In outlining how Ingram succeeded in this beyond all reasonable expectation, Abe interweaves a fascinating and wide-ranging analysis, embedding Ingram's growing cherry obsession into a framework of recent Japanese history and the deleterious impact that the increasing militant conformity of its society during the late 19th and early 20th centuries had on the diversity of cherry cultivation there. This explains the book's title, as it was Ingram's desire for maximum diversity that resulted in him saving key cherry varieties that were disappearing in Japan itself, where planting became concentrated on a single beautiful but uniform form, *Somei-yoshino*.

Despite his focus on the breeding of garden plant varieties during the middle years of his life, including the publication of his great work *Ornamental cherries* in 1948, Ingram never lost his interest in birds. This again came increasingly to the fore during his later years, when he produced highly personal books focused on observations of living birds, such as *In search of birds* (1966), *The migration of the Swallow* (1974) and, at age 98, *Random thoughts on bird life* (1978). Earlier in his life he had, however, combined observation with collecting, producing important works from studies in, for example, Japan and France, and depositing many specimens in the Natural History Museum (NHMUK) collections. To take a single example, it was he who collected on the island of Ushant, Brittany, the first Gray's Grasshopper Warbler *Locustella fasciolata* specimen from Europe (Ingram 1929). Only a single other genuine specimen has been recorded subsequently, in Denmark, although Richard Meinertzhagen perpetrated one of his more egregious frauds with another specimen he claimed also to have collected on Ushant (Kennerley & Prÿs-Jones 2006).

Although there is limited suggestion of this in the work under review, it would seem that Ingram may not always have been the easiest of people to interact with. Thus a retired NHMUK Bird Group curator who was on the staff when he used to visit the collections remarked to me that he was a most disagreeable person to assist because of his sense of entitlement, and a reviewer of his book *Isles of the Seven Seas* (1936) noted that '... generally the author does not feel for the natives of these islands the sympathy that he displays for their birds and plants' (*Geogr. J.* 89: 87, 1937). Nevertheless, he lived a diverse and involving life extending well beyond his ornithological discoveries, and Abe's book performs a valuable and highly readable service in bringing the wider man into gaze.

Robert Prÿs-Jones

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- Ingram, C. 1901. [Mr. Collingwood Ingram sent for exhibition ...]. *Bull. Brit. Orn. Cl.* 12: 39.  
 Ingram, C. 1929. [Note discussing occurrence of *Locustella fasciolata* on Ushant]. *Bull. Brit. Orn. Cl.* 50: 4.  
 Ingram, C. 1981. What has been the cause of the present scarcity of song birds? *Bull. Brit. Orn. Cl.* 101: 312.  
 Kennerley, P. R. & Prÿs-Jones, R. P. 2006. Occurrences of Gray's Grasshopper Warbler in Europe, including a further case of Meinertzhagen fraud. *Brit. Birds* 99: 506–516.

### OBITUARY

#### Martin Wedgwood Woodcock, 14 January 1935–24 February 2019

For many people, Martin Woodcock, who died on 24 February aged 84, will be remembered as a consummate bird artist, an avid birder, a prominent member of the BOC and the African Bird Club—but first and foremost as a gentleman (in both senses of the word)—a vibrant, convivial conversationalist and wonderfully warm and supportive friend who lived his life to the brim. No one who shared his company could ever forget that wicked twinkle in his eyes as his wife, Barbara, served yet more delicious food while Martin set up his next anecdote with another round of good wine or scotch.

Barbara, who survives him, formed a constant part of the 'Woodcock experience'. Unfailingly cheerful and welcoming, she supported his every eccentricity, holding him to account when the conversation became too boisterous, accompanying him on their many birding trips overseas, notably to Africa and South-East Asia, and adding her own successful framing business to the passions of the Woodcock household. A weekend *chez* Woodcocks was a pleasure never to be declined.

Born on 14 January 1935 in Sidcup Kent, Martin painted and drew from childhood and even sent a drawing of a Great Snipe *Gallinago media* to Peter Scott in 1947, of which the recipient was most appreciative in a letter with a 'nice drawing of a Whitefront' on it. He was entirely self-taught. His first sight, at age eight while at Ashdown House Prep School, East Sussex, of Coward's *Birds of the British Isles and their eggs*, and later trips to Blakeney and Cley as a 16-year-old set the mould for the future. His prep school doctor and local G.P. encouraged his love of nature, and he explored Ashdown Forest and its birds by bicycle as Battle of Britain Spitfires chased Messerschmitts in the skies above.

He went to Christ's Hospital School, Horsham, West Sussex, at age ten and spent eight years there before failing to take up an offer to read history at Magdelene College for lack of sufficient maths. Instead, Martin did National Service in the Royal Artillery and was grateful for the long periods of leave which

afforded plenty of time for birding at Cley. There he mingled with the great birders and ornithologists of the day, including R. A. Richardson, who gave him useful advice on his art and illustration, as did Chloe Talbot-Kelly in later years.

On leaving the army in 1955, Martin followed his father into stockbroking and worked for some dreary years (his own description!) in the City, grabbing as many UK and European birding holidays as possible. A significant high point was an extended trip in 1961–62 to visit his only sister, Nan, who was then working in Uganda. Stories from this trip form the first chapter in his delightful self-illustrated memoir *Safari sketchbook: a bird painters' African Odyssey* (2010).

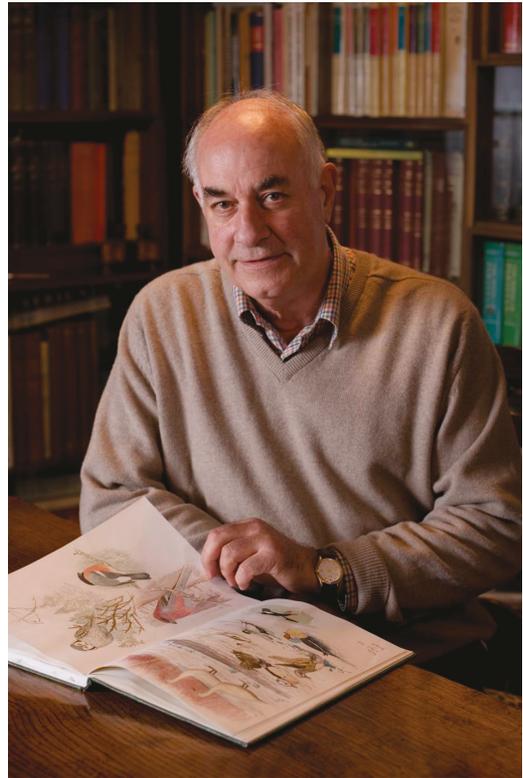
As a member of the BOC from 1961, he met many leading ornithologists and was invited to illustrate Ben King and Edward Dickinson's *Field guide to the birds of South-East Asia*, published by Collins. In 1973, Collins invited him to write about and illustrate birds full time, thereby offering a welcome escape from his increasingly unloved job in stockbroking.

Several other Collins projects were duly commissioned but abandoned due to the exigencies of the market, but his work there included the extremely successful *Collins Gem Guide: Birds*. His self-authored and illustrated *Handguide to the birds of the Indian Sub-Continent* was followed by illustrations for *Quartet's Birds of Oman* by Michael Gallagher, which led to a meeting with Leslie Brown, then planning the monumental *Birds of Africa* to be published by Academic Press, originally envisaged at four volumes. When work began on Vol. 2, of a series that eventually grew to seven volumes covering mainland Africa, Leslie Brown had died to be replaced by an editorial team consisting of Emil K. Urban, Stuart Keith and C. Hilary Fry. Moreover, Martin's two co-illustrators of Vol. 1 had moved on, and Martin found himself the sole artist for some 5,000 illustrations of more than 2,000 species of African birds in all their plumages—a truly formidable task and the work for which he is probably best known.

I joined Academic Press in 1982 and worked with Martin as the publishing editor for the project. It was some 22 years later before the sixth volume was published, and there were numerous difficult times as the editor / author team worked to complete the manuscripts and the project progressed though many changes of management at the publishers. Throughout, Martin was the perfect collaborator; not only were his illustrations superb and continually improving, but they arrived in plenty of time to feed the publication schedule. Not the least of his contributions was his unflinching good humour in the face of deadlines and constant project reorganisation. If he became concerned, it was because there was a problem to solve, and when he had helped resolve it we celebrated together. He provided an outstanding dose of wit and sanity in a sometimes crazy world.

I especially recall Martin's delight at cracking the Congo Peacock *Afropavo congensis* problem. The species is scarce and difficult to find in the wild, so Martin's many field trips to observe African birds first-hand had never brought him face to face with one. Where to find a living bird to flesh out his research on its appearance and improve his illustration? Just in time for press, he managed to locate a specimen kept by an enthusiastic pheasant collector only a short drive away. Martin wasted no time in making a personal visit to bring life to his first illustration and repainted the entire plate with a better version!

Martin was Hon. Secretary of the BOC from April 1965 to April 1969, and continued a close connection with the club subsequently, giving evening talks on the Birds of Thailand and Malaya (1967), Oman (1978) and Three African forests (1994), as well as speaking on the Indian avifauna at a symposium on Asian birds (1977). He published two short papers in the Bulletin in 2003, on Systematics and confusion in the genus *Parmoptila* (*Bull. Brit. Orn. Cl.* 123: 274–277) and Some reflections on the use of skins in bird illustration (*Bull. Brit. Orn. Cl.* 123A: 249–252). He was also a member of the Society of Wildlife Artists for over 25 years and a co-founder of the African Bird Club in 1993. As the latter's first Chair, and later President, he did much to establish it as an influential force for the understanding and conservation of Africa's birds.



Martin Woodcock, at home in Norfolk, 2006 (© R. Jefferson)

His first marriage to Heidi Schön brought three children, and he acquired and brought up two stepchildren when he later married Barbara Skales in 1972. This strong and loving extended family has since grown to include 14 grandchildren.

But perhaps Martin's greatest achievement was also his last. Following diagnosis of an aggressive terminal cancer, the energy with which he embraced life, reached out to his friends and continued to socialise and enjoy his time to the fullest, remains a lesson to us all. Nothing stood in the way of his unflinching humour, his bonhomie, and his sonorous readings from his delightful book of self-penned poetry, *Drawing together*.

Andrew Richford

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### FORTHCOMING MEETINGS

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

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

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

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

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**Monday 16 September 2019—6.30 pm—Pat Morris—*The Hastings Rarities: taking the long view*.**

*Abstract.*—It is now more than 50 years since hundreds of bird records were dismissed as potentially fraudulent on the grounds that it was unlikely that so many rare species would turn up within a short period of time and a limited area around Hastings. Statistical analysis confirmed a significant difference between the numbers of records in that area and time compared to other areas of Kent / Sussex and with later periods. In ornithological terms it makes limited difference, as most of the suspect species have been found subsequently in that area. It has long been widely accepted that fraud occurred and that a local taxidermist, George Bristow, was responsible for perpetrating this. Bristow was unable to defend himself, having died, and the taxidermy profession was besmirched. Although protests were made at the time the issue appears closed. However, worrying doubts remain when the evidence is examined closely. Equally, in retrospect there may be further evidence to confirm Bristow's guilt. A colleague, Philip Redman, has also been studying details of the Hastings affair, and may hopefully be able to join us from Paris.

*Biography.*—Dr Pat Morris is Senior Lecturer in Zoology at Royal Holloway, Univ. of London, and well known for his studies of mammal ecology. He is a past Chairman of the Mammal Society, a former Council Member of the National Trust, and has published >70 scientific papers and c.20 books. A consultant to several major publishers and the BBC Natural History Unit, in his spare time he has pursued a long-standing interest in the history of taxidermy and was appointed the first Hon. Life Member of the Guild of Taxidermists. He was awarded the Founder's Medal by the Society for the History of Natural History and made MBE in the 2015 Honours List 'for services to the natural and historic environment'.

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**Saturday 26 October 2019—One-day joint meeting with the Neotropical Bird Club and Natural History Museum** in the Flett Theatre, Natural History Museum (NHM), London SW7 5BD. The nearest tube station is South Kensington and attendees should use the NHM entrance on Exhibition Road. There is **no charge** to attend, no need to book and all are welcome. The programme is provisionally planned to include the following talks, but a full final programme, including additional talk and speaker details, should be posted at <http://www.boc-online.org> by about late June.

*Avoiding extinctions in the most threatened area in the Neotropics: the Pernambuco Centre of Endemism*—Luís Fábio Silveira (University of São Paulo, Brazil)

*Diversity in avian mimicry*—Alexander Lees (Manchester Metropolitan University)

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

*The physiology / behaviour nexus in a Central American cloud forest songbird, Black-headed Nightingale-Thrush *Catharus mexicanus**—Samuel Jones (Royal Holloway London)

*Using science to protect Ecuador's most threatened birds*—Martin Schaefer (Fundación Jocotoco)

*Conservation of dry forest endemic birds in north-west Peru*—Christian Devenish (Manchester Metropolitan University)

Access to NHM is possible from 10.00 h, when coffee / tea will be available adjacent to the Flett Theatre. The meeting will begin at or shortly after 10.30 h, with a break for lunch around 12.30 h; many food outlets are available both within NHM and nearby in South Kensington. The conference will end by 17.00 h and NHM closes at 18.00 h. For up-to-date details, please check the BOC website: <http://www.boc-online.org>.

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**Monday 18 November 2019—6.30 pm—Tim Birkhead—*The wonderful Mr Willughby: the start of scientific ornithology.***

*Abstract.*—The first scientific bird book was *The ornithology of Francis Willughby*, named in Willughby's honour by his friend John Ray after Willughby's death at the age of just 36 in 1672. These two men were pioneers of the scientific revolution and changed the way we think about birds. Until recently it was widely assumed that Ray was the brains and Willughby a mere 'talented amateur', but after a decade of research I have been able to show that Willughby was every bit as brilliant as his co-author and friend John Ray. In this talk I will tell the story of Willughby's short but spectacularly productive life—a story every ornithologist should know.

*Biography.*—Tim Birkhead is emeritus professor of behavioural ecology at the Univ. of Sheffield. He completed a D.Phil. at Oxford on guillemots (Alcidae) in 1976, before taking a lectureship at Sheffield where he has been ever since. Tim is a Fellow of the Royal Society—the UK's most prestigious scientific body. His main research is on promiscuity in birds, but he is also interested in the history of science. He has maintained a long-term study of Common Guillemots *Uria aalge* on Skomer Island, Wales, for the last 47 years and raised UK£150,000 through crowd funding to keep the study going. Tim has won several awards for his undergraduate teaching. He is also an award-winning author and has written 15 books, including several popular science works. He has featured on BBC Radio 4's Life Scientific, The Infinite Monkey Cage and Inside Science, and his book *The most perfect thing: the inside (and outside) of a bird's egg* was made into a TV programme with David Attenborough, who referred to the book as 'Magnificent'.

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#### 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://www.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](mailto:rmalin21@gmail.com)), if you would kindly inform him if you intend becoming a Friend of the BOC.

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#### The *Bulletin* and other BOC publications

From volume 137 (2017), the *Bulletin* of the BOC has become 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 six months. Prospective authors are invited to contact the *Bulletin* editor, Guy Kirwan ([GMKirwan@aol.com](mailto:GMKirwan@aol.com)), to discuss future submissions or look at <http://www.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](http://www.biodiversitylibrary.org/bibliography/46639#/summary); vols. 132–136 are also available on the BOC website: <http://www.boc-online.org/>

BOC Occasional Publications are available from the BOC Office or online at [info@www.boc-online.org](mailto:info@www.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).

## Helpers at a *Sapayoa* nest are kin

by Benjamin M. Van Doren, Jack P. Hruska, Sarah A. Dzielski & Bronwyn G. Butcher

Received 19 July 2018; revised 1 April 2019; published 17 June 2019

<http://zoobank.org/urn:lsid:zoobank.org:pub:B06B96CD-4B8A-46C7-B663-683EBCAF945B>

**SUMMARY.**—The natural history of the Sapayoa *Sapayoa aenigma*, the sole member of the Sapayoidae and the only New World representative of the ‘Old World suboscines’, is poorly known. Previously, we reported a pair of adult Sapayoos breeding with assistance from two immature males, but their kinship was unknown. Here, we use double-digest restriction site-associated DNA sequencing (ddRAD-seq) to conduct parentage and relatedness analyses among this group. We found that the members of the adult pair were unrelated, but all other dyads were probably first order (parent-offspring or full sibling). In addition, the helper males were very unlikely to have sired either of the chicks. We conclude that the group consisted of two unrelated adults and two offspring from a previous brood. These results provide important context for social behaviours observed within the group, which included mounting events; such behaviour may be involved in group cohesion.

Sapayoa *Sapayoa aenigma* is the sole member of one of the world’s least known bird families, Sapayoidae (Winkler *et al.* 2015). Resident in wet Chocó forests of south-west Panama, western Colombia and north-west Ecuador, *Sapayoa* has perplexed taxonomists for decades; only recently have molecular studies revealed that it is nested within the Old World suboscines (Sibley & Ahlquist 1990, Fjeldså *et al.* 2003, Chesser 2004, Irestedt *et al.* 2006, Moyle *et al.* 2006, Selvatti *et al.* 2015). Nonetheless, its precise relationships within this group remain debatable. Furthermore, a paucity of natural history data limits the potential for comparative studies with other Old World suboscines.

The first descriptions of the nest and nestlings of the Sapayoa suggested that parental care was undertaken by two adults (Christian 2001). However, Dzielski *et al.* (2016) subsequently reported the presence of helpers at a Sapayoa nest, and thus that cooperative breeding occurs. At that time, we were unable to determine if the helpers were related to the breeding pair, which is a common scenario among cooperatively breeding species (Skutch 1999, Cockburn 2006). We also documented unusual social behaviours in the breeding group, which consisted of an adult male, adult female and two immature males. Specifically, all four individuals participated in mounting behaviours, which were always preceded by a solicitation display. Usually, the adult female gave the display before being mounted by a male. Additionally, we recorded occasional mountings between males. The function of these behaviours, which occurred during nest provisioning, is unclear. Were they explicitly reproductive in nature, or did they serve a non-reproductive social function?

We proposed three possible non-reproductive functions for these mounting behaviours: enforcement of a dominance hierarchy among members of the group, maintenance of social cohesion within the group, and experience-gaining through practice. Non-reproductive mounting behaviours have been documented in another species, Acorn Woodpecker *Melanerpes formicivorus*, but their function is unknown (MacRoberts & MacRoberts 1976, Koenig & Walters 2014). Given the prevalence of presumed inbreeding avoidance behaviours

in birds (Koenig & Dickinson 2004), the possibility that the Sapayoa nest helpers could be both related to the breeding pair and involved in reproduction warrants investigation.

To shed further light on these behaviours and better understand *Sapayoa* reproductive biology, we sequenced genomic DNA from the same family group of Sapayoa studied by Dzielski *et al.* (2016). We posed two primary questions. (1) Were the two nest helpers related to the breeding pair? (2) Did either of the nest helpers sire one or more nestlings?

## Methods

**Sample collection.**—We obtained genetic material from six *Sapayoa aenigma* collected in Darién National Park, Panama. This material is archived at the Cornell University Museum of Vertebrates, Ithaca, NY (CUMV). Four of these—an adult male (CUMV 55871) and female (CUMV 55868) and two immature males (CUMV 55971–972)—were provisioning a single nest containing two nestlings (CUMV 55869–870). Detailed information concerning all individuals is presented in Dzielski *et al.* (2016). Genomic DNA was extracted from blood preserved in ethanol using Qiagen DNeasy Blood and Tissue kits.

**ddRAD sequencing.**—We used double-digest restriction site-associated (ddRAD) sequencing to identify single-nucleotide polymorphisms (SNPs) across the *Sapayoa* genome for use in parentage and relatedness analysis. We followed the methods of Thrasher *et al.* (2018) to sequence DNA and identify SNPs. The ddRAD libraries from these *Sapayoa* samples were prepared and sequenced along with 232 other samples from species unrelated to this study. We used approximately 200 ng of DNA digested with SbfI and MspI, ligated unique barcode adapters, and pooled samples. We purified DNA, selected fragments of 450–600 bp, and added Illumina sequencing adapters. We pooled samples in equimolar ratios and sequenced the pooled library on an Illumina HiSeq 2500 (100 bp, single end).

**Trim, filter and demultiplex.**—Again following Thrasher *et al.* (2018), we assessed read quality using FASTQC ([www.bioinformatics.babraham.ac.uk/projects/fastq](http://www.bioinformatics.babraham.ac.uk/projects/fastq)) and trimmed sequences to 97 bp using fastX\_trimmer (FASTX-Toolkit). We removed reads containing a single base with a Phred quality score of <10 (using fastq\_quality\_filter). We additionally removed sequences if more than 95% of the bases had a Phred quality score of <20. Using process\_radtags, we demultiplexed the sequences to obtain sequences specific to each individual.

**De novo assembly.**—We assembled the sequences de novo using the Stacks pipeline, following Thrasher *et al.* (2018). First we used denovo\_map.pl to assemble the reads into a catalogue with a minimum stack depth of 5 (m) and allowing up to five mismatches between loci within an individual (M) and five mismatches between loci when building the catalogue (n). Corrections were made by running rxstacks. Loci with a log likelihood less than -20 (lnl\_lim -20) or that were confounded in 25% of the population were removed (conf\_lim 0.25). We then reran cstacks and sstacks with this new catalogue.

**SNPs identified.**—We identified SNPs using the populations module within Stacks, following Thrasher *et al.* (2018). All of our samples were considered in one population and a locus was processed if it was present in 95% of the individuals (r) at a stack depth of  $\geq 10$  (m). The data were restricted to the first SNP per locus (write\_single\_snp) and a minor allele frequency of 0.25 was required to process a nucleotide site at a locus (min\_maf).

**Parentage and relatedness.**—We performed a paternity analysis using Cervus (Marshall *et al.* 1998, Kalinowski *et al.* 2007) to determine whether the father of each nestling was the adult male or one of the helpers. We assumed that the adult female was the mother of both nestlings because she was the only female present at the nest. We also performed a parentage analysis for the nest helpers to determine the likelihood that they were offspring of the adult pair. Finally, we calculated pairwise relatedness coefficients for all individuals

using the R package SNPRelate (Zheng *et al.* 2012). We multiplied coefficients by two so that they scaled from 0–1, with 0.5 being the theoretical expectation for full siblings or a parent-offspring relationship. We calculated bootstrapped 95% confidence intervals for each comparison with 10,000 iterations, sampling with replacement from included loci.

## Results

Post-filtering, we retained 672 SNP loci for analysis. Paternity analysis using Cervus showed that the adult male was far more likely to be the father of the nestlings than either immature male (Table 1). When we considered the adults as possible parents of the helpers, we found that the number of mismatched loci between adults and helpers was comparable to that of adults and nestlings (Table 2). This strongly suggests that the adults were also the parents of the immature male helpers, and is supported by low non-exclusion probabilities (Table 2). Finally, relatedness scores between individuals of the group were relatively high (mean  $0.35 \pm \text{SD } 0.12$ ) and similar for all comparisons, with one exception: the adult male and female showed far lower relatedness scores than all other comparisons (Table 3).

## Discussion

These data show that the adult male and female were less closely related to each other than to all other members of the breeding group. In addition, they confirm that both chicks were offspring of the pair and support the hypothesis that the immature male helpers were young from an earlier brood. A scenario in which young relatives assist an experienced adult pair is common among avian cooperative breeders (Skutch 1999, Cockburn 2006). Among the Old World suboscines, multiple species of broadbills have been observed to breed cooperatively, at least occasionally (Lambert & Woodcock 1996, Bruce 2003). The lack

TABLE 1  
Paternity analysis of nestling Sapayoas *Sapayoa aenigma*, comparing adult and immature males.

Offspring ID	Candidate father	Mismatched loci: adult female and candidate male (no. compared)	Trio LOD score	Most likely father
Chick (male)	Adult male	23 (669)	45.62	*
	Immature male 2	95 (669)	-286.55	
	Immature male 1	105 (668)	-349.47	
Chick (female)	Adult male	36 (671)	67.15	*
	Immature male 2	104 (671)	-281.34	
	Immature male 1	117 (670)	-315.58	

TABLE 2  
Parentage analysis of nestling and immature Sapayoas *Sapayoa aenigma*, showing number of loci inconsistent with parentage by adult male and female.

Offspring	Mismatched loci: adult female (no. compared)	Mismatched loci: adult male (no. compared)	Mismatched loci: both adults (no. compared)	Parent pair non-exclusion probability
Chick (male)	9 (668)	13 (669)	23 (670)	$1.86 \times 10^{-71}$
Chick (female)	24 (670)	12 (671)	36 (672)	$1.30 \times 10^{-74}$
Immature male 1	10 (668)	15 (669)	26 (670)	$2.62 \times 10^{-78}$
Immature male 2	9 (669)	14 (670)	24 (671)	$5.63 \times 10^{-76}$

TABLE 3  
Relatedness matrix scaled from 0–1. Parentheses show bootstrapped 95% confidence intervals.

	Adult female	Adult male	Chick (female)	Chick (male)	Immature male 1	Immature male 2
Adult female	1	0 (0–0.135)	0.341 (0.27–0.401)	0.42 (0.371–0.5)	0.427 (0.38–0.5)	0.5 (0.397–0.5)
Adult male	0 (0–0.135)	1	0.417 (0.372–0.472)	0.417 (0.366–0.5)	0.406 (0.354–0.5)	0.409 (0.358–0.5)
Chick (female)	0.341 (0.27–0.401)	0.417 (0.372–0.472)	1	0.356 (0.304–0.423)	0.329 (0.264–0.396)	0.356 (0.291–0.5)
Chick (male)	0.42 (0.371–0.5)	0.417 (0.366–0.5)	0.356 (0.304–0.423)	1	0.234 (0.165–0.322)	0.344 (0.276–0.413)
Immature male 1	0.427 (0.38–0.5)	0.406 (0.354–0.5)	0.329 (0.264–0.396)	0.234 (0.165–0.322)	1	0.287 (0.209–0.359)
Immature male 2	0.5 (0.397–0.5)	0.409 (0.358–0.5)	0.356 (0.291–0.5)	0.344 (0.276–0.413)	0.287 (0.209–0.359)	1

of relatedness between the adult male and female—the breeding pair—is also consistent with observations in other species and the ‘incest avoidance’ hypothesis.

Our results lend support to the hypothesis that mounting events between individuals in this *Sapayoa* family were not explicitly related to reproduction. We believe that the most likely explanation for this behaviour is to maintain cohesiveness of the breeding group. The adult female expended considerable effort soliciting mountings from both adult and immature males, and in turn these individuals consistently provisioned the nest (Dzielski *et al.* 2016). If soliciting mountings reinforces group bonds or otherwise encourages males to persist in the provisioning effort, the female would benefit from a reduced burden to deliver food. Mountings between males could likewise be explained by the group cohesiveness hypothesis. In contrast, a dominance hierarchy (see, e.g., Briskie 1992, Eason & Sherman 1995) is less likely to explain these observations because males did not vie for access to the female, and a mounting was always preceded by a solicitation display given by the receiving individual.

The most likely scenario is that all related individuals were first-order relatives (full siblings or parents and offspring), yet relatedness values for most pairs fell below the expected 0.5 value. In practice, relatedness values estimated using SNP data can vary far from their theoretical expectation, especially when the sample consists of only a small number of closely related individuals (Wang 2017).

## Conclusion

Overall, this information provides valuable context for the observations reported by Dzielski *et al.* (2016) and indicates that *Sapayoa aenigma* will breed cooperatively with assistance from their kin. This scenario may occur in other Old World suboscines (e.g. multiple broadbill species), but cooperative breeding in these taxa remains to be studied in detail. *Sapayoa* also requires further study, especially the apparently rich array of social interactions that occur in this species.

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## Major range extension for Orange-fronted Plushcrown *Metopothrix aurantiaca* in the central Amazon of Brazil

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**SUMMARY.**—Orange-fronted Plushcrown *Metopothrix aurantiaca* is a unique, but easily overlooked, small furnariid found in the midstorey and canopy of riverine areas in the Amazon. The species' previously published distribution includes parts of southernmost Colombia, eastern Ecuador, eastern Peru, northern Bolivia and western Brazil. In the easternmost part of its distribution (Brazil), *M. aurantiaca* occurs in the states of Acre, Amazonas and Rondônia, east to 64°W. We present nine new records of the species in Brazil, all of them east of its previously known distribution and together extending the range by c.750 km. These new records derive from sampling that includes collecting expeditions, exhaustive *várzea* surveys, and incidental observations. We propose a new continuous distribution for this species restricted to white-water river floodplains with known occurrences.

Orange-fronted Plushcrown *Metopothrix aurantiaca* is a unique, small furnariid with bright plumage and tarsal coloration, distinct from other members of its family (Fig. 1; Renssen 2003). This warbler-like bird forages in pairs or small groups and often associates with mixed-species flocks, feeding mainly by gleaning arthropods from vegetation, even



Figure 1. Orange-fronted Plushcrown *Metopothrix aurantiaca*, Careiro da Várzea, Amazonas, Brazil, 20 October 2018 (Robson Czaban)

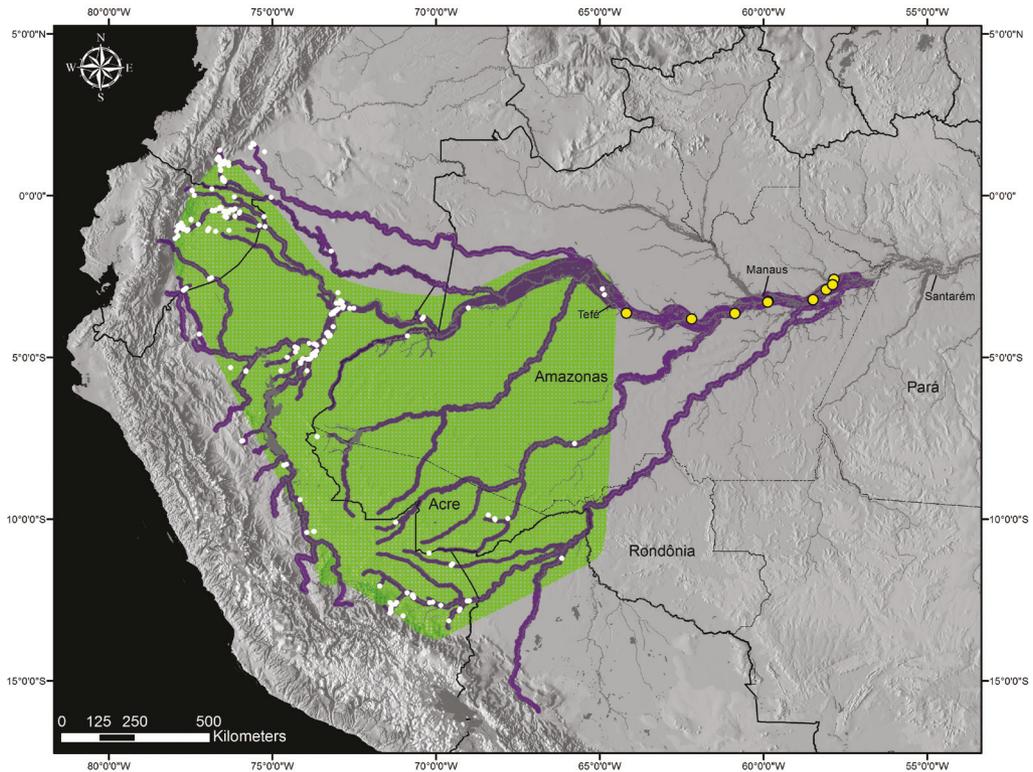


Figure 2. A currently published distribution (green polygon; BirdLife International 2018) of Orange-fronted Plushcrown *Metopothrix aurantiaca* compared to the distribution we propose (purple polygon; see text), based on interpretation of our new records presented here (yellow dots). White dots indicate specific localities within the species' previously known range, derived from eBird (through November 2017), digital vouchers archived at Wikiaves, the Macaulay Library and xeno-canto (June 2018), and specimen localities from the Louisiana State University Museum of Natural Science, Baton Rouge (March 2018), Museu Paraense Emílio Goeldi, Belém (December 2017), and other museums with data archived at the Global Biodiversity Information Facility (July 2018). The shapefile for the revised species distribution we here propose is available on request from the authors.

directly clinging to and hanging from leaves (Remsen 2003, Ridgely & Tudor 2009). Chiefly in the midstorey and canopy of riverine areas in the Amazon, *M. aurantiaca* has also been found in second growth and *terra firme* forest (Hilty & Brown 1986, Parker *et al.* 1996, Schulenberg *et al.* 2010). The species' previously published distribution includes parts of extreme southern Colombia, eastern Ecuador, eastern Peru, northern Bolivia and western Brazil (Ridgely & Tudor 2009). In the easternmost part of its range (Brazil), it occurs in the states of Acre, Amazonas and Rondônia, east to 64°W (Fig. 2). Here, we present nine new records of *M. aurantiaca* in Brazil, all of them east of its previously known distribution and extending the range by c.750 km.

1. 20–23 September 2003, 66 km south-east of Tefé, Amazonas state (AM) (03°37'S, 64°11'W). MCH observed a pair of *M. aurantiaca* on the north bank of the Solimões (Amazon) River; the birds were 500 m from the river edge in the canopy of tall *várzea* forest, which was flooded at the time (3–4 m deep). This and the following record were the only occasions on which the species was noted in 45 days of bird surveys along the full extent of the Amazon in Brazil.

2. 5 November 2003, 15 km east of Itapiranga, AM (02°45'S, 57°53'W). MCH saw, heard and sound-recorded another pair of *M. aurantiaca*, and one was collected on the north bank of the Amazon, at 'Costa do Cucuiari'. The pair was in the canopy of tall *várzea* forest within a mixed-species flock. This record, together with the previous one, within a few weeks of each other, already suggested 15 years ago the full extent of the distribution that our subsequent records have reinforced (Fig. 2, purple polygon).

3. 28 October 2015, 8 km south of Careiro da Várzea, AM (03°15'S, 59°51'W). RC found two birds (apparently a male and female based on plumage differences) beside the BR-319 highway (Fig. 1), south of the town of Careiro da Várzea (<http://www.wikiaves.com/1891099>). The pair was in short-stature *várzea* forest (c.10 m), which was not flooded at the time, but is so during the high-water season (roughly April–August). They were with several Hooded Tanagers *Nemosia pileata*, searching for food under large leaves, where they spent much time hidden from view. Despite this and their superficial similarity to female *N. pileata*, periodic vocalizations confirmed their continued presence in the flock. A similar flock containing both species was seen at the same location more than one month later and again in October 2018 (<https://www.wikiaves.com.br/3152831>).

4. 6 September 2016, 10 km south-west of Itacoatiara, AM (03°13'S, 58°29'W). During a 15-day survey, TOL observed at least 2–3 individuals, possibly including a juvenile, foraging near the margin (c.60 m from water) of a small channel on the south bank of the Amazon, opposite Itacoatiara (<http://www.wikiaves.com/2415687>). Observations were made at two different points along the same channel (spanning nearly 1 km) and might best be considered separate records. The birds were seen foraging acrobatically in the midstorey and consorting with a mixed-species flock that also comprised Scaled Spinetail *Cranioleuca muelleri*, Green-tailed Jacamar *Galbula galbula*, Chestnut-crowned Becard *Pachyramphus castaneus*, White-winged Becard *P. polychopterus*, Bar-breasted Piculet *Picumnus aurifrons*, Yellow-olive Flatbill *Tolmomyias sulphureus* and Red-stained Woodpecker *Veniliornis affinis*. The habitat was flooded *várzea* forest, 15–20 m tall, with a relatively dense understorey composed of lianas and a few *Cecropia* trees near the channel edge.

5. 28 February 2017, 3 km south-east of São Sebastião do Uatumã, AM (02°35'S, 57°50'W). GAL observed and sound-recorded three birds vocalising in the canopy ([www.xeno-canto.org/357168](http://www.xeno-canto.org/357168); <https://ebird.org/view/checklist/S34901685>; <http://www.wikiaves.com/3089947>); after playback, they descended to the midstorey and remained there, gleaning insects from the leaves. Habitat consisted of *várzea* forest (20–30 m tall) with an open understorey and *Cecropia* trees on the south bank of the Uatumã River. This is the easternmost record to date.

6. 18 August 2017, 12 km south of Careiro da Várzea, AM (03°17'S, 59°52'W). BRA & CLR found a presumed pair just east of the BR-319 (<https://ebird.org/view/checklist/S38720102>). The birds appeared to be foraging with a very small mixed-species flock that also included three *Pachyramphus castaneus* and two Chestnut-vented Conebills *Conirostrum speciosum*. The relatively short-stature *várzea* forest was no longer inundated at this season and was immediately adjacent to the road, >4 km from the south bank of the Solimões River. One bird was photographed (<http://www.wikiaves.com/2726712>; <http://www.wikiaves.com/2726713>), but neither was detected vocalising during the brief observation.

7. 15 October 2017, 18 km south-west of Itapiranga, AM (02°54'S, 58°05'W). MCH, CLR & BRA photographed and sound-recorded another presumed pair spontaneously vocalising at the outskirts of a small community bordering a south-bank tributary of the Amazon, in a seasonally flooded landscape north of Urucurituba (<https://ebird.org/view/checklist/S40011003>). When first discovered, there was a lot of activity in the vicinity (including species of *Bucco*, *Picumnus*, *Tityra*, *Dacnis*, *Conirostrum*), but it was unclear whether the pair



Figure 3. Recent Orange-fronted Plushcrown *Metopothrix aurantiaca* specimens collected in November 2017 west of Codajás, Amazonas, Brazil (two in background; GRL 3786, GRL 3787) and west of Manacapuru, Amazonas, Brazil (foreground; GRL 3952), housed at the collection at the Instituto Nacional de Pesquisas da Amazônia, Manaus (Cameron L. Rutt)

of *Metopothrix* was part of a cohesive mixed-species flock. The two birds remained high in the canopy of an emergent tree and neighbouring tall trees where mature *várzea* borders a strip cleared for sparse habitation. This area is c.800 m from the nearest large river and was not flooded at the time. We presumed the birds to be a pair as one (the putative male) had a much more saturated orange forehead and more vividly orange legs and feet (<http://www.wikiaves.com/2855507>).

8. 4–5 November 2017, 15 km west of Codajás, AM (03°48'S, 62°11'W). One was collected (GRL 3786) in the Canal do Juanico, Ilha Grande, by G. Thom & E. Schultz. It was with another three or four *M. aurantiaca* in a mixed-species flock, in the canopy of tall *várzea* forest (>30 m) near a lakeshore. Another pair was seen and heard in the canopy on the south bank of the Solimões River, close to the river edge, where a second individual was collected (GRL 3787; Fig. 3).

9. 5 November 2017, 47 km south-west of Manacapuru, AM (03°38'S, 60°52'W). G. Thom also collected an individual (GRL 3952) along the Paraná dos Mundurucus on the south bank of the Solimões River (Fig. 3). At least two individuals were seen with a large mixed-species flock, foraging in the canopy of *Cecropia* trees, near the border of tall *várzea* forest and a manioc plantation. This specimen and the two from Codajás were all obtained during a 20-day collecting expedition.

The species' previously published distribution (Fig. 2, green polygon) simultaneously over-estimated the extent of occurrence over inappropriate habitat (extensive *terra firme* far from rivers) and under-estimated the true extent east along the Amazon River. The former is a common problem with digital distribution maps for *várzea* birds, which are mapped very unevenly (i.e., some species are restricted to river margins, whereas others are mapped over enormous geographic polygons; Vale *et al.* 2017). All of our records are from tall *várzea* forest in the floodplain of the main Amazon River. Occurrence at *terra firme* sites 'seldom far from rivers' in upper Amazonia (Remsen 2003) may correspond to a phenomenon we have observed in our area, whereby species locally associated strictly with white-water (muddy) floodplains, such as Great Antshrike *Taraba major*, Plain-crowned Spinetail *Synallaxis gujanensis*, and the kapok tree *Ceiba pentandra*, also occur spottily in *terra firme* in pockets of exceptionally rich soils. 'Transition forest' (Terborgh 1971, Remsen & Parker 1983), which

does not flood regularly but is distinctly different from *terra firme* typical of ancient uplands and is virtually absent from the central Amazon, may also account for some records. This apparent variability in habitat selection across the species' range merits future investigation. In any case, at the scale of a range-wide distribution map, tracing the major rivers as we propose (Fig. 2, purple polygon) accounts for virtually all of the plotted localities and, we believe, provides a more accurate and predictive (see below) picture of where the species is found.

Our records extend the species' known distribution eastward by some 750 km. This suggests that *M. aurantiaca* had been overlooked in this region, where it is probably widespread but uncommon in *várzea* forest on both banks of the middle Amazon. This interpretation also leads us to propose a continuous distribution along the rivers where it has been recorded (Fig. 2, purple polygon). Our easternmost records cluster just west of the mouth of the Uatumã River and near the state line dividing Amazonas and Pará, Brazil. It is unclear whether the species can be expected to occur even further downstream along the Amazon. Although *várzea* habitat is relatively continuous along the river and no other species are known to be limited by this tributary, many species are known to occur along only a particular stretch of river, and considerable species turnover of *várzea* birds occurs in the central Amazon (Cohn-Haft *et al.* 2007). We have searched for *M. aurantiaca* between Santarém and the Amazonas state line, to date without success. Thus, we propose treating our records and the state line as the easternmost limit until proven otherwise.

All records to date are from nutrient-rich ('white-water') rivers. Apparent gaps between the numerous records in the headwaters of white-water tributaries near the Andean foothills and those along the Amazon River itself may be an artefact of inadequate sampling or might represent a real phenomenon. Considering our finding of *M. aurantiaca* in localities long visited by ornithologists and birdwatchers, we believe the species is easily overlooked, especially where it occurs at low density. For this reason, we suspect that it indeed occurs in appropriate habitat all along those rivers where it has been found, even when existing records are concentrated in their headwaters, such as the Madeira, Juruá, Purus and Japurá, as mapped in our predicted distribution (Fig. 2, purple polygon).

Future searches for the species should use playback of vocalisations and concentrate on mixed-species flocks in tall *várzea* forest. *M. aurantiaca* can be difficult to spot, high in the forest canopy, where its mostly dull underparts and bright orange legs could be confused for the much commoner *Nemosia pileata*. Its high-pitched vocalisations resemble those of canopy tanagers and the commonest call, a sharp *tss-tss-tss*, sounds almost identical to those of Bar-breasted Piculet *Picumnus aurifrons* and members of the Golden-spangled Piculet *P. exilis* complex (Rêgo *et al.* 2014), with which it can co-occur.

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# Documentation of a hybrid *Spizella* sparrow using spectrographic and genetic analysis

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**SUMMARY.**—We report the first well-documented hybrid between Field *Spizella pusilla* and Clay-coloured Sparrows *S. pallida*. This hybrid combination has previously been suggested from field observations in eastern North America, but not confirmed. We encountered an individual in Lorain County, Ohio, USA, during surveys for the state's second breeding bird atlas. It was a territorial male, singing a buzzy but accelerating trilled song with characteristics of both parents. It responded vigorously to playback of both Field and Clay-coloured Sparrows. In the hand, the bird showed plumage characteristics of both species and intermediate measurements. Using molecular data, we were able to confirm Clay-coloured Sparrow as the mother of the individual, with support for Field Sparrow as the father. This and other recent field observations of this hybrid pairing have been reported at the eastern boundary of the expanding breeding range of Clay-coloured Sparrow, suggesting that this hybrid combination can be expected elsewhere in the Great Lakes region and in New England, where these species are increasingly syntopic.

The six species of sparrows in the genus *Spizella* are common in open habitats across North America. Clay-coloured Sparrow *S. pallida* occurs in central North America, in shrubland, grassland and prairies, throughout the year (Grant & Knapton 2012). Field Sparrow *S. pusilla* is found in brushy pasture and grassland, and second-growth scrub, in eastern North America, also year-round (Carey *et al.* 2008). Both species are migratory, with overlap in their breeding ranges in the Great Lakes region, and in migration and winter in the eastern Great Plains as far south as Texas. There have been several field observations of possible hybridisation behaviour and putative hybrids, but confirmation has been lacking. Here we describe a hybrid between these species, with supporting vocal, morphological and genetic data.

## Methods

**Encounter details.**—The putative hybrid was first seen by EK on 3 July 2008 while undertaking field work for the second Ohio Breeding Bird Atlas project (Rodewald *et al.* 2016). The bird was singing in a small grassland at the Charlemont Reservation of Lorain County Metro Parks, Lorain County, Ohio, USA (41°07.469'N, 82°26.906'W). The bird resembled a Clay-coloured Sparrow, a very rare breeder in the state (Peterjohn 2001), but some coloration and song details were inconsistent with the species. A brief recording of its song was made by ATB using a Kodak DX7440 digital camera on 11 July 2008.

On 16 July 2008, ATB & AWJ returned to the site at 07.15 h. The bird was still singing continuously, and we set up mist-nets in the centre of the bird's apparent territory, based on repeated use of song perches. We initiated playback of a typical Clay-coloured Sparrow

song on a speaker below the net. The bird immediately approached the speaker and spent ten minutes counter-singing against the playback while perched on higher stems. This behaviour occurred within 5 m of the playback equipment, but the bird did not come closer to the mist-nets. We then changed the playback to a typical Field Sparrow song, and the bird immediately flew directly at the speaker and was caught in the mist-net. It was measured and photographed, with several contour feathers and one secondary feather collected before the bird was released.

**Genetic analyses.**—Plucked feathers were stored in a clean 2 mL tube in the field, then refrigerated at 4°C at the Cleveland Museum of Natural History. Feathers were extracted using a Qiagen DNeasy Blood & Tissue Kit (Qiagen Inc., Valencia, CA), with 30 µL of DTT (Dithiothreitol) added to the initial digestion step to digest the feather. We also extracted DNA, using standard protocols, from the other widespread North American species of genus *Spizella* for comparison (Table 1). We amplified two genes using the polymerase chain reaction (PCR); the mitochondrial NADH dehydrogenase subunit 2 gene (ND2) was amplified using primers and conditions from Drovetski *et al.* (2004), and the ninth intron of the nuclear-encoded aconitase 1 gene (ACO1-19) was amplified using primers and conditions from Barker *et al.* (2008). The PCR results were cleaned and sequenced at the CWRU Genomics Center (Cleveland, OH) using BigDye Terminator 1.1 and 3.1 Cycle sequencing kits (Applied Biosystems, Foster City, CA) on an ABI 3730 Genetic Analyzer using the same sets of primers. Sequences were aligned in Geneious version 9.0 (Kearse *et al.* 2012), and aligned and compared to several GenBank sequences of congeners (Table 1).

## Results

**Morphology and song.**—Plumage features were intermediate vs. both putative parental species (Fig. 1). All bare parts—the bill (including gape and mouth lining), legs, feet, and toes—were pinkish orange, resembling a Field Sparrow, but with a dusky tip to the culmen like a Clay-coloured Sparrow. The hybrid had a weak white eye-ring. The grey ear-coverts contrasted with a pale supercilium and the pale malar. The lores were pale brown, and the crown was streaked rusty, with a subtle central crown-stripe. The nape was grey, and the back was streaked black, brown and rusty.

Unflattened wing chord was 65.5 mm; Pyle (1997) reported a range of 61–72 mm for Field Sparrow and 59–67 mm for Clay-coloured Sparrow. The tail was 64 mm. Pyle

TABLE 1  
Museum specimen data and GenBank accession numbers for DNA sequences used in this study. Museum acronyms: CMNH = Cleveland Museum of Natural History; UMMZ = University of Michigan Museum of Zoology, Ann Arbor.

Taxon	ND2 GenBank	ACO9 GenBank	Specimen number	Collector number
<i>S. pallida</i>	FJ547320	n/a		
<i>S. pallida</i>	MK530936	MK530941	UMMZ 242717	n/a
<i>S. pusilla</i>	EF529824	KC007881		
<i>S. pusilla</i>	MK530938	MK530942	CMNH 74050	CLB 949
<i>S. passerina</i>	FJ547319	n/a		
<i>S. passerina</i>	MK530937	MK530943	CMNH 73488	CLB 782
<i>S. breweri</i>	AF290121	n/a		
<i>S. breweri</i>	MK530939	MK530944	CMNH 73031	CLB 489
<i>S. pallida</i> × <i>S. pusilla</i>	MK530940	MK530945	n/a	n/a



Figure 1. Hybrid Field *Spizella pusilla* × Clay-coloured Sparrow *S. pallida* mist-netted in Charlemont Reservation, Lorain County, Ohio, 16 July 2008; the bill and legs have a pink tone resembling Field Sparrow, but plumage characters are intermediate, with a pale malar that is absent in Field Sparrow and rusty tones throughout the body, which are absent in Clay-coloured Sparrow (Andrew W. Jones)

(1997) reported a range of 59–74 mm for Field Sparrow and 55–63 mm for Clay-coloured Sparrow. We identified the bird as an after-second-year adult, based on the relatively small amount of wear on the broad tips of the rectrices, a lack of moult limit in the primaries and secondaries, and the broad shape and minimal wear to the alula and primary-coverts. These ageing criteria are common to both parental species (Pyle 1997).

Two songs were recorded by ATB during his visit on 11 July 2008. These had a buzzy tone that was similar to a typical Clay-coloured Sparrow. The song was an extended introductory note followed by a series of notes on the same relative frequency but decreased in length, and with a decrease in time between each note (Fig. 2).

**Genetic analyses.**—There were 134 variable sites within the ND2 data among the four species of *Spizella*, including the hybrid. Within these sites, the hybrid differed from the two Clay-coloured Sparrow sequences at just three loci. Pairwise differences between the hybrid and the other species were as follows: Clay-coloured Sparrow: 0.2 and 0.4%, Chipping Sparrow *S. passerina*: 8.8%, Brewer’s Sparrow *S. breweri*: 8.5% for both, and Field Sparrow: 7.9 and 8.0%. Within the ACO1-19 data, there were three variable sites among Clay-coloured, Field and the hybrid sparrow. Two loci had singleton alleles restricted to one of the two Field Sparrow samples and were therefore uninformative in determining parentage of the hybrid. The third variable locus had a fixed difference between the Clay-

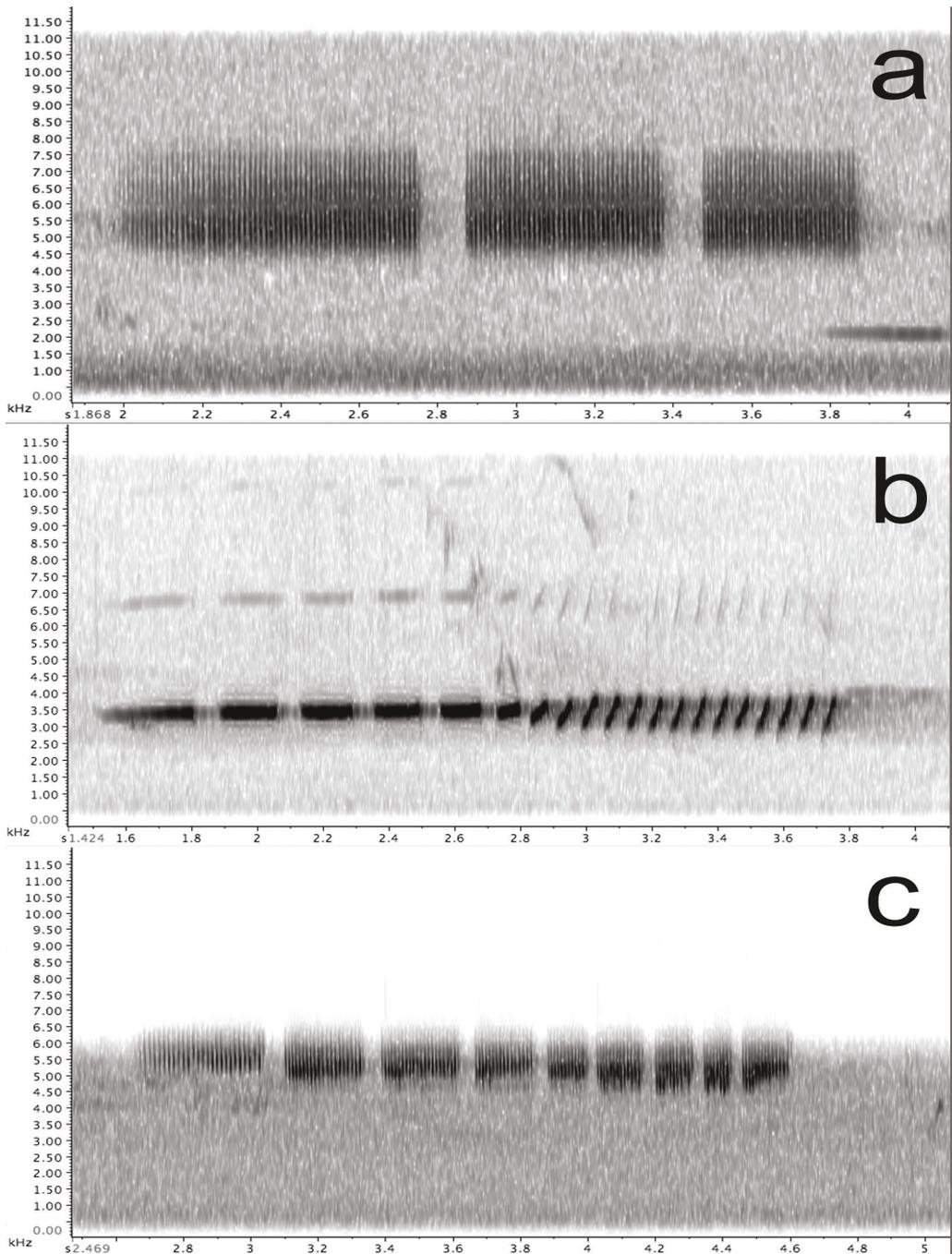


Figure 2. Sonograms of song from three *Spizella* sparrows. A: Clay-coloured Sparrow *S. pallida*, recorded in Oscoda County, Michigan, by A. Chartier on 27 June 2008 (xeno-canto.org, XC31304). B: Field Sparrow *S. pusilla*, recorded in Grant County, Wisconsin, by P. Marvin on 21 May 2011 (XC167935). C: Field × Clay-coloured Sparrow hybrid, recorded in Lorain County, Ohio, by A. T. Boone on 11 July 2008 (Macaulay Library ML113644741). The hybrid individual's song has the buzzy tones of a Clay-coloured Sparrow, but the accelerating cadence of a Field Sparrow.

coloured and Field sparrow samples, with all samples being homozygous. The hybrid was heterozygous, carrying one Clay-coloured Sparrow allele and one Field Sparrow allele. The small amount of DNA that we extracted from the feathers was used up in the ND2 and ACO1-19 PCR reactions, so no additional nuclear loci were available.

## Discussion

The combination of intermediate song characteristics, aggression to both parental songs, plumage appearance, bare-part colours, intermediate measurements, and a heterozygous nuclear allele confirm that this bird was a hybrid between a male Field Sparrow and a female Clay-coloured Sparrow.

Field and Clay-coloured Sparrow hybridisation has been suggested by multiple observers in the literature and eBird reports (Sullivan *et al.* 2009). Nests have been reported with both species attending them in Allegany County, New York (Brooks 1980) and Holmes County, Ohio (Weaver 2002). An adult that was thought to be a Clay-coloured × Field Sparrow hybrid was reported in Grand Isle County, Vermont, with intermediate plumage and song characteristics matching the present individual (Hoag 1999). Two additional reports are available at eBird with photographs of adults that are very similar to the present case, but with more rusty tones on the head and eyestripe, and no information concerning vocalisations (Hunterdon County, New Jersey; <https://ebird.org/view/checklist/S7726349>, accessed 10 August 2018; Muskingum County, Ohio; <https://ebird.org/view/checklist/S45469502>, accessed 10 August 2018). Finally, there are observations from Le Haut-Saint-Laurent County, Quebec, Canada, where an apparent hybrid male successfully fledged offspring with a female Clay-coloured Sparrow. The apparent hybrid sang a pure Clay-coloured Sparrow song, and resembled a pure Clay-coloured Sparrow except for rusty tones in the crown and supercilium, and a pink bill. This individual was perhaps a backcross hybrid (L. Tremlay pers. comm., <https://ebird.org/view/checklist/S46915359>, <https://ebird.org/view/checklist/S46943720> and <https://ebird.org/canada/view/checklist/S46980332>, accessed 26 September 2018).

Most studies of differential responses to playback involving hybrid birds are directed at patterns of response across hybrid zones, with a focus on the two parental species (e.g., Billerman & Carling 2016). In many well-studied systems, song is not strongly differentiated across the hybrid zone (e.g., Pearson & Rohwer 2000, Kenyon *et al.* 2017). Within Emberizidae, one similar rare hybrid case was examined for response intensity. A hybrid between a female White-throated Sparrow *Zonotrichia albicollis* and a male Dark-eyed Junco *Junco hyemalis* was held in captivity and presented with playback; it responded most strongly to its own song, at comparable intermediate levels to both parental species, and least strongly to a control (Jung *et al.* 1994). These studies consistently display aggression to both parental species. In the present case, the hybrid *Spizella* responded more strongly to Field Sparrow song. The hybrid's father was a Field Sparrow, and this species' song is likely the one it would have initially imprinted on as a nestling.

Clay-coloured and Field Sparrows are closely related. Klicka *et al.* (2014) found strong support for a monophyletic genus *Spizella*, with Clay-coloured likely sister to a clade of five species including Field Sparrow. Clay-coloured Sparrow has hybridised with both Brewer's Sparrow (Rotenberry *et al.* 1998) and Chipping Sparrow (Middleton 1998). Field Sparrow has not been documented to hybridise with other species except perhaps Vesper Sparrow *Poocetes gramineus* (Doolittle 1929). Hybridisation between Field Sparrow and Clay-coloured Sparrow may be increasingly common. All reported crosses reviewed here are within the breeding range of Field Sparrow, and coincide with the eastern edge of the Clay-coloured Sparrow range, where the latter species is increasingly observed during the

breeding season (Grant & Knapton 2012). Here, hybridisation between the two taxa may be more likely as edge-of-range individuals lack suitable mates.

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# The history of Aplomado Falcon *Falco femoralis* subspecies diagnoses

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**SUMMARY.**—I present the historical details associated with early 20th century descriptions of Aplomado Falcon subspecies. I identify potential weaknesses in these diagnoses that justify re-examination of traditional taxonomy, and stress that climate change, habitat modification and large-scale reintroduction efforts may have altered or eliminated any valid subspecies boundaries that once existed. I recommend that conservation efforts in the Northern Hemisphere focus on the Chihuahuan Desert of Mexico where Aplomado Falcons have declined severely in recent years.

In North America in the late 19th century, acceptance of subspecies as valid taxonomic units led to proliferation of numerous trinomials. This process accelerated in the first half of the 20th century (Coues 1871, Stejneger 1884, Stresemann 1975, Haffer 1992, Barrow 1998). By 1945 the number of named avian subspecies had exceeded 28,500, with new trinomials being coined at a rate of *c.*200 per year (Mayr 1946). In part, this trend reflected awareness that species are not fixed entities but demonstrate geographic variability potentially indicative of ongoing speciation (Ridgway 1879). New subspecies resulted partly from demotion of closely related, similar-looking species, but also from subdivision of single species into separate geographic forms (Stejneger 1884, Haffer 1992, Barrow 1998). Disruption of the Linnaean binomial system, the lumping of many formerly separate species, the trivial nature of diagnostic characters, and the resulting instability of nomenclature generated abundant criticism on both sides of the Atlantic (Coues 1884, Sharpe 1896, Allen 1890, Clark 1902, Sclater 1904, Ridgway 1923). In 1886, the American Ornithologists' Union (AOU) proposed restricting subspecies designations to geographic forms interconnected by intergradation within contiguous geographic distributions (AOU 1886).

Further proliferation of new subspecies led to demands for more consistent and less subjective criteria. Clark (1904), for example, proposed that size differences of less than 5% should not provide the basis for a subspecies diagnosis. He also urged that diagnostic characters be sufficiently conspicuous to be translatable into 'intelligible language or figures'. Allen (1905) and Merriam (1919) opposed such restrictions. Subsequently, Grinnell (1921) and Ridgway (1923) urged that proof of intergradation be revived in the interest of slowing further changes to nomenclature. But Chapman (1924), like Allen, objected to any 'unreasoning adherence to a purely arbitrary man-made law'. Swarth (1931) agreed, stating that 'science is not a game, to be won or lost according to set rules'. At another extreme, Hartert (1910) and Huxley (1939) proposed limiting subspecies designations to isolated (at least ecologically) and distinctive subpopulations, thereby making such diagnoses inappropriate for geographic forms interconnected by more gradual or 'clinal' variation (Huxley 1939). Nevertheless, taxonomists persisted in basing diagnoses on extremely small sample sizes of measured specimens, subjective

assessments of plumage differences, and inaccurate knowledge of the location of breeding vs. wintering distributions (Mayr 1935, Parkes 1982, Wilson & Brown 1953). Due to these and many other concerns, Mayr (1951) decried the waste of time spent by taxonomists 'describing and naming trifling subspecies'. Wilson & Brown (1953) called the system 'illusory and superfluous' and hoped it would eventually be relegated to 'nomenclatural limbo'.

Although controversy regarding subspecies has continued beyond the 20th century it still basically revolves around the concept's utility, its definition, and how best to evaluate putative races (Haig *et al.* 2006, Patten 2010, Winker 2010, McCormack & Maley 2015, Patten & Remsen 2017). Despite these concerns, the AOU has consistently emphasised that subspecies have value in demarcating unique coloration and morphology associated with specific geographic regions, migratory routes, habitats and behaviours; and to study the early stages of speciation (AOU 1886, 1983, 1998). Subspecies can also play a critical role in conservation biology if they identify evolutionarily unique populations and facilitate efforts to preserve the evolutionary potential of declining species (Haig *et al.* 2006, Phillimore & Owens 2006, Haig & D'elia 2010). In this regard, 79 subspecies currently appear on international lists of avian taxa designated Endangered or Threatened under the US Endangered Species Act of 1973 (as amended, 16 U.S.C. 1531 *et seq.*). Complicating such listings is the possibility that many subspecies, especially those described in the late 19th and early 20th centuries, may be invalid based on modern morphometric, colorimetric and genetic standards (Zink 2004, Dickinson & Remsen 2013, Patten & Remsen 2017, and others). Dickinson & Remsen (2013) cautioned that current global checklists may still recognise 'hundreds' of invalid subspecies. This possibility has spurred ongoing efforts to re-evaluate 'older' subspecies (Dickinson & Remsen 2013, Gill & Donsker 2019). Because of the risk of misallocating conservation resources, subspecies currently listed as threatened or endangered perhaps deserve highest priority in this endeavour (Crandall *et al.* 2000, Zink 2004, Fitzpatrick 2010, Patten 2010).

A potential case in point is provided by the Aplomado Falcon *Falco femoralis*, a widespread Neotropical raptor, well known to ornithologists since at least the early 19th century. By the early 20th century it was known to breed in Panama and various parts of South America but also in the south-west USA and north-east Mexico (Salvin & Godman 1904). Some authorities interpreted the lack of specimens from most of Mexico and northern Central America as a significant gap in the breeding range (Salvin & Godman 1904, Griscom 1932). This, plus one other supposed 'gap' in Argentina and perceived differences in size and coloration, served to justify subdividing the species into three, sometimes four, subspecies (Todd 1916, Swann 1922, Chapman 1925). Although Aplomado Falcon is considered Not Threatened or Least Concern (Bildstein *et al.* 1998, BirdLife International 2018, CITES 2018), in 1986 the northern subspecies so-called 'Northern Aplomado Falcon' *F. f. septentrionalis*, was listed as 'Endangered' under the US Endangered Species Act (Shull 1986, Keddy-Hector 1990). This rested on evidence of extensive pesticide contamination in eggs of eastern and southern Mexican Aplomado Falcons, as well as equivocal evidence of population declines in the south-west USA in the early 20th century (Kiff *et al.* 1980, Hector 1987, Keddy-Hector 2000). At no time during preparation (by this author) of materials to justify the Endangered status was the validity of the northern subspecies questioned. Here, I attempt to rectify this deficiency by providing a historical analysis of the evidence used to designate this and the other subspecies of this charismatic falcon.

TABLE 1

Averages, minima and maxima of wing chord measurements (mm) of Aplomado Falcon *Falco femoralis* subspecies as presented by different authorities (sample sizes in parentheses).

Subspecies	Male	Female	Reference
<b>INITIAL DIAGNOSES</b>			
<i>F. f. septentrionalis</i>			
Arizona (2)	267 (1)	294 (1)	Todd (1916) <sup>a</sup> ,
Arizona, Texas, Tamaulipas (10)	259 (6) 253–263	289 (4) 283–294	Todd & Carriker (1922) <sup>a,b</sup>
<i>F. f. femoralis</i>			
Colombia, Bolivia, Argentina (12)	240 (6) 230–248	267 (6) 263–271	Todd & Carriker (1922)
<i>F. f. pichincae</i>			
Ecuador (3)	--	290–295	Chapman (1922) <sup>a</sup>
<b>FIELD MUSEUM SPECIMENS</b>			
<i>F. f. septentrionalis</i>			
Texas, Tamaulipas, Nicaragua (11)	255–260	270–304	Hellmayr & Conover (1949) <sup>c</sup>
Not specified (15)	257 (8) 248–267	290 (7) 272–302	Blake (1977) <sup>c</sup>
<i>F. f. femoralis</i>			
Argentina, Bolivia, Brazil, Guyana, Panama, Paraguay, Uruguay, Venezuela (22)	225–252	255–290	Hellmayr & Conover (1949) <sup>c</sup>
Not specified (48)	237 (23) 226–254	263 (25) 245–282	Blake (1977)
<i>F. f. pichincae</i>			
Argentina, Bolivia, Colombia, Chile, Peru (13)	256–278	267–313	Hellmayr & Conover (1949) <sup>c</sup>
Not specified (15)	258 (5) 235–272	298 (10) 290–311	Blake (1977)
<b>COMPOSITE SAMPLES</b>			
<i>F. f. septentrionalis</i>			
Arizona, Texas, Chihuahua, Coahuila, Tamaulipas, Veracruz, Tabasco, Campeche, Chiapas (70)	262 (38) 229–289	293 (32) 267–314	DPK-H unpubl. <sup>a,b,c,d,e,f</sup>
<i>F. f. femoralis</i>			
Argentina, Belize, Bolivia, Brazil, Colombia, Guyana, Nicaragua, Paraguay (53)	238 (34) 220–260	269 (19) 254–285	DPK-H (unpubl.)
Argentina (28)	257 (9) 247–275	280 (19) 266–288	Liébana (2015) <sup>d</sup>
<i>F. f. pichincae</i>			
Bolivia, Chile, Peru (19)	268 (11) 256–280	301 (8) 286–318	DPK-H (unpubl.)

Sources: <sup>a</sup> US National Museum, Washington DC (USNM); <sup>b</sup> Carnegie Museum, Pittsburgh (CM); <sup>c</sup> Field Museum of Natural History, Chicago (FMNH); <sup>d</sup> Trapped, wild adults (Montoya 1995); <sup>e</sup> Museum of Comparative Zoology, Cambridge, MA (MCZ); <sup>f</sup> First-generation breeding project birds taken from nests and measured as adults at Peregrine Fund's Univ. of California Santa Cruz facility.

## History

In 1916, W. E. Clyde Todd, of the Carnegie Museum, proposed that Aplomado Falcons collected in Arizona represented a subspecies that he named *F. fusco-coerulescens*<sup>1</sup> *septentrionalis*. Todd described this form simply as ‘similar in color to *F. fusco-coerulescens*, but decidedly larger’ (Fig. 1). He provided no additional details, discussion of the geographic distribution, or any analysis of size differences. In fact, the account contains measurements of only two specimens, both from the same nesting territory near Fort Huachuca in south-east Arizona (Bendire 1887). These details appear at the end of a four-part series containing similarly brief ‘diagnoses’ of 55 new subspecies, 25 new species and one new genus along with a promise that more details would be forthcoming (Todd 1912, 1913, 1915, 1916).

Six years later, Todd fulfilled his promise by providing measurements of 11 North American (Arizona, Texas, and Tamaulipas) and ten South American (Argentina, Bolivia, Colombia) specimens (Todd & Carriker 1922). The wing chords of the two groups do not overlap and the North American sample averages 8% larger than that from South America (Table 1). Just one comment concerning plumage appears, in reference to the dark abdominal band of the northern birds: ‘the black area on the lower parts more extensive’. But Alexander Wetmore (1926) of the Smithsonian considered that plumages of birds in the two regions were ‘identical’, as did John Cassin in his characterisation of the first US specimen: ‘precisely identical with the South American bird’ (Cassin 1855). Swann (1936) mostly agreed: ‘scarcely differs in plumage from the southern typical form . . . slate of upper parts with a brownish shade’ but added ‘tail more widely banded with white’. Hellmayr & Conover (1949), after reviewing the large series of Aplomado skins at the Field Museum of Natural History, Chicago, supported and augmented Todd’s description: ‘Differs from the South American races by its light grayish upper parts (this being especially noticeable on the crown), extensive and solid black pectoral zone, and the light tone of the zinc-orange abdominal area’. Wetmore (1965) ultimately agreed: ‘distinguished by lighter-gray upper surface, with the breast solid black, and somewhat larger size’. Emmet Blake’s characterisation, also based on Field Museum specimens, is essentially identical and emphasises the larger size, complete abdominal band, and ‘paler, more grayish upper surface’ (Blake 1977). Like Hellmayr & Conover, Blake also mentioned the relative paleness of the lower abdomen ‘and tibiae’.

In 1925, Frank Chapman of the American Museum of Natural History, New York, described *F. fusco. pichincha*, based on the larger size of three females collected in the Andes of Ecuador (Chapman 1925). Wing chords of these specimens were as large as those of the largest North American birds (Table 1). Chapman also described the black area of the abdomen and flanks of Ecuadorian specimens as ‘smaller and divided medianly’. Swann (1936) later copied and extended Chapman’s description: ‘darker above, especially on the crown; zinc orange tints averaging deeper on the breast, the black area smaller and divided medianly’ and called this the ‘Andine Aplomado Falcon’. Hellmayr & Conover (1949) reiterated that *F. fusco. pichincha* is ‘considerably darker throughout, upper parts duskier, the pileum especially so; the ochraceous abdominal area deeper in tone; the black pectoral zone less extensive and more or less broken medially’. Blake (1977) once again agreed with

<sup>1</sup> Vieillot (1817) derived *Falco fusco-coerulescens* from Azara’s (1802) description of ‘*obscuro azulejo*’, one of the smaller Neotropical falcons (‘*losalconillos*’). This name had priority until Peters & Griswold (1943) pointed out that Azara’s description of *obscuro azulejo* better fit the smaller Bat Falcon *F. rufigularis*. Priority then shifted to Temminck’s (1822) *F. femoralis* (‘*Faucon a culotte rousse*’) that he based on actual specimens and Azara’s species description of an *alconillo* that he called the ‘*aplomado*’.



Figure 1. Female and male specimens of Aplomado Falcon subspecies, from left to right: *F. f. septentrionalis*, *F. f. femoralis* and *F. f. pichincae* (© Field Museum of Natural History, Chicago)

Hellmayr & Conover and emphasised the larger size (than the nominate form), incomplete abdominal band, and darker, more intense coloration.

A footnote in Griscom (1932) referred to a fourth subspecies. This acknowledged Swann's (1922) split of South American Aplomado Falcons east of the Andes into northern and southern forms. Swann (1922, 1936) credited Vieillot (1817) with describing the nominate form that Swann called the Southern Aplomado Falcon *Rhynchofalco*<sup>2</sup> *fusc. fusc.* and Temminck (1822) with describing the Lesser Aplomado Falcon *R. fusc. femoralis*. In Swann's view, Southern Aplomado Falcon was a larger, migratory form in Argentina and Chile, whereas Lesser Aplomado Falcon was a smaller, non-migratory form inhabiting the rest of South America east of the Andes. He distinguished the latter as 'more bluish slate, less brownish' (than *R. fusc. fusc.*), with the tail having 'much less white in it'. Wetmore (1939) opposed this and stated that Swann's Southern Aplomado Falcon was invalid because typical Lesser Aplomado Falcons had been collected at the type locality of the Southern Aplomado Falcon. He also felt that 'The geographic races of this falcon are not clearly outlined at the present time'. Peters & Griswold (1943) rejected Swann's Southern Aplomado but stated that Aplomado specimens from 'Chile and southern and western Argentina' were larger than typical *F. f. femoralis*. Hellmayr & Conover (1949) did the same, but suggested that the nominate form 'might have to be subdivided, as suggested by Swann', apparently because specimens from southern Argentina (Chubut) were almost as large as typical *F. f. pichincae* and possessed a 'medially broken blackish pectoral zone',

<sup>2</sup> *Rhynchofalco* is a monotypic genus or subgenus name proposed for Aplomado Falcon by Ridgway (1873) that reflected his belief that *F. femoralis* was not that closely related to Bat Falcon and Orange-breasted Falcon *F. deiroleucus*, which he and others placed in genus *Hypotriorchis*.

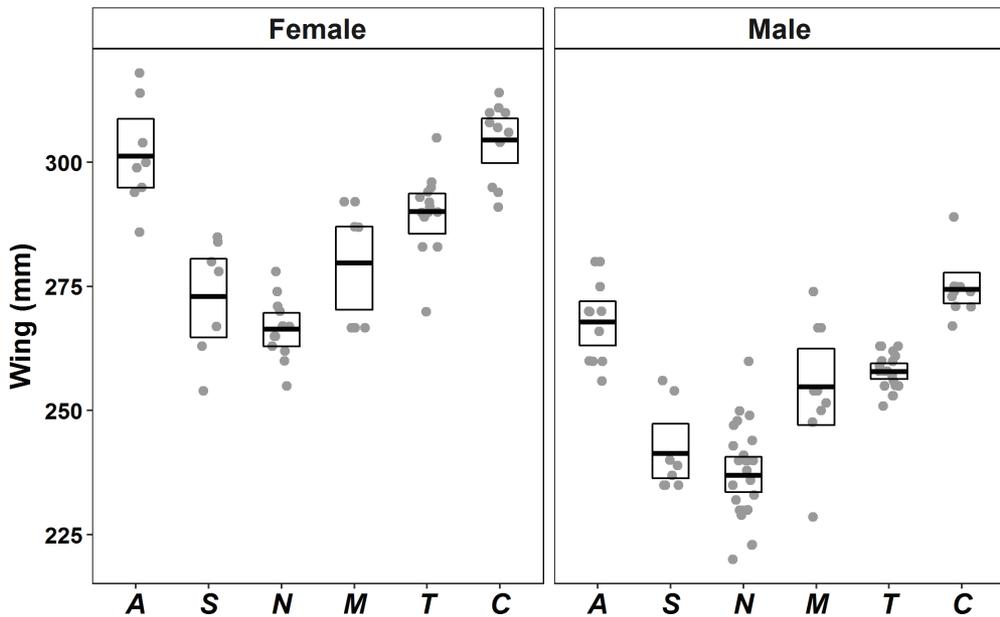


Figure 2. Comparison of means and bootstrapped 95% confidence limits of wing chord measurements (uncorrected for shrinkage) of Aplomado Falcon *F. femoralis* regional groups arranged to show variation in size along gradients of elevation and latitude: 'A' = *F. f. pichincha* from the Andes of Chile, Ecuador, Peru and western Bolivia; 'S' = *F. f. femoralis* from southern South America, in Argentina and Paraguay; 'N' = *F. f. femoralis* from Central America and northern South America east of the Andes and north of Argentina and Paraguay; 'M' = *F. f. septentrionalis* from the tropical coastal plains of Mexico; 'T' = *F. f. septentrionalis* from the coastal plain of north-east Mexico and southern Texas; and 'C' = *F. f. septentrionalis* from the Chihuahuan Desert of Arizona, Chihuahua and Coahuila.

while also being, like *F. f. septentrionalis*, 'very light and gray above'. This, however, partially conflicted with Peters & Griswold (1943) who described specimens from this region as 'brownier and darker' than typical *F. f. septentrionalis*.

Complicating all of this was the assumption that Aplomado Falcons were highly migratory (Swann 1922, Bent 1938, Wetmore 1939, Hellmayr & Conover 1949, Brown & Amadon 1968, Blake 1977). Swann (1922) and Wetmore (1939), for example, stated that the larger Aplomado Falcons of Peru were actually wintering *F. f. septentrionalis* from the USA and Mexico. Wetmore (1939) even suggested that Swann's larger, paler Southern Aplomado might be wintering *F. f. septentrionalis*. This view obviously conflicted with Swann's (1922) belief that Southern Aplomado Falcons migrated north in winter and partly explains Wetmore's reticence as to the validity of Southern Aplomado Falcon. But Hellmayr & Conover (1949) accepted Swann's scenario as an explanation for the mixture of smaller darker, and larger paler Aplomado specimens in east-central Argentina (Buenos Aires province). They proposed that this region was not inhabited by breeders, but only by 'migratory visitors, the small dark-backed ones coming from the north [*F. fusc. femoralis*?], the larger, paler ones being wanderers from Patagonia'. Eggs (Western Foundation of Vertebrate Zoology, Camarillo, and National Museum of Natural History, Washington DC) and field studies, however, show that the species does breed in Buenos Aires and surrounding provinces (Bó 1996, De Lucca & Saggese 1996, De Lucca & Quaglia 2012, De Lucca *et al.* 2013, Salvador 2013, Liébana 2015, De Lucca & De Lucca 2017). Residents from this population are also larger than typical *F. f. femoralis* (Liébana 2015; Table 1).

In the Northern Hemisphere, the paucity of specimens from Middle America coupled with disproportionate collecting in the south-west USA (Keddy-Hector 2000, Keddy-Hector *et al.* 2017) created the impression that more than 2,000 km separated Aplomado Falcons breeding in Arizona, New Mexico, Texas and Tamaulipas from the nearest resident population in western Panama. This notion appears to have supplanted an initial supposition that the species was resident throughout most of Mexico and Central America (Baird *et al.* 1874). Salvin & Godman (1904), for example, stated 'though not infrequent in Mexico, it is probably only a winter visitor there'. Griscom (1932) described the geographic distribution as 'remarkably disconnected' and thought that Aplomado Falcons of the south-west USA must winter in Guatemala. He also considered western Panama (Agua Dulce) the northernmost occurrence of resident *F. f. femoralis*. Perhaps reinforcing this belief was the possibility that many (perhaps most) US specimens—those collected by Frank Armstrong at 'Ft. Brown', 'Brownsville' or 'Cameron Co.', Texas—actually came from Mexico (Strecker 1912, Oberholser 1974, Hector 1987, Keddy-Hector 2000, Keddy-Hector *et al.* 2017).

One effect of this 'disconnection' was to make the known breeding range easily meet the liberating suggestion of Merriam (1897, 1919) and Stone (1903) that subspecies designations, in the absence of proof of intergradation, be applicable to isolated populations even if they differed only slightly from nearest neighbouring populations. This also met Huxley's (1939) criterion that a valid subspecies be 'partially or wholly isolated from related groups'. But the gap in the breeding range steadily shrank as collectors supplied specimens from additional parts of Middle America. This was acknowledged by Friedmann *et al.* (1950) who described the Aplomado as resident from the south-west USA south to the Yucatán and possibly even to Guatemala. This view has been confirmed by specimen and sight records from the tropical lowlands of San Luís Potosi, Veracruz, Tabasco, Campeche and Chiapas (Kiff *et al.* 1980, Hector 1981, reviewed by Keddy-Hector 2000, Keddy-Hector *et al.* 2017). Binford (1989) allowed for the possibility that the species was resident in Oaxaca, but felt that his February records only indicated winter residency. He was apparently unaware that, at least on the Caribbean slope, the species has an extended breeding season and resident pairs can commence incubation before the end of February (Keddy-Hector 2000). Howell & Webb (1995) suggested the species also breeds in Guerrero. Hellmayr & Conover (1949) postulated incorrectly that an adult male collected in early August in Nayarit (San Blas) indicated nesting. Breeding has also been documented in Chihuahua and Coahuila, but apparently from nowhere else in the Mexican altiplano or western Mexico (Hector 1981, Montoya 1995, Macías-Duarte 2002, Keddy-Hector *et al.* 2017).

Evidence of nesting also began to appear in Central America north of Panama. For Belize, Russell (1964) listed breeding-season records in February–June. In Nicaragua, Howell (1972) collected breeding-season (February–March) specimens including a presumed pair, of which the female had enlarged ovaries. Both authorities assigned specimens from the Caribbean slope to *F. f. femoralis*. Howell also noted that two immatures collected in April 1904 on the Pacific slope were intermediate in size between *F. f. septentrionalis* and *F. f. femoralis*. Hellmayr & Conover (1949) assigned these immatures to *F. f. septentrionalis* and interpreted them as migrants from the north, the month of collection, however, hints at a local natal site, and suggests the existence of a zone of intergradation connecting the two subspecies along the Pacific slope. A similar pattern occurs on the Caribbean slope, with southern Mexican *F. f. septentrionalis* averaging only slightly larger than *F. f. femoralis* from Central America and northern South America, but smaller than *F. f. septentrionalis* of the Chihuahuan Desert of Arizona, Chihuahua and Coahuila (Fig. 2). The species has also been observed and is probably resident in El Salvador (Jones & Komar 2006), Guatemala (Eisermann & Avendaño 2018) and Honduras (Marcus 1983). Aplomado Falcons were first

reported from Costa Rica in 1980, and there have been more recent sight records, mostly of subadults suggesting these are either vagrants or the product of local resident pairs (Koford *et al.* 1980, Jones & Komar 2011, eBird 2018).

The existence of non-breeding season specimen and sight records at higher latitudes and higher elevations has weakened the notion that this falcon is highly migratory (GBIF2018, eBird 2018). Bildstein (2004, 2006), in fact, classified it as a 'partial migrant' or 'altitudinal migrant'. Keddy-Hector *et al.* (2017) recommended changing this to 'local migrant'. This view is supported to some degree because this species clearly satisfies Bergmann's Rule (Bergmann 1847), with larger falcons inhabiting higher latitudes or higher elevations (Keddy-Hector *et al.* 2017). Rensch (1936), Mayr & Vaurie (1948), Mayr (1956), Zink & Remsen (1986) and Olson *et al.* (2009) suggested that highly migratory species tend not to show this pattern. Ashton (2002) found that 86% of sedentary and 67% of migratory species follow Bergmann's Rule. But Ferguson-Lees & Christie (2001) mentioned partial migration north from Patagonia and also some movement of Peruvian Aplomado Falcons from the high Andes to coastal locations. Sick (1993) described 'small migrant flocks' in August in southern Brazil. Macías-Duarte (2018) has recently documented 300 km dispersal by fledglings from Chihuahuan nests.

Closure of the gap in breeding distribution also narrowed the gap (and increased the overlap) in size between putative northern and nominate forms (Table 1, Fig. 2). Some of this is simply the result of increasing variability as a function of sample size, but enhancing this effect was larger numbers of specimens from coastal localities and tropical latitudes where Aplomado Falcons tend to be smaller. In this respect, wing chords of higher elevation Chihuahuan Desert Aplomado Falcons (Montoya 1995) averaged 7.0–8.5% (male–female) larger than those of southern Mexican (Campeche, Chiapas, Tabasco and Veracruz) birds (DPK-H unpubl.; Fig. 2). Wing chords of southern Mexican falcons averaged 6.2–3.2% (male–female) larger than those of *F. f. femoralis* specimens from Central America and northern South America.

## Discussion and Conclusion

Despite the larger size and allegedly paler coloration of Aplomado Falcons of southern Argentina, most modern authorities recognise only *F. f. femoralis*, *F. f. septentrionalis* and *F. f. pichincha* (Blake 1977, Mayr & Cottrell 1979, Dickinson & Remsen 2013, Keddy-Hector *et al.* 2017). In comparing these forms, Hellmayr & Conover (1949), Friedmann (1950), Wetmore (1965) and Blake (1977) generally agree on the following characters (Tables 2–3): (1) *F. f. septentrionalis* and *F. f. pichincha* both larger than *F. f. femoralis*; (2) *F. f. pichincha* incomplete dark abdominal band; (3) *F. f. pichincha* darker and more deeply coloured; and (4) *F. f. septentrionalis* more greyish dorsally. Only Swann (1936) mentioned broader white tail-bands in *F. f. septentrionalis*. Disagreements probably stemmed from the subjective and constraining process of using single colour categories to generalise variable and subtle differences typically present in whichever series of skins a taxonomist examined. Variable degrees of fading of older specimens, and of the colours of live birds prior to their collection, further complicated assessments, as did confusion as to differences between the more brownish subadult and more bluish or greyish adult dorsal colour. The last factor possibly explains the description of two Panamanian (Veraguas) *F. f. femoralis* as 'dark brown above' (Hellmayr & Conover 1949); Swann's (1936) application of 'brownish' to *F. f. septentrionalis*; and Peters & Griswold's (1943) 'brownier and darker' southern South American Aplomado Falcons. Together these inevitably led to seemingly contradictory characterisations such as Blake's (1977) description of *F. f. septentrionalis* as 'paler, more grayish' than *F. f. femoralis*, and *F. f. femoralis* as 'less bluish gray' than *F. f. septentrionalis*; in the aftermath of Swann's

TABLE 2  
Comparison of diagnostic characters of three Aplomado Falcon *Falco femoralis* subspecies.

	<i>F. f. septentrionalis</i>	<i>F. f. femoralis</i>	<i>F. f. pichincha</i>
Body size	Larger	Smaller	Larger
Coloration	Paler, more greyish	Darker to paler and more greyish	Darker
Abdominal band	Complete	Complete	Incomplete
White tail-bands	Broader	Narrower	Narrower

TABLE 3  
Comparison of diagnostic characters of Aplomado Falcon *Falco femoralis* subspecies, with *F. f. femoralis* subdivided into Swann's (1936) Lesser and Southern Aplomado Falcons.

	<i>F. f. septentrionalis</i>	<i>F. f. femoralis</i>		<i>F. f. pichincha</i>
		'Lesser' form	'Southern' form	
Body size	Larger to smaller	Smaller	Larger	Larger
Coloration	Greyer	Darker	Greyer	Darker
Abdominal band	Complete	Complete	Incomplete	Incomplete
Tail-bands	Broader	Narrower	Broader	Narrower

(1936) description of *F. f. septentrionalis* as having a 'brownish shade' and *F. f. femoralis* as 'more bluish slate' than *F. f. septentrionalis*.

That the descriptions of plumage are idiosyncratic is obviously just one of several reasons to question the validity (and utility) of these subspecies. In particular, the initial diagnoses depended on unacceptably small sample sizes of specimens (two for *F. f. septentrionalis*, three for *F. f. pichincha*), inaccurate initial impressions of breeding status and migratory behaviour, and of course lack of genetic or statistical analyses. Another concern is that the diagnostic characters are not consistent geographically (Wilson & Brown 1953, Barrowclough 1982). Incomplete abdominal bands occur in *F. f. pichincha* and southernmost *F. f. femoralis*; pale greyish upperparts in *F. f. septentrionalis* and southernmost *F. f. femoralis*; darker or at least less pale coloration in *F. f. pichincha* and tropical *F. f. femoralis*; broader white tail-bands in *F. f. septentrionalis* and southern *F. f. femoralis*; and larger body size occurs in northernmost *F. f. septentrionalis*, *F. f. pichincha* and southernmost *F. f. femoralis* (Tables 2–3).

Such deficiencies indicate that these subspecies should be re-evaluated using modern tests of diagnosability (Amadon 1949, Patten & Unitt 2002, Dickinson & Remsen 2013, Patten 2015, Patten & Remsen 2017). This requires evidence that for each quantifiable diagnostic trait at least 75% of the measurements of one subspecies overlap with no more than 1% of those of another subspecies, and vice versa (Amadon 1949, Patten & Unitt 2002, Baker *et al.* 2002). This test, in effect, determines whether diagnostic characters vary discontinuously (non-clinally) across some pre-established boundary (Huxley 1939, James 1970, 2010, Patten 2010). This re-evaluation is already in progress via an examination of geographic variation in size, proportions and plumage of specimens and live birds. Future work should also characterise the genetic basis for this variation.

Complicating any modern re-evaluation is the possibility that climate change, habitat modification and large-scale reintroduction efforts have altered or eliminated any regions of non-clinal variation that may have formerly constituted valid boundaries between

subspecies. This implies that any re-analysis based on measurements of older specimens may no longer reflect current patterns of geographic variation. Likewise, any re-analysis and generalisations (including my own) based on more recent distribution records and morphological variation may no longer be relevant to patterns present in late 19th and early 20th century specimens. Several studies have documented recent and rapid changes in avian body size—usually decreases—associated with rising global temperatures (Johnston & Selander 1964, Tornberg *et al.* 1999, Root *et al.* 2003, Root & Schneider 2006, Parmesan 2006, Yom-Tov & Yom-Tov 2006, Hitch & Leberg 2007, Sorte & Thompson 2007, Teplitsky *et al.* 2008, Gardner *et al.* 2009, Popy *et al.* 2010, Van Buskirk *et al.* 2010, Chen *et al.* 2011, Gardner *et al.* 2011, Matthews *et al.* 2011, Kirchman & Schneider 2014). Much of this shift is probably related to the influence of climatic regimes (temperature and humidity) on body size because the latter determines rates of heat loss or gain (Bergmann 1847, James 1970, 1991). This suggests that rising global temperatures have reduced the advantage of being large (for better heat conservation) in seasonally cooler climates and increased the advantage of being small (for better heat dissipation) in hotter, more humid environments (James 1970). This is obviously relevant to Aplomado Falcon because body size is or was the most important character used to diagnose subspecies. Diagnosability, as the degree of overlap in body size or any other character, depends on the degree to which subspecies disperse and interbreed at putative boundaries, and this depends on the extent to which climate regimes and habitat fragmentation have inhibited or promoted gene flow along latitudinal and elevational gradients.

Recent climate change and habitat disturbance have probably influenced geographic variation and the extent of interbreeding by Aplomado Falcons at potential subspecies boundaries by determining the spacing and extent of suitable grassland-savanna habitat. Deforestation has reversed a climate-driven trend toward expansion of tropical forest that began in the late Holocene (see review by Werneck 2011). In this regard, conversion of tropical forest to pasture has increased availability and contiguity of habitat in the tropical lowlands (Dirzo & Garcia 1992, Estrada *et al.* 1997, Achard *et al.* 2002, De Labra *et al.* 2013). This is especially evident on the Caribbean slope of Mexico where the species has clearly benefitted from removal and thinning of tropical deciduous and evergreen forests (Keddy-Hector *et al.* 2014, 2017). Deforestation may also account for its increasing presence in Guatemala (Eisermann & Avendaño 2018) and perhaps other parts of Central America.

In the subtropical to temperate grasslands of the Chihuahuan Desert and coastal prairies of southern Texas and north-east Mexico, climate change has probably reduced available habitat by promoting conversion of desert (or 'semi-desert') grasslands to shrubland or chaparral during the past two centuries (Buffington & Herbel 1965, Powell 1994). Exacerbating climate influences has been overgrazing by livestock and the expansion of dry-land farming. This has eliminated much desert grassland and promoted the rapid decline and near-extirpation of Chihuahuan Desert Aplomado populations studied by Montoya (1995), Macías-Duarte (2002) and Macías-Duarte *et al.* (2016). Prolonged drought has contributed to this decline by reducing prey availability and, in turn, falcon productivity (Macías-Duarte *et al.* 2004, 2016).

Large-scale translocation of Aplomado Falcons has the same potential as climate change and habitat alteration to blur or eliminate subspecies boundaries via increased gene flow (Storfer 1999, Avise 2004, Williford *et al.* 2014). This is particularly relevant to *F. f. septentrionalis* because, during 1985–2013, 1,893 captive-reared southern Mexican Aplomado Falcons were released in Texas and New Mexico. A surviving population of c.40 resident pairs in southern Texas is now managed to maximise productivity (Hunt *et al.* 2013). Many of these birds were released in close proximity to extant populations in Chihuahua and

southern New Mexico. Given uncertainty as to the validity of *F. f. septentrionalis* and the current southernmost extent of its distribution, it is possible that falcons released into the USA were more similar, in genetic, phenotypic and ecological terms to tropical lowland *F. f. femoralis* of Central America and northern South America than to the larger, upland, desert grassland-inhabiting *F. f. septentrionalis*. This was addressed preliminarily by Fleischer *et al.* (1998) who compared mtDNA and microsatellite DNA from Chihuahuan Desert falcons with captive southern Mexican individuals. Although this analysis found little difference between the two populations, the authors cautioned that their methodology was perhaps inadequate to detect some differences. The study also did not analyse mtDNA or microsatellite DNA from nearby putative *F. f. femoralis* populations. Ball *et al.* (1988), Winker (2009), Pérez-Emán *et al.* (2010), Oyler-McCance *et al.* (2010), James (2010), Patten (2015), Patten & Remsen (2017) and others have noted the limitations of neutral genetic markers like mtDNA to detect divergence in heritable variation of locally adaptive phenotypes.

These realities raise a concern as to the effect of this type of translocation, via releases of progeny of tropical lowland Aplomado Falcons, on declining populations in northern Mexico (Cunningham 1996, Snyder *et al.* 1996, Araki *et al.* 2007, Fraser 2008, Griffiths & Pavajeau 2008, Jacobsen *et al.* 2008, Leberg & Firmin 2008, Robert 2009). Introductions and translocations have the potential to dilute alleles responsible for adaptive phenotypic features and disrupt culturally transmitted adaptive behaviours, but might also provide long-term benefits by increasing genetic diversity and the evolutionary potential of target populations (Tallmon *et al.* 2004, Whiteley *et al.* 2014). They may also be controversial from a legal standpoint if such efforts flood populations of listed subspecies with genotypes of unlisted races.

The potential for detrimental impacts to declining Chihuahuan Desert populations is troubling, mainly because the larger size and desert to semi-desert habitat of these birds sets them apart both phenotypically and ecologically from lower elevation Aplomado Falcons that now range more or less continuously from southern Texas to South America. This distinctiveness was the basis for Todd's (1916) diagnosis of *F. f. septentrionalis*. Responsible action requires careful consideration of the potential impacts of such introductions before flooding this region with descendants of smaller tropical lowland falcons. The primary objective, as a means to preserve evolutionary potential and viable metapopulation structure, should be to preserve this desert-grassland, higher elevation form and its gene pool. One way to achieve this is to provide legal protection for the Chihuahuan Desert or Mexican Altiplano Aplomado Falcon as a 'distinct population segment' as provided for under the US Endangered Species Act (Haig *et al.* 2006, Haig & Delia 2010). Such protection would sharpen the focus of conservation actions on a region where Aplomado Falcons are actually in trouble, and away from the Gulf coast of Texas and Caribbean slope of Mexico where no recent declines have been reported and the species appears relatively secure (Keddy-Hector *et al.* 2017).

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# Clarifying the distributions of Abyssinian Crimsonwing *Cryptospiza salvadorii* and Red-faced Crimsonwing *C. reichenovii* in Tanzania

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**SUMMARY.**—Abyssinian Crimsonwing *Cryptospiza salvadorii* and Red-faced Crimsonwing *C. reichenovii* both occur in Tanzania but their distribution on Mt. Meru and in the Crater Highlands is poorly understood. Similarly, the southernmost record of *C. salvadorii* in Tanzania, in the Uluguru Mountains, is ambiguous. We conducted an in-depth literature review and detailed specimen evaluation of these two taxa and here clarify their ranges in northern Tanzania. We failed to find definitive evidence for the presence of *C. salvadorii* in the Uluguru Mountains.

Abyssinian Crimsonwing *Cryptospiza salvadorii* and Red-faced Crimsonwing *C. reichenovii* occur in Tanzania and a few other countries in sub-Saharan Africa. *C. salvadorii* is found from Ethiopia south to northern Tanzania and eastern Democratic Republic of Congo (Zimmerman *et al.* 1996, Keith 2004, Payne 2010). *C. reichenovii* occurs in East Africa from the Albertine Rift Mountains to the Eastern Arc Mountains, and south to the highlands of Mozambique and Zimbabwe, with disjunct populations in the Cameroon-Nigeria highlands and Bioko, and western Angola (Keith 2004, Payne 2010).

Numerous sources covering East African birds (Mackworth-Praed & Grant 1960, White 1963, Hall & Moreau 1970, Britton 1980, Short *et al.* 1990, Zimmerman *et al.* 1996, Keith 2004) provide the southern limit of the range of *C. salvadorii* as forested areas in northern Tanzania on Mt. Kilimanjaro, Mt. Meru and the Crater Highlands. However, there is a record from the Uluguru Mountains reported by Friedmann & Loveridge (1937) that was later questioned by Stuart & Jensen (1985). Our primary aim here is to evaluate this Uluguru record, and to clarify the distribution of this taxon, as well as that of its congener *C. reichenovii*, in northern Tanzania.

## Methods

Information concerning *C. salvadorii* and *C. reichenovii* on Mt. Meru, Mt. Kilimanjaro, the Crater Highlands and adjacent volcanos, and the Uluguru Mountains, was reviewed via the literature and an examination of specimens from Tanzania housed in major collections in Europe and North America. With the exception of a few cases, all of the specimens evaluated and discussed in this paper are listed by museum collection, registration number and collector in the Appendix. Museum acronyms are as follows: FMNH = Field Museum of Natural History, Chicago; MCZ = Museum of Comparative Zoology, Harvard University, Cambridge, MA; NHMUK = Natural History Museum, Tring; YPM = Peabody Museum of Natural History, Yale Univ., New Haven, CT; ZMB = Museum für Naturkunde, Berlin; ZMUK = Zoologisk Museum, Copenhagen. A map is provided to facilitate a coherent understanding of our evaluation of distributional records of these two crimsonwings in Tanzania (Fig. 1).

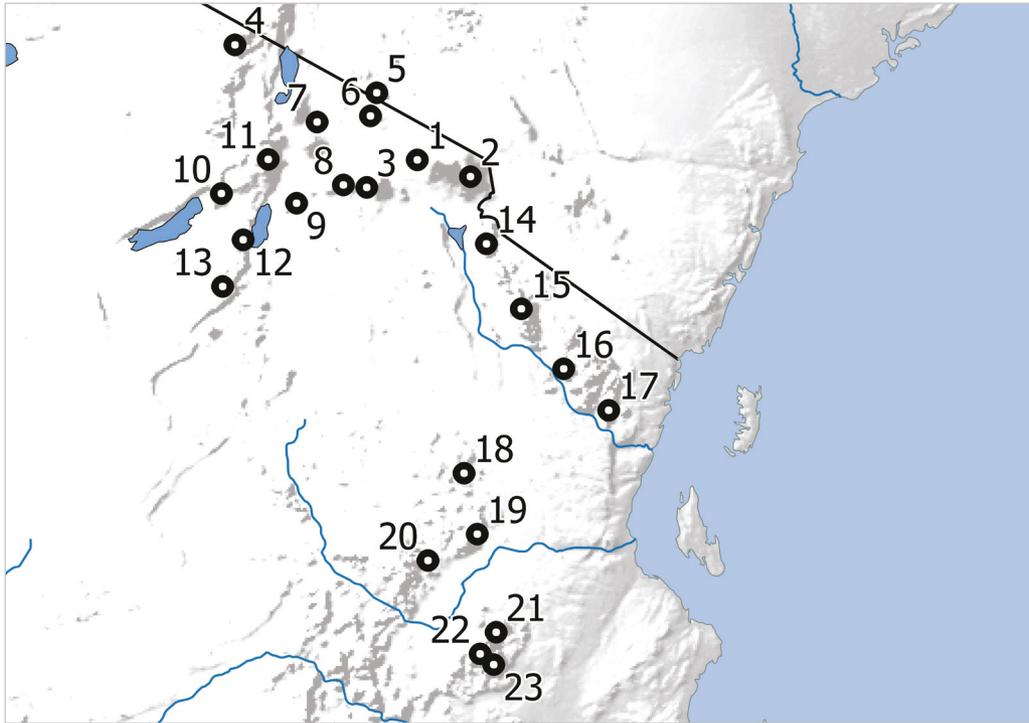


Figure 1. Distributions of Abyssinian Crimsonwing *Cryptospiza salvadorii* and Red-faced Crimsonwing *C. reichenovii* in northern Tanzania and in the Eastern Arc Mountains. Localities as follows: (1) Engare Nairobi, Mt. Kilimanjaro, (2) Mandara, Mt. Kilimanjaro, (3) Olmotoni, Mt. Meru, (4) Loliondo, (5) Ol Doinyo Orok (Kenya), (6) Longido, (7) Kitumbeine, (8) Monduli, (9) Essimingor, (10) Oldeani, (11) Ngorongoro, (12) Marang Forest, (13) Nou Forest, (14) North Pares, (15) South Pares, (16) West Usambaras, (17) East Usambaras, (18) Nguu Mountains, (19) Nguru, (20) Ukagurus, (21) Bagilo, Ulugurus, (22) Tchenzema, Ulugurus, (23) Ukwama, Ulugurus. Two other localities could not be marked due to issues of scale: Mgeta (07°02'S, 37°34'E) and Lukwangule (07°14'S, 37°62'E) are just north and east of Tchenzema, respectively. Map created using QGIS 2.18 (QGIS Development Team (2019) with background layers from <https://www.naturalearthdata.com/>.

## Distribution in northern Tanzania

The ranges of *C. salvadorii* and *C. reichenovii* in northern and eastern Tanzania are of interest because their contact zone is purportedly Mt. Kilimanjaro and Mt. Meru (Keith 2004, Payne 2010), but is actually the Crater Highlands as we demonstrate here (Fig. 1). Reports of both *C. salvadorii* and *C. reichenovii* on Mt. Meru are ambiguous. In his annotated list of the birds of Arusha National Park, based on his own records, a small skin collection in the park museum, and notes from D. F. Vesey-FitzGerald, Beesley (1972) reported both *C. salvadorii* and *C. reichenovii* on Mt. Meru. However, he stated 'These two species are treated together, and although none has yet been obtained, I believe their identification is correct.' During his 1905–06 expedition to Mt. Kilimanjaro and Mt. Meru, Sjöstedt (1908) recorded *C. salvadorii* only on Mt. Meru, at 3,500 m. Moreau & Sclater (1935) also reported *C. salvadorii* on Mt. Meru, based on two male specimens from c.1,700 m at Ngare Olmotoni (= Olmotoni: Fig. 1; Appendix). They also reported the first record of the species on Mt. Kilimanjaro, in the west at Ngare Nairobi (c.1,750 m), and in the south at 'Bismarck Hill' (= Mandara, c.2,700 m; Fig. 1; Appendix) (Moreau & Sclater 1935). There is also a 2009 specimen of *C. salvadorii* from Mt. Meru in FMNH (Appendix). Finally, a specimen listed in VertNet.org as *C. reichenovii* from Mt. Meru at YPM (leg. G. Heinrich) is in fact an adult female *C. salvadorii*

(1,800 m, 21 June 1962; Appendix). There are no confirmed reports of *C. reichenovii* on Mt. Meru, and the report of this species in Keith (2004) might reflect Beesley's (1972) statement. Regarding Mt. Kilimanjaro, dated specimens as well as mist-netted birds all confirm *C. salvadorii* as the only crimsonwing on the mountain (Cordeiro 1994, Dulle *et al.* 2016); the record by NJC of a pair of *C. reichenovii* on the west slope above Ngare Nairobi (Cordeiro 1994) and repeated by Keith (2004), must be rejected as no male (with its diagnostic red lores) was observed clearly at the time.

*C. salvadorii* occurs (R. E. Moreau specimens in NHMUK; Appendix) on Kitumbeine, Longido, Monduli and Essimngor, the four forested mountains nearest to Mt. Meru and Mt. Kilimanjaro (Fig. 1). It is also present on Mt. Oldeani, the highest forested peak in the Crater Highlands (Moreau & Sclater 1938) (Fig. 1). North of the latter, *C. salvadorii* occurs in Loliondo (Selempo 1994) and Ol Doinyo Orok at 1,800 m on the Kenyan side of the border, near Longido (Bennun *et al.* 1986) (Fig. 1).

*C. reichenovii* appears to be the more widespread crimsonwing species in the Crater Highlands and forests to the south along the Gregory Rift. There are records of this species from Nou and Marang Forests (Moreau & Sclater 1938, Elliott & Fuggles-Couchman 1948; also two specimens in ZMUC from Marang Forest at 1,600 and 1,850 m; Fjeldså 2015) and more generally, the Crater Highlands (Elliott & Fuggles-Couchman 1948) (Fig. 1). Of interest, there is also a specimen of *C. salvadorii* from Nou Forest (leg. J. Kiure, 19 April 2004, ZMUC: Fjeldså 2015). Records of *C. salvadorii* from Nou Forest at a higher elevation of 2,400 m (Fjeldså 2015; Appendix) and of *C. reichenovii* at c.1,950–2,100 m (Moreau & Sclater 1938; Appendix), represent the only currently known Tanzanian location where both species of crimsonwing are found (Fig. 1). Whether they co-occur at similar elevations in Nou Forest is unknown.

Of particular interest, these two species co-occur on four different Albertine Rift mountains. Four *Cryptospiza* species inhabit the Ugandan side of the Ruwenzori Mountains (Willard *et al.* 1998). *C. reichenovii* was found at the lowest elevations (1,960 m) and *C. salvadorii* at 2,700 m, but neither species was found at 2,075 m (Willard *et al.* 1998). On the other hand, Dusky Crimsonwing *C. jacksoni* and Shelley's Crimsonwing *C. shelleyi* overlapped with their congeners, at 1,960–2,700 m and 1,960–3,400 m, respectively. Another study in the Ruwenzori Mountains, Uganda, recorded *C. jacksoni* (1,800–2,700 m), *C. shelleyi* (2,100–3,000 m), and of the two species we focus on, *C. reichenovii* occurred at 1,800 and 2,400 m, with an unresolved identification of *C. salvadorii* / *C. reichenovii* at 2,100 m (Dehn & Christiansen 2001). In the Itombwe Massif, Democratic Republic of Congo, Prigogine (1980) similarly recorded no overlap in elevational ranges among *C. reichenovii* (1,590–1,850 m), *C. shelleyi* (1,890–2,050 m) and *C. salvadorii* ( $\pm$  2,530 m). In the Nyungwe Mountains, Rwanda, where all four *Cryptospiza* occur, the overall ranges overlapped for *C. reichenovii* (1,700–2,500 m) and *C. salvadorii* (1,750–2,350 m), especially in the Bururi Valley (Dowsett-Lemaire 1990). Finally, Turner (in prep.) reports *C. reichenovii* and *C. salvadorii* as sympatric at 2,150–2,450 m in Bwindi-Impenetrable National Park, Uganda. In summary, the evidence of altitudinal range overlap between *C. reichenovii* and *C. salvadorii*, when they co-occur on the same mountain, is probable in the Ruwenzoris, but only definite on two of the four Albertine Rift mountains.

## Do both *Cryptospiza* species occur in the Uluguru?

Lack of definitive evidence of altitudinal overlap between *C. reichenovii* and *C. salvadorii* in their entire Tanzanian range has an important bearing on the report of both species co-occurring 400 km south of Mt. Kilimanjaro, in the Uluguru Mountains, Tanzania (Friedmann & Loveridge 1937, Friedmann & Stager 1964). Svendsen & Hansen (1996)

noted that *C. reichenovii* occurs at 900–2,520 m in the Uluguru. The supposed Uluguru record of *C. salvadorii* in Friedmann & Loveridge (1937) involved a female collected by A. Loveridge at Mbeta (probably = Mgeta at c.1,100 m) in the Uluguru Mountains on 24 July 1922. Friedmann was unable to assign this bird to any known subspecies (Friedmann & Loveridge 1937). His comments on this specimen, which is at MCZ, were as follows:

'This single specimen is obviously *C. salvadorii* and not *C. reichenowi*, but it does not fit any of the races of the former. Sclater [Sclater 1930] does not record the species from Tanganyika Territory at all, but Shelley [Shelley 1905] notes that, '. . . in its most southern range the species has been met with by Dr. Stuhlmann at Uluguru.'

'The bird is darker below than *ruwenzori* [= *C. salvadorii ruwenzori*], but is olive-green, not brown as in the Nyasaland form *australis* [= *C. reichenovii australis* following Mackworth-Praed & Grant 1955]. It may belong to a hitherto unknown race intermediate between these two, but more material is needed to make certain of this. For the present the bird may best be designated as above, and its absolute determination left for a more propitious occasion.

'The bird is in fairly fresh plumage; the amount of red on the lower back is intermediate between *borealis* [= *C. s. salvadorii* following Grant & Mackworth-Praed 1945] and *ruwenzori*; the crown is duskier olive-green than in most specimens of either of these. The wing is short, only 50 mm, as against 55–56 mm in females of *ruwenzori* and 56 mm in *borealis*.' (Friedmann & Loveridge 1937: 375)

First, it is important to note that in Friedmann's statement quoted above ('Sclater [Sclater 1930] does not record the species from Tanganyika Territory'), Moreau (1938) corrected Sclater's error that *C. salvadorii* did not occur in Tanzania, as Sclater had previously described *C. s. kilimensis* from Mt. Kilimanjaro in 1934. Franz Stuhlmann, referred to by Shelley (1905), collected plants during 1894–95 in the Uluguru Mountains (Polhill & Polhill 2015), but he also collected bird specimens, some of which were described by Reichenow (1895, 1904). Reichenow's (1895) first mention of the crimsonwing collected by Stuhlmann, presumably from the Uluguru, was listed as '*Cryptospiza salvadorii*'. Further descriptions followed in his tome on African birds, where *C. reichenovii* is considered mostly a species of western Africa with an additional distribution near Lake Victoria, and *C. salvadorii* considered to range across the mountains of eastern Africa (Reichenow 1904: 174). Reichenow mentioned the Stuhlmann specimen from the eastern Uluguru, and for *C. salvadorii* stated more generally ['es bedarf fernerer untersuchung, ob *C. australis* von *C. salvadorii* zu sondern ist'] that this taxon 'also requires further investigation on whether or not it is *C. australis* [now = *C. reichenovii australis*] or *C. salvadorii*', but listed localities from Kenya, Tanzania and Malawi for *C. salvadorii*, with Malawi records under *C. australis*. The Stuhlmann specimen at the Museum für Naturkunde (ZMB 2000/20225), Berlin, was identified as *C. reichenovii australis* (Fig. 2), and we conclude that Reichenow was correct in assigning this specimen to '*C. australis*' and stating that more work was needed to resolve the identification of his grouping.

In addition to the early Stuhlmann record of a putative *C. salvadorii* in the Uluguru (Reichenow 1904, Friedmann & Loveridge 1937, Friedmann & Stager 1964), there is also Loveridge's record of this species from there some years later (Friedmann & Loveridge 1937). Loveridge's specimens were examined at MCZ and two were subsequently sent on loan from MCZ, and compared to a series of *C. reichenovii* and *C. salvadorii* from Kenya and Tanzania at FMNH. There are four Loveridge *Cryptospiza* specimens collected in the Uluguru (Appendix), all of which were mentioned by Friedmann & Loveridge (1937). One (MCZ 134085) has long been considered *C. salvadorii*, and the other three (MCZ 134082, 134083, 134084) were identified as *C. reichenovii* in the same paper.



Figure 2. The female *Cryptospiza* specimen collected by F. Stuhlmann in October 1894 at 2,500 m in the Uluguru Mountains, Tanzania, initially identified as Abyssinian Crimsonwing *C. salvadorii* (presumably by A. Reichenow) and now correctly identified as Red-faced Crimsonwing *C. reichenovii australis*, Museum für Naturkunde, Berlin (© S. Frahnert)

*Birds of Africa* (Keith 2004) reported the ranges of wing and tail measurements, respectively, for females of *C. salvadorii kilimensis* (wing 56–58 mm, mean = 57.0 mm; tail 40–44 mm, mean = 41.9 mm) and *C. r. reichenovii* (wing 52–57 mm, mean = 53.9 mm; tail 36–41 mm, mean = 39.4 mm). As such data were not provided for *C. r. australis*, the race in the Eastern Arc Mountains to Malawi and Mozambique (Britton 1980, Keith 2004), we measured seven females of *C. r. australis* from Malawi, Mozambique and the Uluguru Mountains from the FMNH series. One Uluguru adult female (MCZ 134084) measured 54 and 39 mm for wing and tail, whereas the juvenile female (MCZ 134085) correspondingly measured 50 and 41 mm, respectively. Wing and tail measurements of *C. r. australis* were 52–56 (mean = 54.9) and 36–40 (mean = 39.2) mm, respectively. Comparing these measurements places the adult MCZ specimen within the range of *C. reichenovii* rather than *C. salvadorii*.

Data from the original labels of the MCZ *Cryptospiza* specimens collected by A. Loveridge from the Uluguru Mountains further clarified the anomalies leading to the misidentification of this taxon as *C. salvadorii*. The identification of *C. salvadorii* was based on the immature specimen (MCZ 134085; collected 24 July 1922) (Friedmann & Loveridge 1937). Differentiation of juveniles and immatures of the two species is difficult (Clement 1993, Stevenson & Fanshawe 2002). Friedmann & Loveridge (1937) were probably unaware that they based their identification on a juvenile, but made no comparisons with six other specimens of *C. reichenovii*, collected by A. Loveridge at Bagilo, in the Uluguru Mountains (Friedmann 1928, Friedmann & Loveridge 1937).

Plumage comparisons of the adult MCZ specimen with a series of females of *C. salvadorii kilimensis* and *C. reichenovii australis* also revealed that the MCZ specimen is more olive on the breast and chest, as well as the head, back and mantle, giving it a slightly darker appearance consistent with *C. reichenovii* (Fig. 3). In contrast, the overall tones of female *C. salvadorii kilimensis* are greyer on the mantle and back, and paler grey-tan on the breast (Fig. 3). In contrast to adult plumage, the immature MCZ specimen more closely matches juvenile *C. r. australis*, but the richer browner coloration and less red on back and mantle is not 100% distinguishable from immature *C. s. kilimensis* (Fig. 4).



Figure 3. Comparative dorsal (top) and ventral (bottom) views of female Red-faced Crimsonwing *Cryptospiza reichenovii australis* and Abyssinian Crimsonwing *C. salvadorii kilimensis*, including the Loveridge specimen from the Uluguru Mountains. Specimens (left to right) as follows: *C. r. australis* (Bagilo, Uluguru Mountains, Tanzania, leg. A. Loveridge, 5 May 1922, MCZ 134084); *C. r. australis* (Bunduki, Uluguru Mountains, Tanzania, leg. J. G. Williams, 6 November 1948, FMNH 188139); *C. r. australis* (Nyika Plateau, Malawi, leg. N. Goswami, 12 November 2009, FMNH 468432); *C. s. kilimensis* (Engare Nairobi, Mt. Kilimanjaro, Tanzania, leg. R. E. Moreau, 12 February 1938, FMNH 203748); *C. s. kilimensis* (near Limuru, Kenya, leg. J. G. Williams, 18 July 1950, FMNH 103503); *C. s. kilimensis* (Chyulu Hills, Kenya, leg. unknown, 29 June 1938, FMNH 103500); *C. s. kilimensis* (Chyulu Hills, Kenya, leg. unknown, 1 June 1938, FMNH 103498) (N. J. Cordeiro)



Figure 4. Comparative dorsal (top) and ventral (bottom) views of juvenile / immature specimens of Red-faced Crimsonwing *Cryptospiza reichenovii australis* and Abyssinian Crimsonwing *C. salvadorii* of both sexes, including the Loveridge specimen from the Uluguru Mountains described in Friedmann & Loveridge (1937). Specimens (left to right) as follows: *C. r. australis* (female, 'Mbeta' = Mgeta, Uluguru Mountains, Tanzania, leg. A. Loveridge, 24 July 1922, MCZ 134085); *C. r. australis* (male, Mt. Gorongosa, Mozambique, leg. S. Reddy, 20 August 2011, FMNH 481454); *C. r. australis* (female, Mt. Gorongosa, Mozambique, leg. C. Salema, 15 August 2011, FMNH 481450); *C. r. australis* (male, Dabaga Highlands, Iringa, Tanzania, leg. J. G. Williams, 26 March 1952, FMNH 217021); *C. salvadorii ruwenzori* (female, Nairobi, Kikuyu, Kenya, leg. V. G. L. van Someren, 24 May 1918, FMNH 203742) (N. J. Cordeiro)

It would be surprising if *C. salvadorii* occurs in the Ulugurus and Mt. Kilimanjaro and not in intervening Eastern Arc montane forests (North and South Pare, West and East Usambara, Nguu, Nguru and Ukaguru: Fig. 1) where, instead, *C. reichenovii* is present (Fjeldså *et al.* 2010). However, the Lukwangule Plateau in the southern portion of the Ulugurus rises to 2,630 m, higher than any mountain further north in the Eastern Arc. It is also noteworthy that Brown Woodland Warbler *Phylloscopus umbrovirens* has an overall similar distribution to *C. salvadorii* with an isolated population on the Lukwangule Plateau (Britton 1980, Urban *et al.* 1997). This perhaps added some weight to accepting the possibility of a similar disjunct distribution of *C. salvadorii* in the southern Ulugurus. Considerable ornithological research and collecting has been done in the Eastern Arc Mountains since the 1930s (Fjeldså *et al.* 2010), but there have been no records of *C. salvadorii*. *C. Werema* mist-netted birds throughout the Ulugurus and only recorded *C. reichenovii* (Werema 2016, Werema & Howell 2016). The Lukwangule Plateau represents the only possible location where *C. salvadorii* might be found in the Eastern Arc based on elevation. However, specimens of two males and one female collected there by Moreau at 2,150 m are *C. reichenovii* (all at NMHUK; Appendix). Two sight records of putative *C. salvadorii* were claimed for the Ulugurus in October 1993 (Svendsen & Hansen 1996). Both were singles outside of the forest, at 1,430 m near Ukwama, and at 1,600 m at Tchenzema (Svendsen & Hansen 1996; see Fig. 1), in habitat and at elevations consistent with *C. reichenovii* (Britton 1980). The authors stated ‘the birds were seen under good conditions, the Tchenzema bird being observed for 5 minutes at only 10 m distance’, but they provided no details of the sex or age of the birds in either observation.

Both *Cryptospiza* species discussed here occur as pairs, and our collective observations suggest that vagrant singles are mostly immatures. Following our examination of specimens, we conclude that all of the specimens and observations claimed as *C. salvadorii* from the Uluguru Mountains were misidentified *C. reichenovii*, as follows: (i) F. Stuhlmann’s first *Cryptospiza* specimen from 1894 was indeed *C. reichenovii*; (ii) the previous identification of Loveridge’s Uluguru immature *Cryptospiza* specimen as *C. salvadorii* can be rejected; (iii) the identification of another of Loveridge’s specimens from the same mountain and in the same year as *C. reichenovii* is confirmed; (iv) all other dated crimsonwing records, including a more recent collecting expedition (Friedmann & Stager 1964), and all other known specimens from the Uluguru Mountains in the museum collections we studied can be identified as *C. reichenovii*; and (v) the only definitive record of the two species co-occurring in Tanzania is from Nou Forest, although overlap in elevation is apparent elsewhere where both species co-occur (i.e. at least two of four Albertine Rift mountains).

Therefore, with no other records of *C. salvadorii* from the Ulugurus, including during the intensive mist-net sampling by *C. Werema*, we reject the identification of the two sight records in 1993 (Svendsen & Hansen 1996) as *C. salvadorii*. We surmise that Stuart & Jensen (1985) were the first to correctly treat early reports of *C. salvadorii* in the Ulugurus as probably misidentified *C. reichenovii*, but despite their concern, until now, no one investigated this claim. Unless a specimen or definitive photograph is obtained that proves otherwise, we conclude that *C. reichenovii* alone occurs in the Uluguru Mountains, Tanzania.

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## Appendix

List of all specimens consulted for this study (locality, museum acronym, registration number, sex, and collector). Refer to Fig. 1 for localities and to Methods for museum acronyms.

### Abyssinian Crimsonwing *Cryptospiza salvadorii*

Mt. Kilimanjaro, Ngare Nairobi: NHMUK 1934.6.18.61 (m), 1934.6.18.62 (m), leg. R. E. Moreau; Mandara: NHMUK 1934.6.18.63 (m), 1934.6.18.64 (f), leg. R. E. Moreau.

Mt. Meru, Ngare Olmotoni: NHMUK 1939.6.19.274 (m), 1939.6.19.224 (m), leg. R. E. Moreau; unspecified location: FMNH 484698 (sex not recorded), leg. M. Munissi; near Momela: YPM 96397 (f), leg. G. Heinrich.

Oldeani, Crater Highlands: NHMUK 1935.12.25.330 (m), 1935.12.25.331 (m), 1935.12.25.332 (m), leg. R. E. Moreau.

Essimngor, northern Tanzania: NHMUK 1935.12.25.333 (m), leg. R. E. Moreau; 1938.3.13.35 (sex unknown, juv), leg. E. G. Rowe.

Ketumbeine, northern Tanzania: NHMUK 1937.6.22.203 (f), 1937.6.22.204 (f), 1937.6.22.205 (f), 1937.6.22.206 (f), 1937.6.22.209 (f), leg. R. E. Moreau.

Monduli, northern Tanzania: NHMUK 1937.6.22.207 (f), leg. R. E. Moreau.

Longido, northern Tanzania: NHMUK 1937.6.22.208 (f), 1937.6.22.210 (m), leg. R. E. Moreau.

Nou Forest, Crater Highlands (ZMUC 094982), leg. J. Kiure.

### Red-faced Crimsonwing *Cryptospiza reichenovii*

Nou Forest, Crater Highlands: NHMUK 1935.12.25.322 (f), 1935.12.23.323 (f), 1935.12.25.324 (m), 1935.12.25.325 (f), 1935.12.23.326 (f), 1935.12.25.327 (f), 1935.12.25.329 (f), leg. R. E. Moreau.

Uluguru Mountains, Lukwangule Plateau: NHMUK 1937.12.27.334 (m), 1937.12.27.335 (m), 1937.12.27.337 (f), leg. R. E. Moreau; location not specified: MCZ 134082 (m), MCZ 134083 (f), leg. A. Loveridge; location not specified: ZMB 2000/20225 (f), leg. F. Stuhlmann; Bagilo: MCZ 134084 (f), leg. A. Loveridge; Mgeta: MCZ 134085 (f), leg. A. Loveridge.

# Adding value to collections: improving the data associated with Crested Ibis *Nipponia nippon* specimens held in the Natural History Museum, Tring

by Robert Prÿs-Jones

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**SUMMARY.**—In the bird collection of the Natural History Museum at Tring (NHMUK), and no doubt in many analogous collections elsewhere, older specimens are increasingly likely to have become divorced from some, or even all, of the data that once accompanied them. As the utility of such specimens for research depends in large part on their accompanying data, it is important, though time-consuming, to try to restore missing data to them. Stimulated by a genomic research project request to sample all Crested Ibis *Nipponia nippon* specimens in the NHMUK collection, this paper presents a case study of such an attempt. The results are used to highlight the importance that such investigation is factored into projects aiming to make museum specimen data available online.

In early 2014, the Natural History Museum at Tring (NHMUK) received a request for DNA samples from all of its skin specimens of Crested Ibis *Nipponia nippon* as part of a genomic research project examining the genetic changes the species has undergone during the crash in its population size and distribution over the past 150 years (Feng *et al.* 2019). The most recent published catalogue of such specimens is that presented by Knox & Walters (1994), from which all relevant data are summarised in Table 1. Since then no additional specimens of the species have been received by NHMUK.

Table 1 indicates that NHMUK formerly held 23 or 24 relevant specimens collected between *c.*1840 and 1910, the uncertainty arising because one of two specimens found unregistered when the data were gathered (1988) was considered potentially to have been a previously registered specimen that had become detached from its label. As at least three specimens appeared to be missing from the collection, this left 20 available for sampling. To place this in context, from museums worldwide in total only *c.*60 historic museum specimens of this now extremely rare species were available to the genomic research project (Feng *et al.* 2019).

Contributing specimen molecular samples to a project such as this provides both obligations and opportunities to museum curators. Considering obligations first, both the quality and quantity of data on the label(s) attached to each specimen, in particular that associated with collection locality and date, are key to its utility, as indeed such data are to most research undertaken on museum specimens. Given the relative ease with which older specimens in particular might have become separated from their relevant data, and the problems with interpretation that can arise in relation to the available information (Rasmussen & Prÿs-Jones 2003, Steinheimer 2010), this suggested that a close study of museum register, catalogue and other archival data, in conjunction with the published literature, might improve the data quality and quantity available in Knox & Walters (1994) and shown in Table 1.

Turning to opportunities, where genomic data permit specimens to be grouped geographically, this can provide a cross-check as to the origin of specimens of vague or

TABLE 1

Data for NHMUK Crested Ibis *Nipponia nippon* skin specimens from Knox & Walters (1994), listed in the order and in accordance with the headings they use. Information in brackets is inference. The column 'CBBM' refers to the specimen's entry in Sharpe & Ogilvie-Grant (1898).

Reg. no.	Locality	Country	Date	Source	Age	Sex	Posture	CBBM Notes
1		Japan			ad		mount	<i>b</i> Not found 1988.
2	Shanghai	China		J. Webb	ad		mount	Not found 1988. Details taken from CBBM.
3	1842.1.19.90	Japan		Leyden Museum; Temminck; Leadbeater	ad		skin	
4	1852.2.5.12						skin	Reg. no. appears incorrect.
5	1891.10.19.20	Korea		C. W. Campbell		female	skin	
6	1892.4.2.492	China		Tweeddale coll.	ad		skin	
7	1892.4.2.493	China	May	W. Pryer; Tweeddale coll.	imm	male	skin	
8	1897.10.30.2	Korea	1 Feb 1891	C. W. Campbell	ad	female	skin	Not found 1988.
9	(1897.10.30.3)	Japan	April	Blakiston; Seebohm coll.		female	skin	Reg. no. inferred.
10	1897.10.30.4	Japan		H. Pryer	ad		skin	
11	1897.10.30.5	China	18 Nov 1872	R. Swinhoe	ad	male	skin	
12	1897.10.30.6	China	18 Nov 1872	Swinhoe coll.	imm	female	skin	
13	1900.9.9.12	N China		Rev. Father Hugh			skin	
14	1900.9.9.13	N China		Rev. Father Hugh			skin	Not found 1988. Details from register.
15	1908.1.5.20	China	6 Jun 1901	S्यान coll.	ad	female	skin	
16	1980.1.5.21	China	2 Jun 1901	S्यान coll.	ad	male	skin	
17	1908.1.5.22	China	2 Jun 1901	S्यान coll.	ad	male	skin	
18	1908.1.5.23	China	4 Jun 1901	S्यान coll.		male	skin	
19	1908.1.5.24	China	4 Jun 1901	S्यान coll.	ad	female	skin	
20	1908.1.5.25	China	Nov 1896	S्यान coll.	ad	male	skin	
21	1908.1.5.26	China	Nov 1896	S्यान coll.	ad	female	skin	
22	1912.9.23.14	China	1 Jan 1910	Duke of Bedford coll.	ad	male	skin	
23	1988.17.1	(Asia)					skin	
24	1988.17.2	(Korea)	15 Jan 1901			male	skin	Damaged; bill broken

TABLE 2

Data for NHMUK Crested Ibis *Nipponia nippon* skin specimens based on the archival and molecular research outlined herein. Information in brackets is inference. Chinese locality names given in each case are modern Anglicised ones where possible, notably for provinces; otherwise, they are from the original label, with spelling standardised where possible using Bartholomew (1922). The column 'CBBM' refers to the specimen's entry in Sharpe & Ogilvie-Grant (1898). Plumage colour data are pers. obs.

Reg. no.	Locality	Country	Date	Collector	Donor/vendor	Plumage	Sex	Posture	CBBM	Notes
3	1842.1.19.90	Japan	pre-1843	? H. Bürger	Leiden Museum via Leadbeater	white	female	skin	a	
1	?	Japan	?	?	?	white	male	mount	b	Not found 1988 or 2018
4	1852.2.5.2	China	1843-51	R. Fortune	H. Cumming	white	male	skin		
2	1852.3.19.2	Shanghai	pre-1853	J. Webb	J. Russell Reeves	white	female	mount	e	Not found 1988 or 2018.
5	1891.10.19.20	Seoul	Dec 1888 or Jan 1889	C. W. Campbell	C. W. Campbell	white	female	skin	c	
6	1892.4.2.492	Shanghai	pre-1893	?	Marquess of Tweeddale	white	female	skin	d	
7	1892.4.2.493	Shapooshan dist., Zhejiang Province	May 1875	W. Pryer	Marquess of Tweeddale	dark grey	male	skin	f	
8 & 23	(1897.10.30.2)	Seoul	Dec 1888 or Jan 1889	C. W. Campbell	H. Seebohm	white	male	skin		Almost certainly specimen re-reg. as 1988.17.1.
9	(1897.10.30.3)	Hakodate, Hokkaido	27 Apr 1873	T. Blakiston	H. Seebohm	dark grey	female	skin		Reg. no inferred.
10	1897.10.30.4	Yokohama, Honshu	pre-1888	H. Pryer	H. Seebohm	white	male	skin		
11	1897.10.30.5	Ningbo, Zhejiang Provine	18 Nov 1872	R. Swinhoe	H. Seebohm	grey flecks	male	skin		
12	1897.10.30.6	Ningbo, Zhejiang Provine	18 Nov 1872	R. Swinhoe	H. Seebohm	grey flecks	female	skin		
13	1900.9.9.12	Shaanxi Province	pre-1901	Rev. Father Hugh	Rev. Father Hugh	white		skin		
15	1908.1.5.20	(Kienteh area), Anhui Province	6 Jun 1901	F. W. Styan	F. W. Styan	pale grey	female	skin		
16	1980.1.5.21	(Kienteh area), Anhui Province	2 Jun 1901	F. W. Styan	F. W. Styan	pale grey	male	skin		
17	1908.1.5.22	(Kienteh area), Anhui Province	2 Jun 1901	F. W. Styan	F. W. Styan	pale grey	male	skin		
18	1908.1.5.23	(Kienteh area), Anhui Province	4 Jun 1901	F. W. Styan	F. W. Styan	pale grey	male	skin		
19	1908.1.5.24	(Kienteh area), Anhui Province	4 Jun 1901	F. W. Styan	F. W. Styan	grey	male	skin		
20	1908.1.5.25	Luonan, Shaanxi Province	Nov 1896	F. W. Styan	F. W. Styan	white	female	skin		
21	1908.1.5.26	Luonan, Shaanxi Province	Nov 1896	F. W. Styan	F. W. Styan	white	female	skin		
22	1912.9.23.14	c.50 km S of Feng-hsiang fu, Shaanxi Province	1 Jan 1910	M. P. Anderson	Duke of Bedford coll.	white	male	skin		
24	1988.17.2	Seoul	15 Jan 1901	Miss E. Scarlett	Miss E. Scarlett	white	female	skin		



uncertain provenance. Most generally important, however, the genomic results would provide unambiguous sex determination. Many specimens, especially older ones of phenotypically monomorphic species, including Crested Ibis (He *et al.* 2013), lack label indication of sex, and even where this is provided it is likely to be unclear whether it is based on gonad examination. In practice, sexing is found to be erroneous in a non-negligible minority of cases (e.g. Rasmussen & Prŷs-Jones 2003).

Using the approaches mentioned above, this paper reports on a specimen-by-specimen examination of all such issues and summarises the results in Table 2, an updated version of Table 1 to facilitate comparative assessment of the added value that such an approach can bring. The archival methodology is outlined below; the molecular methodology is presented in Feng *et al.* (2019). Although the Natural History Museum was legally part of the British Museum for more than 200 years from the 1750s until 1963 (Stearn 1981), using first the acronym BM and later BM(NH), I use the current official acronym NHMUK throughout this paper for simplicity, as no confusion should thereby be caused.

## Archival methodology

The assembly of a bird collection by NHMUK began in the 1750s, with the great majority of its constituent material being either donated or purchased. However, due both to poor preparation techniques and inadequate curatorial care, few specimens from pre-1800 survive, and the vast majority date from the great era of bird exploration and collecting spanning 1850–1950. Even post-1800, documentation of what was received, its provenance, and what was subsequently disposed of left much to be desired until the 1830s, when the first systematic attempts both to register (on arrival, with a unique identification number both in the register and on the specimen's label) and to catalogue (i.e. place within a taxonomically ordered list) individual specimens commenced (Knox & Walters 1992, Wheeler 1996, Thomas 2012).

The search for archival data pertaining to each Crested Ibis specimen drew on the following potential sources:

1. The label(s) attached to the specimen in question, usually comprising an original collector's label and a museum curator's label. However, at least half of all specimens received up to c.1860 were mounted for display (Günther 1912), whereupon they normally had their original label removed, giving considerable scope for data to be lost or incorrectly transcribed.
2. From 1837, the specimen register entry made on its museum arrival, which in addition to the individual specimen's number includes an identification, often only to genus or less in earlier years, and highly variable additional data concerning provenance, date of collection, collector, etc. Pre-1945, each specimen received a four-part registration number, in which the first three parts represented respectively the year, month and day of the earliest registration of the particular collection in which it was received, and the fourth part the number of the specimen within that collection; subsequently, three-part registration numbers were used (year, batch no., specimen no.). In the absence of other, more precise dating, the first part of the registration number therefore defines the latest possible year in which the specimen could have been collected.
3. Various NHMUK catalogues, including: the partial, manuscript Vellum Catalogues (c.1835–43), in which entries from c.1840 onwards were increasingly erratic; the published G. R. Gray catalogues of the 1840s / 1850s, which were very incomplete in their taxonomic coverage; and the invaluable, complete 27-volume *Catalogue of the birds*

in the *British Museum*, published 1872–98. The relevant volume (no. 26) for Crested Ibis in the last-named is Sharpe & Ogilvie-Grant (1898).

4. Information contained in surviving correspondence, notably from the donor / vendor. Occasionally this may include relevant data not transcribed onto the specimen's label or into its register or catalogue entries. NHMUK has voluminous archives, but searching for such information from before the 1880s, when NHMUK was moved to a new building in South Kensington and thereby physically separated from the rest of the British Museum, is complicated because potentially relevant material often remained at the latter or, indeed, may have subsequently been passed by that organisation to the British Library.
5. Specimen collectors' catalogues or diaries that may have survived and been deposited in a public institution, not infrequently NHMUK itself.
6. The published literature, where information relating to many specimens was included in journals or books either before or after their arrival in the NHMUK.

Searching of sources 1–3 above is usually relatively straightforward and comprehensive, but exhaustive searches are rarely feasible for 4–6. The analysis provided below should therefore not be considered the final word in restoring data to the specimens under consideration, but rather one that took account of the 'law of diminishing returns' in the context of time spent vs. information retrieved.

## Results

The results of the investigation undertaken are summarised in Table 2, arranged in approximate chronological order of each specimen's arrival in NHMUK, as revealed by their registration number. Individual specimens are best cross-referenced between Tables 1 and 2 by means of the numbers (1–24) in the left-hand column of each, as a few registration number errors / omissions occurred in Knox & Walters (1994). The sources of information additional to, or altered from, that in Table 1 are summarised below, considering archival results first, listed by registration number in the order presented in Table 2, and molecular subsequently.

### *Archival*

**1842.1.19.90.**—This was almost certainly the first Crested Ibis specimen to reach NHMUK, being the only one mentioned in Gray (1844: 91), who stated: 'Japan. – From the Leyden Museum.'; no Crested Ibis entry appears in the Vellum Catalogues. The specimen was received from the London dealers Leadbeater within a batch of duplicates from Leiden Museum (Sharpe 1906), whose director from 1820 was C. J. Temminck. In 1835 Temminck provided the first description of the Crested Ibis from a single complete skin received from P. F. von Siebold in Japan. Leiden subsequently received further Japanese specimens, notably from Heinrich Bürger, who was Siebold's assistant in Japan during 1825 to 1835, and NHMUK's specimen is probably one such (H. van Grouw pers. comm.). The specimen was formerly mounted, but the annotation 'No 13 Burton 14.5.84' on its only label shows it was sent for demounting by the taxidermist Burton on that date. This was part of a programme for turning much of the former (mounted) display collection into a (skin) research collection (Knox & Walters 1992); in consequence the subsequent entry for the specimen ('a') in Sharpe & Ogilvie-Grant (1898: 16) is annotated 'sk' (skin) and not 'st' (stuffed).

**Specimen lacking known reg. no.**—This is mounted specimen ‘*b*’ in Sharpe & Ogilvie-Grant (1898: 16), who otherwise merely stated ‘Japan. Purchased’. Neither it nor the other mounted specimen (‘*e*’—see below) mentioned by Sharpe & Ogilvie-Grant (1898), who regrettably do not provide registration numbers, is now at NHMUK. As it was not mentioned by Gray (1844), the specimen almost certainly arrived subsequently. Precisely when is almost impossible to determine without knowledge of its vendor, as its registration, if undertaken, was seemingly made at most at the generic level (‘*Ibis*’) alone.

**1852.2.5.2.**—This is the specimen referred to by Knox & Walters (1994: 45) as 1852.2.5.12, with the comment ‘reg. no. appears to be incorrect, as the register claims it was assigned to a different species.’ Examination of its only label, a museum one, on which is written only the registration number, reveals the number is in fact 1852.2.5.2, as the digit ‘1’ has been faintly crossed out. This is confirmed by the tiny metal preparation tag also present (see Varley *et al.* 2016 for a photo of such a tag), on which the registration number is very faintly scratched and for which the final part can be confirmed as ‘2’. The register entry for this specimen gives ‘*Ibis* China’, part of a batch of five specimens (1852.2.5.1–5) noted as being ‘Fortune colln.’ and purchased from Hugh Cuming, a well-known conchologist who also dealt in a wider array of natural history specimens including birds (Sharpe 1906, Dance 1980). The collector was almost certainly Robert Fortune, who spent much time in south-east China during the decade preceding 1852, initially collecting plants on behalf of the Royal Horticultural Society and later tea varieties for the East India Company (Rose 2009). For unclear reasons, the specimen is not included in Sharpe & Ogilvie-Grant (1898).

**1852.3.19.2.**—Knox & Walters (1994) had no registration number for this mounted specimen, now missing, listed as ‘*e*’ by Sharpe & Ogilvie-Grant (1898). However, a register search for the collector J. Webb reveals that it is almost certainly 1852.3.19.2 (‘*Ibis*. Shanghai’), part of a series of 25 registered specimens presented via John Russell Reeves.

**1891.10.19.20 and 1897.10.30.2.**—Both specimens were collected in Seoul, Korea, by Charles W. Campbell, the former (specimen ‘*c*’ in Sharpe & Ogilvie-Grant 1898) being received by NHMUK directly from him, whereas the latter was acquired subsequently as part of the Seebohm collection. On specimen 1891.10.19.20, the original Campbell label contains a mixture of English and Korean writing, the former indicating it was bought in a Seoul market. Knox & Walters (1994) suggested specimen 1897.10.30.2 was missing, but that a detached label found probably belonged to it. This is clearly correct as the label is in the same style as that on 1891.10.19.20, but with ‘Seebohm Coll.’ also appended. They further suggested that the detached label included a date ‘1/2/(18)91’, but this appears to be a misinterpretation. No obvious date of collection is given for either specimen, but Campbell (1892) reveals, firstly, that he was in Seoul in 1888 and 1889 and, secondly, that he obtained his Crested Ibis specimens in December and January. Finally, 1897.10.30.2 is almost certainly the supposedly data-less specimen 1988.17.1 of the two ‘unregistered’ specimens located and registered by Knox & Walters (1994).

**1892.4.2.492.**—As Knox & Walters (1994) indicate, the only data available that can be linked to this specimen (‘*d*’ in Sharpe & Ogilvie-Grant 1898) are ‘Shanghai’ and ‘Tweeddale Coll.’ In particular, who the collector might have been is unknown.

**1892.4.2.493.**—William Pryer, the collector of this specimen (‘*f*’ in Sharpe & Ogilvie-Grant 1898) acquired by NHMUK via the Tweeddale collection, was brother to the ornithologically better known Harry Pryer (Sharpe 1906). Although Knox & Walters (1994) give merely ‘May’ for date of collection, the label clearly indicates it was taken in May 1875, in wet fields. The Zhejiang province collection locality of ‘Shapooshan district’ on the original label was

untraced by Collar *et al.* (2001), but may well be Shapushan, Wuding County (F. Steinheimer *in litt.* 2019).

**1897.10.30.3.**—Knox & Walters (1994) are clearly correct in concluding that 1897.10.1.3, as written on a label on this Thomas W. Blakiston specimen acquired via the Seebohm collection, is a curatorial *lapsus*. Furthermore, although its original Blakiston label states merely ‘♀ April Hakodadi, Japan 1199’, more can be inferred. In Blakiston’s own catalogue which, together with many of his specimens, remains in Japan (Yamashina *et al.* 1932, Kato 2012), the entry for specimen no. 1199 reveals that its collection date was 27 April 1873 and that Blakiston sent it to Robert Swinhoe in February 1875 (M. Kato *in litt.* 2018). As it is in grey plumage, there is little doubt that it must be the specimen referred to by Swinhoe (1875: 455), in a paper on specimens he received from Blakiston, as ‘A full-grown immature grey specimen of this species has come ...’. On his death, Swinhoe’s collection was acquired by Seebohm.

**1897.10.30.4.**—As Harry Pryer, the collector of this specimen acquired by NHMUK via Seebohm, died early in 1888 (*Ibis* 30: 381, 1888), it must have been collected prior to this.

**1897.10.30.5 and 6.**—Both of these Swinhoe specimens were acquired via the Seebohm collection. Swinhoe (1873) wrote an account of their taking, along with a third bird, at Western Lake, Ningpo. A. Anderson is given as the collector of 1897.10.30.6 in the NHMUK register, which is contradicted by the specimen’s labels and clearly a curatorial registration error.

**1900.9.9.12 and (13).**—Knox & Walters (1994) stated that NHMUK received two specimens from Father Hugh (born John Aloysius Scallan), but that they could only find 1900.9.9.12. In fact, the supposed 1900.9.9.13 almost certainly never existed. In his write-up of material received from Father Hugh, Sharpe (1901: 175) refers to just one specimen: ‘Un mâle parfaitement adulte, en plumage blanc, montrant une belle nuance rose, et portant la huppe complètement développée.’ Furthermore, the NHMUK register entry line for specimen 1900.9.9.13 is left blank, rather than having the ditto marks expected if a specimen existed whose data matched 1900.9.9.12. Blank registration lines not infrequently occur in registers from this period and earlier, either in error or because even a genus-level identification of the specimen under consideration had not been reached when registration occurred.

**1908.1.5.20–26.**—All of these specimens were acquired as part of a large collection received from Frederic W. Styan following his return to Britain in 1904 after more than 25 years in China (*Ibis* 77: 210, 1935). Styan made extensive use of one or more native collectors, but nevertheless his specimens generally possess good data. The five specimens 1908.1.5.20–24 were all collected in June 1901, with the label locality being noted merely at the province level; however, Styan (1902) indicated that shortly thereafter his collector was ‘near Chinteh, in Anhwei Province, on the south bank of the Yangtse’. Previously, Styan (1891: 337) had defined the ‘Chin Teh Hills’ as being c.110 km downstream of Kiukiang (modern Jiujiang), which provides a potentially more precise indication of provenance in south-west Anhui province, i.e. in the vicinity of Kienteh (Bartholomew 1922). For specimens 1908.1.5.25–26, the statement in Knox & Walters (1994) that they were collected in ‘Shansi’ (= modern Shanxi province) is a misleading mis-transcription of ‘Shensi’ (= modern Shaanxi province, immediately west of Shanxi) on their original labels. The original label collection locality ‘Lu Nan hsien’ is the modern Luonan (Collar *et al.* 2001).

**1912.9.23.14.**—As noted on its original label, the specimen was taken by Malcolm P. Anderson, who collected extensively in China for the 11th Duke of Bedford. During late

1909 and early 1910 he was in south-east Shensi (modern Shaanxi) province (Thomas 1911), initially around Shangchou (c.33°40'N, 110°20'E) and later near Mt. Tai-pei-san (c.34°N, 107°30'E). Based on locality names in Bartholomew (1922), it appears that his Crested Ibis specimen came from c.50 km south of either Fêng-hsien (c.33°50'N, 106°40'E) or, more probably, Feng-siang-fu (c.34°30'N, 107°20'E).

**1988.17.1.** — See under 1897.10.30.2 (above).

**1988.17.2.** — This is the second of two specimens that Knox & Walters (1994) found to lack a registration no. and therefore provided one. As they noted, its label states it was collected in Korea on 15 January 1901, but they failed to determine the collector / donor name. This is in fact 'Scarlett', subsequently confirmed by checking labels of other specimens from this donor. The next step of tracking this name down in the registers was complicated because Sharpe (1906) had overlooked it. A register search showed that 'The Hon. Miss E. Scarlett' passed a total of 12 Korean specimens to NHMUK, two registered as 1900.12.15.1–2 and space for ten created in the series 1901.9.18.1–10, although only the first five were actually registered, all also collected in January 1901. It appears probable that a decision was made during the registration process not to register the other five specimens, but instead to retain them as duplicates for potential gift or exchange, as not infrequently happened in the late 1800s and early 1900s (Günther 1912). That the Crested Ibis specimen both had a broken bill and belonged to a species then already well represented in the NHMUK collection makes such a decision more likely. Had the collector's name and the relevant registration series been recognised earlier, the appropriate registration number to have been used would have been in the series 1901.9.18.

### *Molecular*

Based on their genomic analysis, Feng *et al.* (2019) could group the 57 Crested Ibis specimens for which they had extracted usable DNA, including 19 from NHMUK (1900.9.9.12 failed), into three major, discrete geographical areas: north-west China, eastern China and north-east Asia (including north-east China, the Russian Far East, Korea and Japan). For all 16 NHMUK specimens labelled with reasonably precise geographical provenance, the molecular results confirmed their areas of origin. For two further specimens (1897.10.30.2 and 1988.17.2), for which it had been necessary to infer their provenance as being Korea in both cases, the molecular data placed them in the appropriate north-east Asian grouping. For the final specimen (1852.2.5.2) with only 'China' noted on its label, its molecular grouping with eastern China specimens agrees with the archival demonstration that it was a Robert Fortune specimen, as his collecting activity appears to have been confined to this area. Archival and molecular results are therefore fully congruent.

Regarding sexing, of the 19 NHMUK specimens that yielded usable DNA, eight had previously been sexed male, seven female and four were unsexed (Table 1). Based on the molecular sexing, ten were found to be male and nine female, but this included a sex change for four of the 15 supposedly sexed birds, i.e. 27% (Table 2). For a rare species in which any phenotypic differences between the sexes appears to be at most slight, this substantial improvement in sexing knowledge for museum specimens is clearly important.

## Discussion

Comparison of Tables 1 and 2 highlights how much additional data can be added or re-attached to historical specimens by means of a focused archival search. Moreover, whereas Knox & Walters (1994) implied NHMUK had accessed 23 or 24 Crested Ibis

specimens, of which either three or four could not currently be found, in fact it appears only ever to have held 22, of which just the two mounted ones are missing. Specimens that remained mounted and on display after the separation made between a mounted display collection and a skin / demounted research collection in the late 1800s (Günther 1912) were at particular risk in this regard. They usually no longer had labels attached to them, any data deemed necessary for the public being stuck on their stands, and they suffered the wear and fading associated with long-term display. Many such specimens were eventually disposed of and, although numerous data-less ex-display specimens survive, no Crested Ibis is among them.

Regarding the molecular sexing results, although a significant percentage of older bird specimens of many species tend to be mis-sexed (e.g. Rasmussen & Prŷs-Jones 2003), Crested Ibis is a species whose phenotypic sexing and ageing had historically been particularly confused due to its long-misunderstood plumage changes associated with breeding. Despite a factually correct interpretation being published in the late 1800s, it was widely overlooked (Yasuda 1984). Only during the second half of the 1900s did it become widely understood that the birds acquire a grey breeding plumage in early spring (late January–February) by cosmetic application of a tar-like secretion from a specialised skin region of the head and neck. Non-breeding plumage is white (Uchida 1970, Wingfield *et al.* 2000). Details from NHMUK specimens confirm that birds are dark grey during the breeding period in April / May, lightening in colour during June, and by November showing at most slight grey flecks in some; others taken in November and through January are white (Table 2).

This paper's core message is not intended to be a criticism of Knox & Walters (1994) who, with a limited budget and time, produced an important catalogue of all then recognised extinct and endangered birds in the NHMUK collections using the data conveniently available. Rather, it is meant to highlight the extent to which older specimens in particular may have become divorced from relevant data that can be restored, but only via time-consuming curatorial searching (*cf.* Steinheimer 2010). These results can be further enhanced with more accurate sexing data from genomic analysis, which can also potentially cross-check provenance information. Although the discussion here has focused on Crested Ibis, a similar situation is doubtless true for most other species for which many specimens were collected pre-1900, as I discovered in relation to NHMUK holdings of Seychelles Kestrels *Falco araea* for an earlier molecular study (Groombridge *et al.* 2009).

Understanding of this point has assumed special importance in the light of the ever-increasing practice of databasing museum specimen information to make it available online. Although in principle clearly highly desirable in order to facilitate a wide array of research, this creates a situation in which the research users of such data become increasingly isolated from the museum curatorial staff who can advise them regarding its reliability and pitfalls. Although time-consuming, and consequently expensive, in projects aimed at creating online databases it is important that resources be made available so that knowledgeable curatorial staff can validate and, if possible, enhance the information before it is disseminated.

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# Two undescribed species of bird from West Africa

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**SUMMARY.**—Taxonomically undifferentiated western and eastern populations of Dusky Long-tailed Cuckoo *Cercococcyx mechowii* and Yellow-spotted Barbet *Buccanodon duchaillui* are known to have very different voices. The cuckoo has two song types, a melodious three-note whistle and a plaintive whinnying in West Africa west of the Bakossi Mountains in Cameroon, and a much less melodious, higher-pitched three-note whistle and a much faster whinnying in Central Africa east of the Bakossi Mountains. The barbet has an accelerating song of some 6–11 hoots west of the Dahomey Gap and a rapid rolling purr to the east. Even though in plumage and morphometrics there is no unambiguous diagnostic distinction between these two vocal groups, analysis of their vocalisations demonstrates a high degree of differentiation. We consider the western groups as species, naming the cuckoo for Françoise Dowsett-Lemaire and the barbet for Robert Dowsett.

Dusky Long-tailed Cuckoo *Cercococcyx mechowii* and Yellow-spotted Barbet *Buccanodon duchaillui* share much the same geographical range, extending through the Upper and Lower Guinea forest belt of West Africa, from Sierra Leone east discontinuously at the Dahomey Gap to Nigeria and thence Uganda (and for the barbet western Kenya), and south to northern Angola (del Hoyo & Collar 2014). They also share a curious characteristic, that their populations either side of a relatively narrow line (not the same line, however) have, quite recently, been found to possess markedly different songs. The revelation concerning the cuckoo appears first to have been made by Dowsett-Lemaire (1997), and in the case of the barbet by Borrow & Demey (2001). We cite the latter's information on both species in quotation marks in the following paragraph.

Each population of Dusky Long-tailed Cuckoo has two song-types. From Sierra Leone to western Cameroon, birds have (1a) a song of 'three rising notes, *hu hee wheeu*', and (1b) 'a less frequently uttered whinnying series of rather plaintive notes, first accelerating and then slowing and descending *tiutiutiutiutittiui-tiu-tiu-tiu...*, reminiscent of [a] *Halcyon* kingfisher'. From western Cameroon eastwards, birds have (2a) a faster song, 'with three similar, less melodious notes *wheet-wheet-wheet*' and (2b) 'a fast, descending *wheewheewheewheewhee...*, almost twice as fast as [the] equivalent in Upper Guinea'. For Yellow-spotted Barbet, the main call in the west of the range is 'a series of 7–10 accelerating *oop* notes similar to a song of Hairy-breasted Barbet' *Tricholaema hirsuta*, while in the east birds give 'a characteristic purring *rrurrrrrr...* (lasting 1–2 seconds), unique among [African] barbets, uttered by adult and juvenile'.

These remarkable circumstances have apparently gone unstudied. Both species are treated as monotypic in all recent world lists (Dickinson & Remsen 2013, del Hoyo & Collar 2014, Christidis *et al.* 2018, Clements *et al.* 2018, Gill & Donsker 2018), following the rejection of the cuckoo's proposed forms *wellsi* by Chapin (1928) and *occidentalis* (as a *nomen nudum*) by Dowsett & Dowsett-Lemaire (2015), and the barbet's proposed forms *ugandae* by Chapin (1939), *bannermani* by White (1965) and *gabriellae* (albeit in this case without explanation) by Short & Horne (2001). Yet vocalisations in almost all non-passerines, including cuckoos

(Payne 1997) and barbets (Kirschel *et al.* 2009), are innate and not learnt, so that any strong vocal difference is bound to reflect a strong taxonomic difference. Certainly there is no other known case in the Cuculidae or any of the barbets (Capitonidae, Megalaimidae, Lybiidae) in which a single taxon separates into two distinct vocal groups. To the contrary, some species of cuckoo in particular are now understood to separate on voice with relatively little distinction in morphology, e.g. Whistling Hawk-Cuckoo *Hierococcyx nicolor*, Northern Hawk-Cuckoo *H. hyperythrus* and Sunda Cuckoo *Cuculus lepidus* (King 2002, 2005).

It might briefly be imagined that seasonal, age or sex differences could account for a single taxon possessing more than one vocalisation, but the complete geographical separation of vocal types places such a notion beyond plausibility (one might also note the indication above that the purr of eastern barbets is given 'by adult and juvenile'). We therefore investigated the cases of Dusky Long-tailed Cuckoo and Yellow-spotted Barbet with three questions in mind. First, are there subtle differences in plumage or morphometrics by which the different-voiced populations can be discriminated? Second, are these populations sufficiently different in voice to be considered separate species? Third, can we confirm that the lines separating the different-voiced populations fall for the cuckoo at the Sanaga River in Cameroon (as suggested by Dowsett & Dowsett-Lemaire 2015) and for the barbet at the Dahomey Gap between Ghana and Nigeria (as remarked by Borrow & Demey 2001)?

## Methods

We examined and measured specimens held in the American Museum of Natural History, New York, USA (AMNH), Muséum National d'Histoire Naturelle, Paris, France (MNHN), Musée Royal de l'Afrique Centrale, Tervuren, Belgium (MRAC), Natural History Museum, Tring, UK (NHMUK), Naturhistorisches Museum, Vienna, Austria (NMW) and Museum für Naturkunde, Berlin, Germany (ZMB). Specimens examined were as follows. *Cercococcyx mechowi*, west of the Sanaga River in Cameroon: one male (MNHN), five males (but in the analysis three; see below), two females and one unsexed (NHMUK) and one male and two females (ZMB); and east of the Sanaga River: one unsexed (MNHN), ten males, four females and two unsexed (MRAC), five males (but in the analysis seven) and five females (NHMUK), one male and one female (NMW) and three males and two females (ZMB). *Buccanodon duchaillui*, west of the Dahomey Gap: two males (AMNH), one male (MNHN) and 14 males (NHMUK); and east of the Dahomey Gap: three males (AMNH) and 22 males (NHMUK). Mensural data were taken in millimetres using digital callipers accurate to two decimal points for bill from skull to tip, wing (chord) and tail (from point of insertion to tip). For *Cercococcyx mechowi* both sexes were sampled, owing to the paucity of specimens, and wings and tails were measured with a rule; for *Buccanodon duchaillui* only males were sampled, and the length of the red forecrown patch was also measured, from the base of the bill to the tip of the furthest red feather. Following evidence emerging from our research, we transferred two males of *Cercococcyx* in NHMUK (1923.10.26.69 and 1926.8.8.619), collected in the Fouban area of Cameroon, although west of the Sanaga River, to the eastern sample (see below concerning BLNScc20101 and the legend to Table 1a).

We assembled and analysed sound-recordings of the songs of the two species. We used all available online archives (Xeno-canto, Macaulay Library and Internet Bird Collection), the collection at the British Library and a commercial publication (Chappuis 2000) (see Appendix). From these we selected homologous self-advertising calls, prepared sonograms and manually measured basic sound parameters using CoolEdit Pro. To distinguish the two song types in the cuckoo, we call the first (1a and 2a above) 'short songs' and the second (1b and 2b above), because they are less frequent and seemingly more related to direct

interactions, 'long calls'. We also searched online for video evidence to confirm the identity of the singers reported on sound-recording websites.

To gauge the degree of difference between populations in voice, plumage and dimensions we made use of the system of scoring proposed by Tobias *et al.* (2010), in which an exceptional character (radically different coloration, pattern, size or sound) scores 4, a major character (pronounced difference in body part colour or pattern, measurement or sound) 3, medium character (clear difference, e.g. a distinct hue rather than different colour) 2, and minor character (weak difference, e.g. a change in shade) 1; a threshold of 7 triggers species status, which cannot be achieved by minor characters alone, and only three plumage characters, two vocal characters and two biometric characters (in both cases assessed for effect size using Cohen's *d* where 0.2–2.0 is minor, 2–5 medium and 5–10 major) and one behavioural or ecological character (allowed 1) may be counted; this system gives a score of 3 for parapatric relationships, 2 for a narrow (<200 km) hybrid zone (being evidence of strong resistance to phenotypic merging) and 1 for a broad (>200 km) hybrid zone.

To determine where the voices of the species change we mapped recordings and made inquiries of observers, in the case of *Cercococcyx* taking note of Dowsett & Dowsett-Lemaire (2015), who identified the Sanaga River in Cameroon as the line of separation, but also of the assertion by Chappuis (2000) that 'The zone of transition is situated in the region of the Cameroon mountains where the two populations are parapatric'.

TABLE 1A

Means  $\pm$  standard deviations of measurements (in mm) of all specimens of western and eastern populations of Dusky Long-tailed Cuckoos *Cercococcyx mechowi*. Means of two male specimens (NHMUK 1923.10.26.69 and 1926.8.8.619) are bill 23.1, wing 136.0, tail 197.5; this consistency with eastern birds, plus the recording of a bird from the same area (near Fouban, Cameroon) singing an eastern-type song, led to these specimens being included in the sample of eastern birds (see Methods). <sup>1</sup> Sample size = 30; <sup>2</sup> sample size = 34; <sup>3</sup> sample size = 34.

	<i>n</i>	bill	wing	tail
Western population	10	22.82 $\pm$ 0.81	132.7 $\pm$ 3.59	185.6 $\pm$ 7.50
Eastern population	36	22.85 $\pm$ 0.87 <sup>1</sup>	134.6 $\pm$ 4.02 <sup>2</sup>	196.8 $\pm$ 7.83 <sup>3</sup>

TABLE 1B

Means  $\pm$  standard deviations of measurements (in mm) of male specimens of western and eastern populations of Dusky Long-tailed Cuckoos *Cercococcyx mechowi*. <sup>1</sup> Sample size = 19; <sup>2</sup> sample size = 20; <sup>3</sup> sample size = 20.

	<i>n</i>	bill	wing	tail
Western population	5	23.0 $\pm$ 0.96	132.4 $\pm$ 5.18	188.4 $\pm$ 5.13
Eastern population	21	22.84 $\pm$ 0.76 <sup>1</sup>	134.9 $\pm$ 4.32 <sup>2</sup>	195.6 $\pm$ 8.20 <sup>3</sup>

TABLE 1C

Means  $\pm$  standard deviations of measurements (in mm) of female specimens of western and eastern populations of Dusky Long-tailed Cuckoos *Cercococcyx mechowi*. <sup>1</sup> Sample size = 9; <sup>2</sup> sample size = 11.

	<i>n</i>	bill	wing	tail
Western population	4	22.4 $\pm$ 0.42	132.8 $\pm$ 1.5	179.5 $\pm$ 5.92
Eastern population	12	23.02 $\pm$ 1.12 <sup>1</sup>	134.7 $\pm$ 3.95 <sup>2</sup>	198.4 $\pm$ 7.80

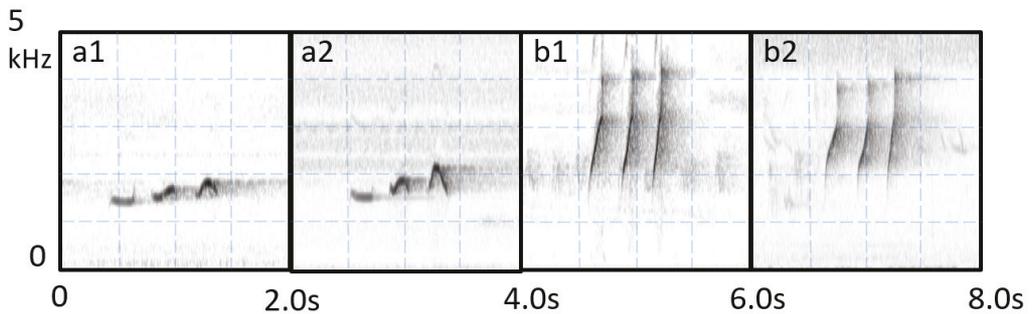


Figure 1. Sonograms of short song of western (a) and eastern (b) populations of Dusky Long-tailed Cuckoos *Cercococcyx mechowi* (a1: ML42772, Liberia, G. S. Keith; a2: CD, Nigeria, C. Chappuis; b1: CD, Gabon, C. Éraud; b2: XC137037, Uganda, J. Engel).

## Results, 1: evidence

### *Cercococcyx mechowi*

Like Payne (2005), we could not discriminate any diagnostic plumage or mensural character between birds from west and east of the Sanaga River. Western birds are marginally smaller, with a tail c.10 mm shorter than those from the east (Table 1a; effect size  $-1.46$ , score 1). Chappuis (2000), evidently examining different material (we are unsure where; there is too little in MNHN to assess size), also considered eastern birds to be larger than western. However, the sample sizes are small and great caution is needed with these results; when broken down by sex, the difference in tail length lessens in males (Table 1b; effect size  $-1.05$ , but  $n = 5$  for western birds) but increases in females (Table 1c; effect size  $-2.73$ , but  $n = 4$  for western birds).

However, the voices of the populations are, as indicated by others, highly divergent. A video (<https://www.youtube.com/watch?v=jM4fjSzc8jk>) shows a singing bird in Ghana and establishes that indeed birds in the western part of the range are the source of the short song analysed below. Another video ([hbw.com/ibc/1151514](http://hbw.com/ibc/1151514)) made in Uganda documents the two distinct vocalisations, short song and long call, uttered by eastern individuals.

The short song of both consists of three (occasionally two) notes, but in western birds it is a leisurely rich whistled *tiuu-wip-wip* and in eastern birds a faster, higher, far less melodious *swiitwiitwiit*, in both cases stereotypical with very little variation. Analysis demonstrates that western birds have a song consisting of longer notes which reach a much lower frequency (Tobias criteria score 4) and have a much narrower frequency band (score 4), along with various other differing characters (Table 2), such that in sonograms they appear as dramatically different acoustic structures (Fig. 1a,b). Moreover the long calls, which are quite variable (and even might prove to be of two types in western birds), involve notes delivered about twice as fast in eastern populations (Fig. 3a,b), a further point of difference which would count highly if the Tobias criteria permitted three vocal characters to be scored.

The number of songs and calls sampled for this analysis is not large for the western group (see Appendix), but the results are geographically almost entirely consistent. The most obvious exception is a recording by C. Chappuis of a long call typical of eastern birds made at 'Nkounden, near Fouban, Cameroon' (BLNS cc20101), a site 120 km north-east of the Bakossi Mountains and 50 km west of the Sanaga River (Fouban also being the area from which two birds similar in size to eastern birds have been collected: see Methods and legend to Table 1a). Also requiring mention here are the long calls of a bird

TABLE 2

Means  $\pm$  standard deviation of measurements of components in the short songs of western ( $n = 11$ ) and eastern ( $n = 37$ ) populations of Dusky Long-tailed Cuckoos *Cercococcyx mechowi*.  $s$  = seconds; e.s. = effect size; Ts = Tobias score (those used in the analysis in bold).

	western	eastern	e.s. (Ts)
Min. duration of note (s)	0.180 $\pm$ 0.011	0.093 $\pm$ 0.013	7.2 (3)
Max. duration of note (s)	0.214 $\pm$ 0.021	0.137 $\pm$ 0.013	4.4 (2)
Max. frequency (Hz)	2178 $\pm$ 161	4045 $\pm$ 144	12.2 (4)
Max. frequency range (Hz)	622.2 $\pm$ 150.2	2369 $\pm$ 182	10.5 (4)
Total phrase length (s)	0.921 $\pm$ 0.053	0.672 $\pm$ 0.036	5.5 (2)

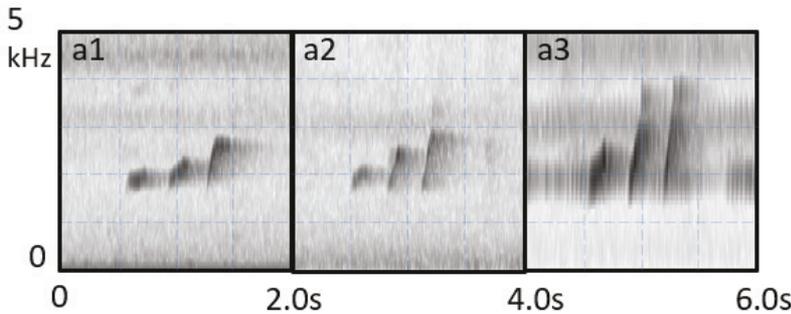


Figure 2. Sonograms of the short song of unassigned populations of Dusky Long-tailed Cuckoos *Cercococcyx mechowi* from the Bakossi Mountains, Cameroon, here considered intermediate between those of western and eastern populations (see Fig. 1) (a1: BLNS136888, M. Mills; a2: BLNS80394, F. Dowsett-Lemaire; a3: BLNS182020, M. Mills).

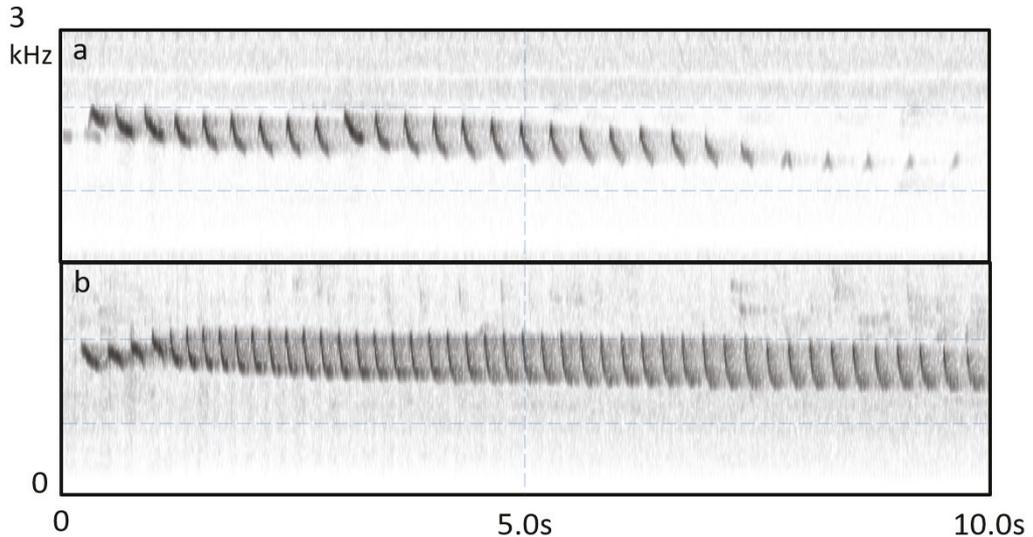


Figure 3. Long calls of western (a) and eastern (b) populations of Dusky Long-tailed Cuckoos *Cercococcyx mechowi* (a: CD, Nigeria, C. Chappuis; b: XC241398, Uganda, M. St-Michel).

on three consecutive days at Mt. Nlonako in western Cameroon (XC407506/ML91480081 and ML537132/134/167), which have, however, been judged not to emanate from a cuckoo but from another bird, probably a young raptor (F. Dowsett-Lemaire & R. J. Dowsett *in*

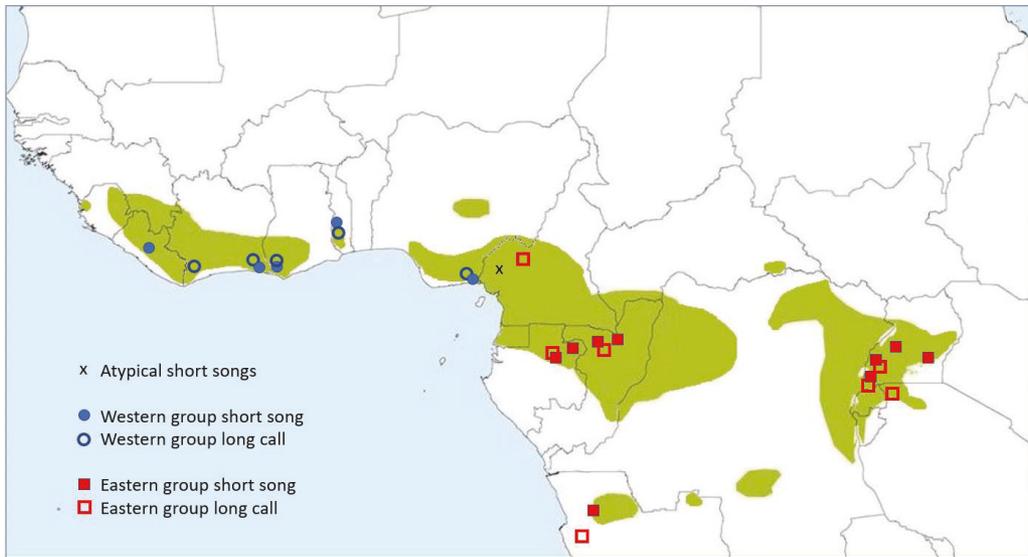


Figure 4. The global distribution of Dusky Long-tailed Cuckoo *Cercococcyx mechowi* with point localities for vocal groups based on recordings listed in the Appendix. The green area is the range as indicated in BirdLife International (2018) (with minor adjustments). The coloured point localities are explained in the internal legend. The Sanaga River lies east of the x for the atypical short songs. The open red square to the north-east of the x marks the Fouban area, where eastern-sized birds have been collected (see Methods and Table 1a), although it lies west of the Sanaga River.

*litt.* 2019). These calls have a pace which would place them in the eastern group, but they sound quite different from those further east. The site of the recordings is *c.*200 km from the Sanaga River, and less than 50 km from the Bakossi Mountains, where song typical of western birds has been reported (Dowsett & Dowsett-Lemaire 2015). However, while we accept the rejection of this anomalous record as a cuckoo, three other recordings clearly of cuckoos, BLNS 80394, 136888 and 182020, all from the Bakossi Mountains, reveal somewhat intermediate short songs, suggesting that at least some ‘eastern birds’ penetrate west of the Sanaga River and that these intermediate song types may reflect hybridisation over a very narrow zone (Fig. 2). However, with the exception of these intermediate short songs at this single locality, there is no indication of any clinal change in voice (Fig. 4).

### *Buccanodon duchailloi*

We were unable to discriminate any diagnostic morphological differences between birds west and east of the Dahomey Gap, which appears to form the dividing line between the different-voiced populations (see Fig. 6), since birds in the Omo Forest Reserve, just east of Lagos in western Nigeria, sing with ‘a single long purr’ (S. Egbe *in litt.* 2018). It is *possible* that western birds have slightly fewer black markings on the breast-sides, flanks and belly, but this is probably an artefact of the particularly well-prepared specimens from Liberia by A. D. Forbes-Watson which comprise the bulk of the western sample we examined. Western birds are very slightly larger in size, with tails a mean 2 mm longer, yielding an effect size of 1.25 and a Tobias score of 1 (Table 3). The mean size of the red crown patch is, however, fractionally smaller (effect size  $-0.52$ ; permissible score 1), but involves such extensive overlap as to be as useless a diagnostic character in the museum as it clearly would be in the field.

Birds in the western population sing a simple, accelerating series of typically 6–11 soft rich *uup* hoots, *uup uup-uup-uup-uupuupuup*. A video ([hbw.com/ibc/1459316](http://hbw.com/ibc/1459316)) documents

TABLE 3

Means ± standard deviations of measurements (in mm) of male specimens of western and eastern populations of Yellow-spotted Barbet *Buccanodon duchaillui*. 'Crown' = red crown patch. <sup>1</sup> Sample size = 24.

	<i>n</i>	bill	wing	tail	crown
Western population	17	16.42 ± 0.55	76.71 ± 2.11	42.12 ± 1.43	16.78 ± 1.82
Eastern population	25	16.18 ± 0.89	74.84 ± 2.76	39.96 ± 1.97	17.81 ± 2.15 <sup>1</sup>

TABLE 4

Means ± standard deviation of measurements of components in the songs of western (*n* = 15) and eastern (*n* = 22) populations of Yellow-spotted Barbet *Buccanodon duchaillui*. Acceleration was determined by dividing the combined duration of the first two notes by the combined duration of the last two notes including the intermediate pause. *s* = seconds; *e.s.* = effect size; *Ts* = Tobias score (those used in the analysis in bold).

	western	eastern	<i>e.s.</i> ( <i>Ts</i> )
Number of notes	8.533 ± 1.685	72.8 ± 16.76	5.38 (3)
Longest note (s)	0.245 ± 0.037	0.026 ± 0.004	8.32 (3)
Pace (notes per s)	4.165 ± 0.724	37.542 ± 3.54	13.06 (4)
Acceleration	2.211 ± 0.311	1.467 ± 0.159	3.01 (2)

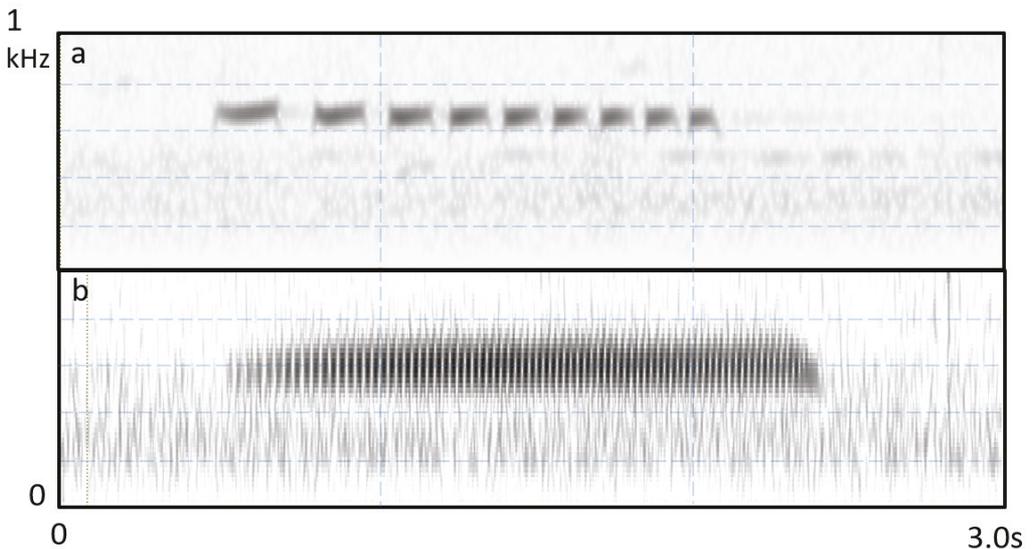


Figure 5. Songs of western (a) and eastern (b) populations of Yellow-spotted Barbet *Buccanodon duchaillui* (a: XC400183, Ghana, P. Åberg; b: ML46607, Tanzania, D. Moyer).

this song, and shows how a large patch of pink bare skin on the neck-side, sufficient to qualify as a visual signal, is exposed and pulses as the bird delivers its hoots. Eastern birds, by contrast, produce a sound very similar in tone and pitch to these hoots, but as a rapid rolling guttural purr, *rrrrrrrrrrru*; whether bare skin is exposed during the delivery is apparently unknown, but Chapin (1939) was brought a 'brood of nestlings' which also gave this call, in which 'the head was extended, beak downwards, and the neck swelled decidedly, the skin showing at its sides'. Analysis (Table 4) reveals that western birds have a song with many fewer notes (no score permissible) which are much longer (score 3),



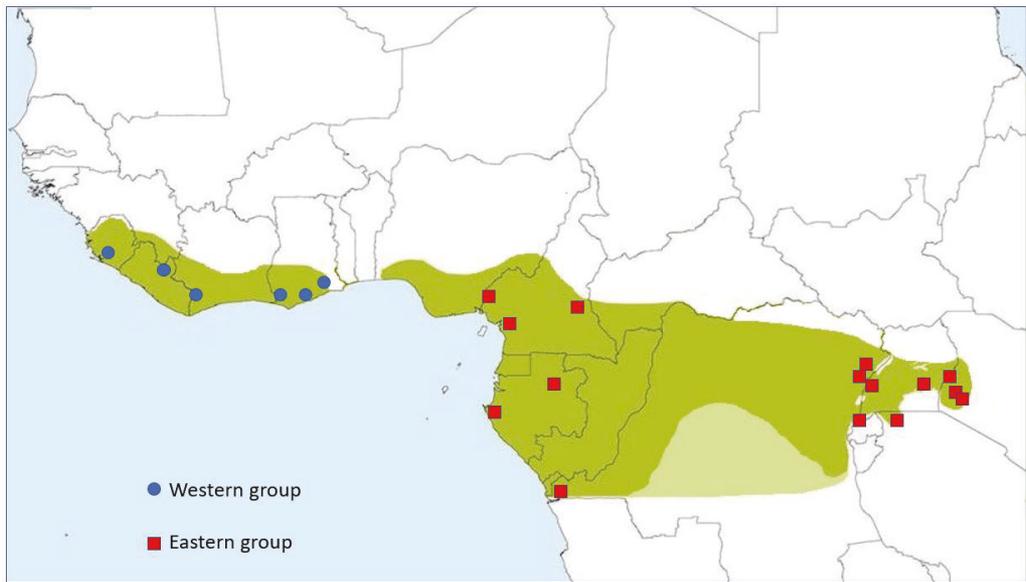


Figure 6. The global distribution of Yellow-spotted Barbet *Buccanodon duchaillui* with point localities for vocal groups based on recordings listed in the Appendix. The green area reproduces the range as indicated in BirdLife International (2018) (with minor adjustments, and pale green indicating uncertain occurrence). The coloured point localities are explained in the internal legend.

delivered far more slowly (score 4) but *accelerando* (no score permissible) (Fig. 5a,b). Also, in western birds amplitude is fairly constant while in eastern birds it shows a clear initial increase to reach a maximum after which it fades towards the end (no score permissible).

M. Mills informs us (*in litt.* 2018) that he once heard a barbet in Uganda deliver some hoots, although he made no note of the time, place or similarity to the hoots of western birds, and hoots are also mentioned as a secondary vocalisation in East African birds by Stevenson & Fanshawe (2002). However, the number of songs sampled for this analysis was substantial (see Appendix) and all yielded geographically consistent results. If eastern birds hoot, they must do so very rarely; and in the absence of further evidence to confirm this phenomenon or to indicate its similarity or difference to the hoots of western birds, we elect to set this testimony aside in the hope that future studies will elucidate the matter.

## Results, 2: interpretation

Although we were able to find one minor distinction each in tail length between the western and eastern populations of the two species under review, we acknowledge that these involve average but not absolute differences, and are therefore indicative but not diagnostic. Nevertheless, the differences between the voices of western and eastern populations of Dusky Long-tailed Cuckoo and Yellow-spotted Barbet score sufficiently highly using the Tobias criteria for each population to be recognised as a separate species. The cuckoo scores 8 on voice, 2 for possible narrow hybrid zone and 1 for tail length, total 11, the barbet 7 on voice and 1 for tail length (crown patch score of 1 is technically permissible but too trivial, and is set aside here), total 8. The type localities for the species are both in the east of their ranges (*Cercococcyx mechowi* in Angola, *Buccanodon duchaillui* in Gabon), so the two new species refer to the western populations. In the following descriptions, colour names and numbers follow Smithe (1975).

*Cercococcyx lemaireae* sp. nov.

## Whistling Long-tailed Cuckoo

*Holotype*.—NHMUK 1977.20.179. Grassfield, Mt. Nimba, Liberia, 550 m, 11 August 1967, collected by A. D. Forbes-Watson.

*Diagnosis*.—Indistinguishable in morphology from *C. mechowii*, albeit with a tendency to slightly shorter wings and tail; but highly divergent in voice, with a short song consisting of a leisurely rich whistled *tiu-wip-wip* (notes longer, at a much lower frequency and with a much narrower frequency band) rather than the faster, higher, far less melodious *swiitwiitwiit* of *C. mechowii*, and a long call delivered half as fast as that of *C. mechowii*; both vocalisations are presumably used in self-advertisement.

*Description of the holotype*.—Crown, nape, mantle and back dark grey (Blackish Neutral Gray 82), with wings similar but tinged dark brown (Sepia 219), and each primary and secondary carrying small dull rufous (near Mikado Brown 121C) triangles *c.*10 mm apart along the outer edge of the outer vane. Uppertail the same colour as the wings but appearing blackish (near Sepia 119) when feathers not fanned, with narrow whitish tips and very small buffy (near Pale Pinkish Buff 121D) notches *c.*10 mm apart on the edges of both vanes of each rectrix (also a few tiny white notches along the shafts of the outer rectrices). Sides of face dark grey (Medium Neutral Gray 85) with sparse whitish flecks on lores, cheeks and ear-coverts; chin to lower belly densely and boldly barred blackish (between Dark Brownish Olive 129 and Blackish Neutral Gray 82) on discoloured whitish background shot with buff (between Warm Buff 118 and Yellow Ocher 123C) across breast and on lower belly where the barring ceases; undertail-coverts warm buff (near Yellow Ocher 123C). Undertail blackish grey (near Sepia 119) with the notches of the uppertail showing whitish rather than buffy. Iris dark brown, eye-rim lemon yellow. Bill (upper mandible) blackish, (lower mandible) tip blackish, rest yellow tinged greenish. Feet: lemon yellow. Testis 6 mm. Weight 54.2 g (A. D. Forbes-Watson label inscription). Bill from skull 22.5 mm, wing 135 mm, tail 193 mm.

*Remarks*.—*C. lemaireae* extends from Sierra Leone east to western Cameroon, with *C. mechowii* occupying the area from central Cameroon east to Uganda. As noted above, an informal name for the new species, '*occidentalis*', is a *nomen nudum* (Dowsett & Dowsett-Lemaire 2015). The type locality ('Bitye, R. Ja, Cameroon') of Bannerman's (1919) subspecies *wellsi*, long considered invalid—the form was not even mentioned by Irwin (1988) or Payne (1997, 2005) and our check of the type specimen (NHMUK 1920.6.26.108) reaffirmed this view (we included it in our mensural sample)—lies within the range of the eastern population (Dowsett & Dowsett-Lemaire 2015), so the name is unavailable in this context. The proposed English name seeks to capture the key tonal difference this species reveals in its voice, and we suggest retention of 'Dusky Long-tailed Cuckoo' for the now-restricted *C. mechowii*; but we acknowledge that with 'Whistling Yellowbill' *Ceuthmochares australis* and 'Whistling Hawk-Cuckoo' *Hierococcyx nisicolor* the Cuculidae may be sufficiently stocked with sibilant species. An alternative, in the interests of syllable reduction, might be to call the two species 'Western Dusky Cuckoo' and 'Eastern Dusky Cuckoo', although this would be to lose the generic English wording matching the etymology of '*Cerco-*' (tail) '*-coccyx*' (cuckoo). The very slightly smaller size of the new form was also noted by Chappuis (2000) and, with a sample size of 1, was speculated on by Chapin (1928).

*Etymology*.—We name this species for Françoise Dowsett-Lemaire, *née* Lemaire, whose achievements, alone and with her husband Bob Dowsett, have illuminated so many distributional, ecological, behavioural (notably vocal), taxonomic and conservation issues in ornithology across the African continent.

*Buccanodon dowsetti* sp. nov.  
Western Yellow-spotted Barbet

*Holotype*.—NHMUK 1977.20.505. Grassfield, Mt. Nimba, Liberia, 550 m, 24 August 1967, collected by A. D. Forbes-Watson.

*Diagnosis*.—Indistinguishable in morphology from *B. duchailloi*, albeit with a tendency to a slightly longer bill, wings and tail, and on average fractionally smaller red crown patch; but highly divergent in voice, the self-advertising song being a simple, accelerating series of typically 6–11 soft rich *uup* hoots, *uup uup-uup-uup-uupuupuup*, as opposed to a rapid rolling guttural purr, *rrrrrrrrrrru*, in *B. duchailloi*, thus involving many fewer but much longer notes delivered far more slowly but *accelerando*.

*Description of the holotype*.—Forehead to mid-crown (line from rear edge of eye) dull crimson (Crimson 108); rest of crown to upper back glossy black (Jet Black 89), becoming matt black on lower back and wings; secondary wing-coverts, scapulars and lower back appearing spotted due to pale yellow (duller than Sulfur Yellow 157) tips, these becoming pale yellow lines on the primary wing-coverts and secondaries, and narrow scalloping on the rump and uppertail-coverts. Tail matt brownish black (near Sepia 219). Bold pale yellow (near Sulfur Yellow 157) line from rear of eye over ear-coverts to neck-side. Ear-coverts, lower face, lower neck-sides, chin, throat and upper breast glossy black, this extending as two broad lines onto middle and lower breast. Upper breast-sides to lower flanks broadly scaled pale yellow on black; centre of mid-breast to undertail-coverts pale yellow with very slight blackish scaling. Soft part colours 'as 785' (collector's number), for which is written: 'Iris brown, bare [eye-rim] black, bill black, feet grey'. 'Testis 5 mm. Weight 37.1 g' (A. D. Forbes-Watson label inscription). Bill from skull 16.5 mm, wing 75 mm, tail 42 mm.

*Remarks*.—*B. dowsetti* ranges from Sierra Leone east to southern Ghana, being wholly absent from Togo and Benin (F. Dowsett-Lemaire & R. J. Dowsett *in litt.* 2019), with *B. duchailloi* occupying the area from south-west Nigeria east to Kenya. All subspecies hitherto described—*bannermani* Serle, 1949 (type locality Bamenda, British Cameroons, type NHMUK 1949.14.4) and *gabriellae* Bannerman, 1924 (type locality Pangala, French Congo, type NHMUK 1924.7.15.1)—refer to the eastern population; it is perhaps worth noting that *gabriellae*, rejected without explanation by Short & Horne (2001), appeared valid to Chapin (1939), as it does to us. The proposed English name predicates that eastern *B. duchailloi* will become known as 'Eastern Yellow-spotted Barbet'.

*Etymology*.—We name this species for Robert J. (Bob) Dowsett, who has for half a century been the standard-bearer for African ornithology, producing (with various co-authors but notably his wife Françoise Dowsett-Lemaire) a series of national avifaunas of immense authority and rigour, documenting the birds of multiple protected areas, studying the migrations of Palearctic passerines, and providing the taxonomic backbone for the entire Afrotropical region.

## Discussion

While an attempt to name a new species *Caprimulgus kwalensis* on the basis of a sound-recording (Davis 1978) was rejected for lack of a specimen (Vuilleumier *et al.* 1992), we know of only a single case where a species has previously been established on the basis of vocalisations without possessing any (not even average) plumage or morphometric differences: Mees's Nightjar *Caprimulgus meesi* was identified as a new taxon from islands in Wallacea that were until then thought to be inhabited by taxonomically undifferentiated

populations of Large-tailed Nightjar *C. macrurus* (Sangster & Rozendaal 2004). Almost in the same category, however, is the recent split of Sula Cuckoo-dove *Turacoena sulaensis* from the supposedly monotypic White-faced Cuckoo-dove *T. manadensis*, based entirely on vocal differences in a paper that did not seek to check the validity of the weak morphological characters on which the commonly synonymised '*sulaensis*' was proposed in 1900 (Ng & Rheindt 2016).

In a CD booklet that was regrettably doomed to be widely overlooked, Chappuis (2000) argued that the two vocal types of *Cercococcyx mechowi* each merited species rank based on the facts that (a) differences in the innate vocalisations of cuckoos have the exact equivalence of visual differences, (b) each vocalisation is unaltered in any way across the large expanse of the ranges in question, (c) playback of eastern vocalisations to western birds produced no reaction, and (d) the larger eastern birds paradoxically have the higher-pitched voice. We commend this judgement and, of course, concur with it unreservedly. A strong divergence in voice with little or no divergence in physical appearance is far more indicative of the likelihood of real reproductive incompatibility than a strong genetic divergence with 'no readily apparent differences... in vocalizations', as presented in the proposed split of the two subspecies that comprise Barred Long-tailed Cuckoo *C. montanus* (Engel *et al.* 2014)—an arrangement not adopted to date by any of the main world lists of bird species (del Hoyo & Collar 2014, Christidis *et al.* 2018, Clements *et al.* 2018, Gill & Donsker 2018).

Ideally, Chappuis' playback experiment would be extended by playing western calls to eastern birds, and a similar pair of experiments undertaken for the two populations of the barbet. However, as the study of *Turacoena sulaensis* shows, the absence of such evidence need not and should not be an obstacle to the advancement of taxonomic hypotheses if these are based on other strong evidence. We are, in any case, reassured that Chappuis has already gone halfway in this issue with the cuckoo, and that playback experiments with African barbets demonstrate that they can discriminate even subtle differences in voice (Kirschel *et al.* 2009), even if this does not mean they remain unresponsive to poor imitations or indeed to calls of other species (F. Dowsett-Lemaire *in litt.* 2019). We strongly encourage playback trials with all of the taxa here delineated, but expect the results to support the conclusions we reach.

Such work would most interestingly be undertaken in the areas where the species replace each other. Confirmation of the Bakossi Mountains as a narrow hybrid zone for the cuckoo would be welcome, as would a study of the environs of the Sanaga River as an area of taxon interchange—from the maps in Borrow & Demey (2001) it appears to be for Yellow-footed Honeyguide *Melignomon eisentrauti* vs. Zenker's Honeyguide *M. zenkeri* and Blue-moustached Bee-eater *Merops mentalis* vs. Blue-headed Bee-eater *M. muelleri*. An exploration of the wooded areas that mark the break in forest continuity known as the Dahomey Gap, especially in western Nigeria, would help confirm the point where the barbets change over.

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**Appendix.** Sources for the vocalisations of Dusky Long-tailed Cuckoo *Cercococcyx mechowi* and Yellow-spotted Barbet *Buccanodon duchaillui*. All recordings were listened to as a means to check specific features, while a subset of these (of sufficient quality) was used to measure basic sound parameters: for *Cercococcyx* short song west 12 recordings (11 measured), short song east 42 (37); long call west 5 (5), long call east 11 (10),

unassigned 7; for *Buccanodon west* 20 (15), east 51 (22). BLNS = British Library (Wildlife and Environmental Sounds), CD = Chappuis (2000), ML = Macaulay Library, IBC = Internet Bird Collection, XC = Xeno-canto.

### *Cercococcyx mechowi*

**Short song (western group):** XC179067, Ghana, G. Wagner; ML23322 and 42772, Liberia, S. Keith; ML101953, Ivory Coast, I. Sinclair; ML146935, Ghana, M. Robbins; CD, Nigeria, C. Chappuis; private, Togo, F. Dowsett-Lemaire; BLNS180102/106/108/109, Ghana, M. Mills; BLNS33605, T. Bara, Ivory Coast; (**eastern group**): XC59080, Uganda, M. Claassen; XC137036/7, Uganda, J. Engel; XC138905/156751, Uganda, B. Piot; XC157034, Uganda, H. Groot; XC166360/166368/166386, Uganda, S. Bot; XC179678, Uganda, C. Wanyama; XC186102, Uganda, N. Perrins; XC241396, 241398/9, 241401, 283229, 287831, 280240 and 292240, Uganda, M. St-Michel; XC303069/70, Uganda, S. Dereliev; XC342702, J. Betleja; XC432516, Uganda, B. Edmonston; ML94116/94719, Tanzania, D. Moyer; ML102134, Gabon, I. Sinclair; ML107792/3, Tanzania, C. McBride; CD, Gabon, C. Énard; private, 'Congo', F. Dowsett-Lemaire; BLNS137243/244/513/526 and 212814 and 221271, Uganda, M. Mills; BLNS137805 and 199770, Angola, M. Mills; BLNS15559, Uganda, P. Boston; BLNS32790 and 32765, Gabon, T. Gullick; BLNS25520, 'Congo', P. Huguet. **Long call (western group):** XC419773, Ivory Coast, E. Leroy; ML101953, Ivory Coast, I. Sinclair; CD, Nigeria, C. Chappuis; private, Togo, F. Dowsett-Lemaire; BLNS180109, Ghana, M. Mills; (**eastern group**): XC312502, Uganda, M. St-Michel; ML26327, Uganda, S. Keith; ML94166/8, Tanzania, D. Moyer; IBC1130656, Uganda, J. del Hoyo; private, 'Congo', F. Dowsett-Lemaire; BLNS137243/221271, Uganda, M. Mills; BLNS137805, Angola, M. Mills; BLNScc20101, Cameroon, C. Chappuis; BLNS1524, Gabon, T. Gullick. **Unassigned** ML537132/537134/537167, Cameroon, M. Robbins; XC407506, Cameroon, J. Cooper; BLNS80394, Cameroon, F. Dowsett-Lemaire; BLNS136888 and 182020, Cameroon, M. Mills.

### *Buccanodon duchaillui*

**Western group:** XC104304/5, Ghana, M. Nelson; XC169720, Ghana, S. Bot; XC353155, Ghana, H. Matheve; XC360423, Ghana, J. Lidster; XC395749, J. Honkala; XC397057, Ghana, P. de Rouw; XC400182/183 and 400460, Ghana, P. Åberg; XC419616, Ghana, B. Edmonston; XC353565, Ivory Coast, E. Leroy; ML23321/29, Liberia, S. Keith; XC24893, Sierra Leone, F. Lambert; BLNS35136, Ivory Coast, A. Greensmith; BLNS180110/111/112 and 180128, Ghana, M. Mills. **Eastern group:** XC99886/7/8/9, Cameroon, M. Nelson; XC263478, Cameroon, J. Cooper; ML176505, Cameroon, P. Rodewald; ML212483, 212507, 212522 and 212556, Cameroon, M. Robbins; ML1132, 1173, 1412, DR Congo, P. Kaestner; ML93930/933, Gabon, L. Macaulay; ML102133, Gabon, I. Sinclair; XC101228, Kenya, J. Bradley; XC233336, Kenya, T. Sirotkin; ML51528, 51539, 51558, 51575, Kenya, J. Horne; XC55001, Tanzania, M. Claassen; ML45774, 46560, 46605, 46606, 46607, Tanzania, D. Moyer; XC138932/3, Uganda, B. Piot; XC245978, 246010, 263445, 263449, 264914, 267371, Uganda, M. St-Michel; XC281973, Uganda, R. de By; ML24808/814, Uganda, S. Keith; BLNScc1946, Gabon, C. Chappuis; BLNScc1947, Cameroon, C. Chappuis; BLNScc22616, Kenya, C. Chappuis; BLNS59271, Cameroon, N. Gardner; BLNS80611, 'Zaire', C. Carter; BLNS196321/399/401/402 and 198811 and 199258, Kenya, A. Gregory; BLNS16667, Kenya, R. Vicker.

## Two Palearctic herons on Fernando de Noronha, Brazil

by Eduardo Augusto Ferreira, Rogério de Castro, Rafael Fernandes & Andrew Whittaker

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**SUMMARY.**—We report the first documented record of Purple Heron *Ardea purpurea* in Brazil, and the second record of Little Egret *Egretta garzetta*, both of them on the island of Fernando de Noronha. A single *A. purpurea* was present between March 2017 and March 2018, and an *E. garzetta* on just one date in March 2017.

The archipelago of Fernando de Noronha (03°52'00"S, 32°25'00" W) lies 356 km off north-east Brazil (Fig. 1). The largest island, Fernando de Noronha, is c.10 km long by 3.5 km wide, and part of the archipelago lies within two protected areas: Fernando de Noronha Marine National Park and Fernando de Noronha-Rocas-São Pedro e São Paulo Environmental Protection Area (Bencke *et al.* 2006). The main island has mostly dry deciduous vegetation with a few man-made reservoirs, the largest being Açude do Xaréu (Castro 2009).

At least 75 bird species have been recorded on Fernando de Noronha (Silva-e-Silva 2008), including several migrant or vagrant water and shorebirds, many of the latter at Açude do Xaréu (Silva-e-Silva & Olmos 2006). Five species of Palearctic herons have been

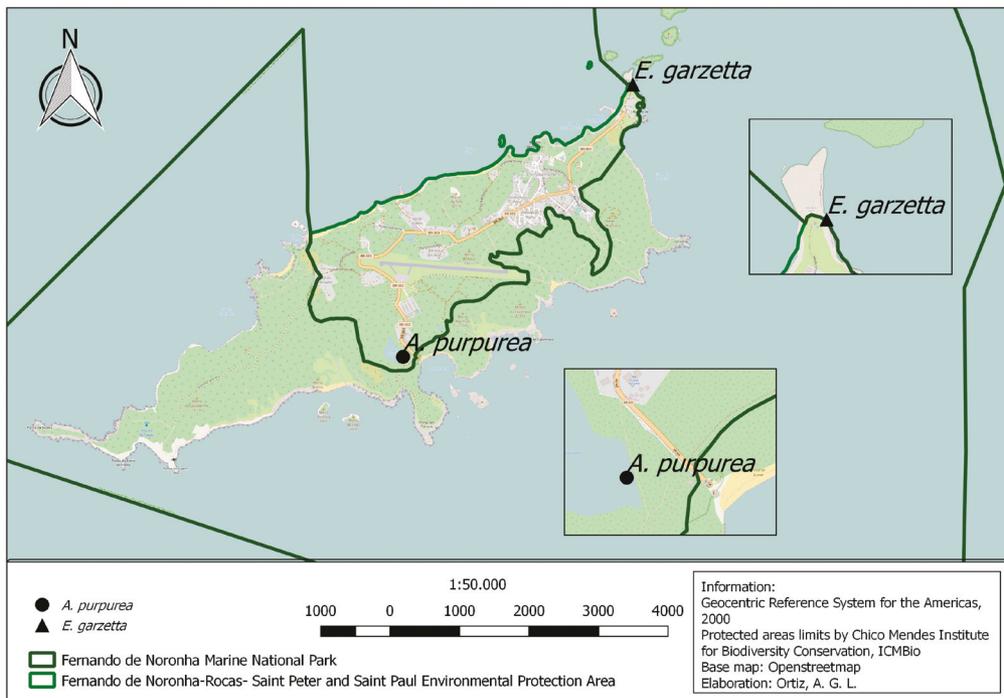


Figure 1. Location of records of Purple Heron *Ardea purpurea* and Little Egret *Egretta garzetta* on Fernando de Noronha.



Figure 2. Purple Heron *Ardea purpurea*, Açude do Xaréu, Fernando de Noronha, Pernambuco, Brazil, March 2017 (Rogério de Castro)

recorded in Brazil: Purple Heron *Ardea purpurea*, Grey Heron *A. cinerea*, Squacco Heron *Ardeola ralloides*, Western Reef Heron *Egretta gularis* and Little Egret *E. garzetta* (Silva-e-Silva & Olmos 2006, Fedrizzi *et al.* 2007, Silva-e-Silva 2008). All records of these species to date are from Fernando de Noronha or Rocas São Pedro e São Paulo, with Purple Heron, Western Reef Heron and Squacco Heron on the former. The many records of *Ardeola ralloides* suggest it is established on Fernando de Noronha (see Whittaker *et al.* in press). However, *Ardea purpurea* was observed only in June 1986, an ‘immature’, which record lacks documentation (Teixeira *et al.* 1987, Piacentini *et al.* 2015), and the only record of *Egretta garzetta* was at Rocas São Pedro e São Paulo (Bencke *et al.* 2005), a small and isolated group of rocky islets 1,100 km north-east of the coast of Rio Grande do Norte and 630 km north-east of Fernando de Noronha. Here we describe the first documented record of *Ardea purpurea* in Brazil, and the second for *E. garzetta*.

On 19 March 2017 RC observed a young *Ardea purpurea* at Açude do Xaréu (Fig. 2; <http://www.wikiaves.com/2504428>). Identification was straightforward. Young have more uniform brown upperparts feathers with buff fringes, and a dull brown bill and legs, showing much less yellow than adults (Martínez-Villata *et al.* 2019a). On 22–24 March 2017, more photographs were taken by EF. The bird was photographed also on 26 April (<http://www.wikiaves.com/2550155>), as well as 14 August (<http://www.wikiaves.com/2666868>) and 29 December, always in the same place (<http://www.wikiaves.com/2842424>). On 14 March 2018 (when in adult plumage) it was photographed again (<http://www.wikiaves.com/2938367>). AW & João Paulo Ferreira da Silva (JP) saw it on 27–28 March and the bird was observed several more times by JP until late April 2018, at either Açude do Xaréu or Açude do Ema.

On 21 March 2017 EAF photographed (Fig. 3) an adult Little Egret *Egretta garzetta* on Fernando de Noronha at Ponta do Air France (03°49’50’’S 32°23’55’’W). The bird was identified by its long thin bill, dark legs and yellow feet, and distinctive head, breast and back plumes (Martínez-Villata *et al.* 2019b). Snowy Egret *E. thula* has bright yellow feet (and rear tarsus), yellow lores and is shorter billed (Bencke *et al.* 2005, Martínez-Villata *et al.* 2019b).



Figure 3. Little Egret *Egretta garzetta*, Ponta do Air France, Fernando de Noronha, Pernambuco, Brazil, March 2017 (Eduardo Augusto Ferreira)

Western Reef Heron *E. gularis* is polymorphic in plumage, which can be dark grey, usually with a white throat, white or intermediate, with a mixture of white and grey (Fedrizzi *et al.* 2007, Martínez-Villata *et al.* 2019b). The latter species has the eyes lemon yellow, maxilla blackish, mandible yellowish, and the bill overall heavier and more decurved than in Little Egret *E. garzetta* and Snowy Egret *E. thula* (Fedrizzi *et al.* 2007, Kirwan *et al.* 2019).

## Discussion

*Ardea purpurea* occurs across Eurasia, Africa and Oceania, with migratory populations in the former (Martínez-Villata *et al.* 2019a). Northern European breeders winter in Africa and are capable of making long, non-stop flights, as demonstrated by seven birds marked with satellite transmitters that flew c.4,000 km from the Netherlands to Morocco in 5–7 days, with one *A. purpurea* travelling almost 5,600 km south-west over the Atlantic until it was lost (van der Winden *et al.* 2010). There are few records of the species elsewhere in the Americas: three in Trinidad & Tobago (Kenefick & Hayes 2006, Behrstock & Kenefick 2012) and six in Barbados (Kirwan *et al.* 2019).

Little Egret is also widespread across Eurasia, Africa and Oceania, as well as Australia and New Zealand (Martínez-Villata *et al.* 2019a). Within the last 70 years the species has been increasingly frequently observed in the Americas, especially in the Lesser Antilles and northern South America, with breeding recorded on at least two islands in the West Indies (Downs 1959, Murphy 1992, Kirwan *et al.* 2019).

Our observations add to the growing body of observations of Palearctic vagrants on Brazilian oceanic islands, including Northern Pintail *Anas acuta*, European Spoonbill

*Platalea leucorodia* (Fedrizzi *et al.* 2007), Eurasian Kestrel *Falco tinnunculus* (Bencke *et al.* 2005), Lesser Moorhen *Gallinula angulata* (Bencke *et al.* 2005) and Black Kite *Milvus migrans* (Nunes *et al.* 2015). Fernando de Noronha seems to be a particularly propitious site for such vagrants due to its size and the presence of (artificial) freshwater bodies with suitable prey including introduced small fish and frogs.

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# A new subspecies of White-eared Honeyeater *Nesoptilotis leucotis* (Meliphagidae)

by Andrew Black

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**SUMMARY.**—White-eared Honeyeater *Nesoptilotis leucotis* ranges broadly across southern Australia, where it is a constituent of eucalypt forest and woodland communities. A recent phylogeographic study recovered deep divergence between western and eastern populations. Within the western phylogroup are two allopatric populations that are differentiated by morphometrics, plumage coloration and voice. The eastern of the two, which occupies mallee woodland on the Eyre Peninsula, South Australia, is described here as a new subspecies.

White-eared Honeyeater *Nesoptilotis leucotis* (Latham, 1801) occupies temperate humid eucalypt forest and semi-arid eucalypt woodland across southern Australia and, until recently, was treated as comprising three subspecies (Schodde & Mason 1999). The subspecies were: an eastern forest form *N. l. leucotis* (Latham, 1801), *N. l. novaenorcaiae* (Milligan, 1904), from western to inland eastern Australia, chiefly in low woodlands of multi-stemmed eucalypts known as mallee (Johnstone & Storr 2004), and *N. l. thomasi* (Mathews, 1912), on Kangaroo Island, where it occurs in both forest and mallee (Baxter 2015).

In a phylogeographic study of 12 southern Australian bird species, Dolman & Joseph (2015) identified two phylogroups within the White-eared Honeyeater, separated by 21 base pair differences in the mitochondrial gene ND2. The break is at the Eyrean Barrier (Ford 1974, 1987, Schodde & Mason 1999: 787), a periodic arid intrusion during Pleistocene times and perhaps earlier, at the longitude of the present-day Spencer Gulf and Lake Torrens. Dolman & Joseph's (2015) findings placed populations previously assigned to subspecies *novaenorcaiae* within both phylogroups, and, to reflect phylogeographic history, led them to restrict *novaenorcaiae*, type locality Wongan Hills, south-west Australia (30°49'S, 116°38'E), to the western group. Black (2018) demonstrated that these genetically divergent western and eastern mallee populations are allopatric as well as distinct phenotypically. He argued that the eastern mallee population consequently required distinction from forest-based nominate *leucotis* there, a view supported by Lamb *et al.* (2018), who identified two subclades within the eastern phylogroup. Black (2018) noted that the name *depauperata* Mathews, 1912, type locality Coonalpyn, South Australia (35°42'S, 139°51'E), was available for the eastern mallee population. He also showed that the western phylogroup comprised two allopatric populations, one in Western Australia, the other on the Eyre Peninsula north to the Gawler Ranges and the Yellabinna region of South Australia, the two separated by the treeless Nullarbor Plain (see Fig. 1). Consequently, he questioned whether they might also be taxonomically distinct.

The present study addresses that question by examining the phenotypes of the two populations within the western phylogroup of White-eared Honeyeater.

## Methods

Specimens of White-eared Honeyeaters were examined from the two populations west of the Eyrean Barrier: 14 adult males of the Western Australian population east to the Great

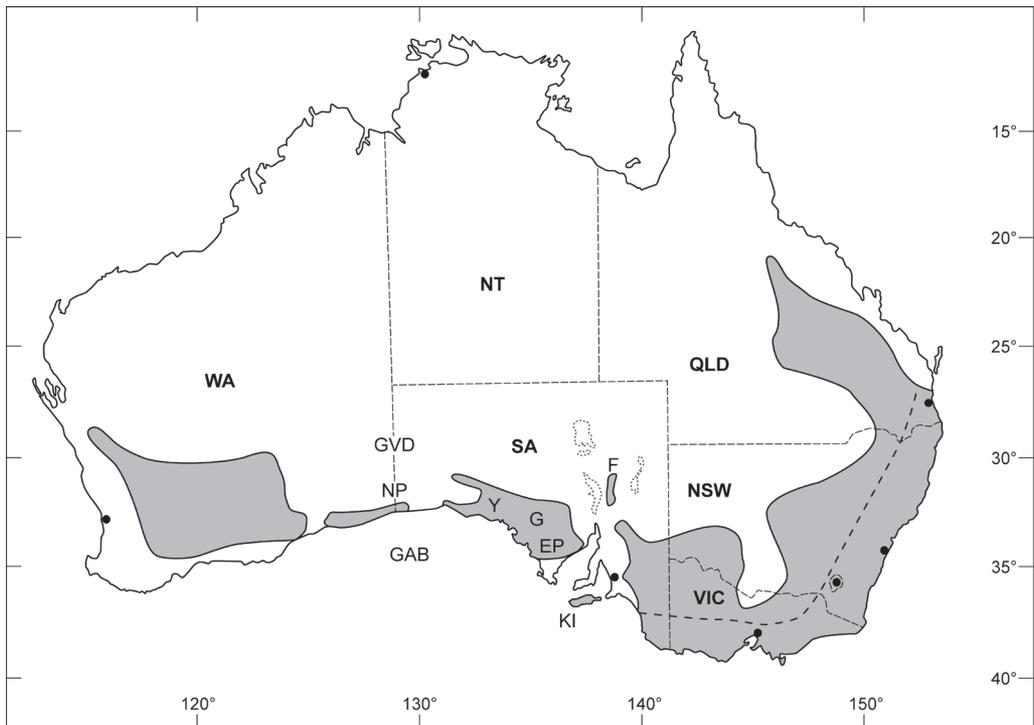


Figure 1. Map showing the distribution of White-eared Honeyeater *Nesoptilotis leucotis*, derived from Johnstone & Storr (2004; for Western Australia), Schodde & Mason (1999; eastern Australia) and Black (2018; South Australia). Two phylogroups range either side of the Eyrean Barrier, represented by the saline Lake Eyre and Lake Torrens (dotted outlines) and the larger Spencer Gulf, with the Eyre Peninsula (EP) to the west and Flinders Ranges (F) to the east. Other than the small Flinders Ranges and Kangaroo Island (KI) isolates, the eastern phylogroup is distributed continuously, with an intergradient zone between inland *N. l. depauperata* and coastal *N. l. leucotis* represented by the dashed line. The western phylogroup contains two allopatric populations, one in southern Western Australia extending across a small discontinuity, south of the Nullarbor Plain (NP) into western South Australia, and another, separated across the NP near the head of the Great Australian Bight (GAB), in the Yellabinna (Y), Gawler Ranges (GR) and EP.

Australian Bight, held at the Western Australian Museum, Perth (WAM), and 12 adult males of the Eyre Peninsula population, at the South Australian Museum, Adelaide (SAMA). Only male specimens were compared because of the small female sample sizes of this sexually dimorphic species (Schodde & Mason 1999, Higgins *et al.* 2001, Black 2018).

Standard measurements were taken: wing, flattened from the 'shoulder' to the tip of the longest primary; tail, from the base to the tip of the longest rectrix when closed; length of the culmen, from the cranio-frontal hinge to the tip; and depth of the bill, at the feather line on the base of the maxilla. All measurements were taken to 0.1 mm, except wing, which was measured to the nearest 1 mm (Table 1).

Plumage coloration of the olive upperparts and yellow underparts was compared using the *Naturalist's color guide* (Smithe 1975).

## Results

**Morphometrics.**—The measurements of males for each population are presented in Table 1. A plot of the significantly differing variables is presented graphically in Fig. 2. It shows that separation between the two populations is substantial, albeit with some overlap.

TABLE 1

Mensural data for male White-eared Honeyeaters *Nesoptilotis leucotis* of the two populations, Western Australia and Eyre Peninsula, presenting means, standard deviation and sample sizes for each variable, and the statistical significance of differences in compared values.

Region and sample size	Wing (mean $\pm$ SD) (n)	Tail (mean $\pm$ SD) (n)	Culmen length (mean $\pm$ SD) (n)	Bill depth (mean $\pm$ SD) (n)
Western Australia	88.3 $\pm$ 2.2 (n = 13)	90.0 $\pm$ 3.2 (n = 13)	18.6 $\pm$ 0.8 (n = 14)	4.5 $\pm$ 0.3 (n = 12)
Eyre Peninsula	91.0 $\pm$ 2.0 (n = 11)	89.1 $\pm$ 2.4 (n = 12)	18.4 $\pm$ 1.0 (n = 12)	4.8 $\pm$ 0.2 (n = 12)
Probability value	0.005	0.4 NS	0.6 NS	0.003



Figure 2. Plot of the variables wing length and bill depth of Eyre Peninsula (orange) and Western Australian (blue) samples of White-eared Honeyeater *Nesoptilotis leucotis*, indicating differentiation between them in morphometrics.

Overall the two populations are of similar size. Tail lengths are not significantly different, but wings are on average shorter in the Western Australian population ( $p = 0.005$ ) with a consequently greater tail / wing ratio. Bills are of similar length, but shallower in Western Australian birds ( $p = 0.003$ ).

**Plumage.**—The Eyre Peninsula population is brighter overall than the Western Australian population (Figs. 3–4). The colour of the underparts in the former approaches highly saturated Spectrum Yellow (55; numbers follow Smithe 1975), that of the latter being a paler, creamy yellow, between Sulphur Yellow (57 or 157) and Cream Color (54). Variation occurs in both populations, with the dullest four of the Eyre Peninsula population overlapping the brightest two from Western Australia, and can be little attributed to plumage wear or specimen age. The dorsum of the Eyre Peninsula population is also brighter and yellower, Yellowish Olive-Green (50) that consistently distinguishes all specimens from the Olive Green (Basic) (46) of the Western Australian population.



Figure 3. Ventral view of White-eared Honeyeater *Nesoptilotis leucotis* specimens (from left to right) SAMA B28176 (paratype of *N. l. schoddei*), east of Kimba, South Australia, 17 July 1963, SAMA B51326 (holotype of *N. l. schoddei*), Port Kenny, South Australia, 17 February 2004 (both from the Eyre Peninsula population), and WAM A11429, Tarin Rock, Western Australia, 23 May 1971 and WAM A19788, Toolina Rockhole, Western Australia, 11 May 1985 (from the Western Australian population), showing the brighter yellow underparts of the Eyre Peninsula population (P. Horton)

## Discussion

Schodde & Mason (1999) found that western, including Eyre Peninsula, populations of White-eared Honeyeater are brighter than those in the eastern mallee. That observation anticipated distinction between the two groups, which are now known to be genetically divergent (Dolman & Joseph 2015) and were subsequently recognised subspecifically, as *N. l. novaenorciae* and *N. l. depauperata* respectively (Black 2018). Black (2018) also found that the Eyre Peninsula population is brighter above and below than all populations of the eastern phylogroup, including the nominate subspecies (Figs. 5–6). The present study now finds that the Eyre Peninsula population has brighter and more yellowish upper- and underparts than the Western Australian population as well. Thus, Eyre Peninsula White-eared Honeyeaters are probably the brightest of all, except potentially the as yet unexamined inland Queensland birds reported by Schodde & Mason (1999) to be ‘small



Figure 4. Dorsal view of the same specimens in the same order as in Fig. 3, showing the brighter and yellowish olive tone in the Eyre Peninsula, South Australia, specimens (P. Horton)

yet bright citrine'. The nature of interactions among mallee and forest populations of the eastern phylogroup needs further, more detailed evaluation, as Schodde and Mason (1999) already observed.

In morphometrics, Eyre Peninsula and Western Australian populations differ slightly but significantly in wing length and bill depth.

In distribution, the same two populations are evidently allopatric, being separated by the Great Victoria Desert and the treeless Nullarbor Plain. Many southern Australian landbirds with Western Australian and Eyre Peninsula representatives, while absent from the Nullarbor Plain, are nonetheless continuously distributed through the mallee corridor of the Great Victoria Desert to the north (Ford 1971, Black & Badman 1986). Others, such as Yellow-plumed Honeyeater *Ptilotula ornata*, Brown-headed Honeyeater *Melithreptus brevirostris*, Shy Heathwren *Hylacola cauta* and the present species, extend through the Yellabinna region into the southern Great Victoria Desert, but are not known to contact Western Australian populations therein. In the south, the Nullarbor Plain extends to the coast at the head of the Great Australian Bight, producing a discontinuity in the mallee vegetation for more than 150 km and forming a narrow barrier to mallee-dependent birds.



Figure 5. Ventral view of White-eared Honeyeater *Nesoptilotis leucotis* specimens (from left to right) SAMA B28176 (paratype of *N. l. schoddeii*), east of Kimba, Eyre Peninsula, South Australia, 17 July 1963, SAMA B55328, *N. l. depauperata*, south of Pinnaroo, South Australia, 13 June 2006, SAMA B25251, *N. l. leucotis*, south of Naracoorte, South Australia, 25 October 1958, and SAMA B3041, *N. l. thomasi*, Kangaroo Island, South Australia, 20 May 1921; showing the brightest underparts of the Eyre Peninsula specimen (P. Horton)

White-eared Honeyeater occurs in mallee either side of that barrier but is not reliably reported from within it (Black 2018, Atlas of Living Australia [www.ala.org.au](http://www.ala.org.au); see Fig. 1).

Black & Stewart (submitted) reviewed many recordings of voice, chiefly song, of the four mainland populations of White-eared Honeyeater and found distinct regional differences. This was particularly pronounced between the western and eastern phylogroups, conforming to the understanding that song divergence in songbirds may reflect or even drive genetic divergence (Päckert 2018). Differences between Western Australian and Eyre Peninsula populations within the western phylogroup were also evident, the former being more complex and more variable. Further standardised comparative sonographic analyses are recommended.

Thus, isolation of Eyre Peninsula and Western Australian populations, albeit only narrowly, has evidently been sufficient to limit gene flow and generate differentiation in plumage pigmentation, proportions and voice. Accordingly, the so-far un-named Eyre Peninsula population is described as a new subspecies.



Figure 6. Dorsal view of the same specimens in the same order as in Fig. 5, showing the Eyre Peninsula specimen to be the brightest and yellowest (P. Horton)

### *Nesoptilotis leucotis schoddei* subsp. nov.

*Holotype*.—Adult male, SAMA B51326, collected by D. Armstrong 1 km north-west of Port Kenny, Eyre Peninsula, South Australia (33°09'45"S, 134°40'03"E) on 17 February 2004. Wing (max. flattened chord) 91 mm, tail (central rectrix from emergence to tip) 90.7 mm, bill length (from skull to tip) 18.7 mm, bill depth (at level of frontal feathering) 4.9 mm (Figs. 3–4).

*Paratypes*.—Adult male, SAMA B28176, collected by W. Head, 15 km east of Kimba, Eyre Peninsula, South Australia (33°08'S, 136°25'E) on 17 July 1963. Wing 92 mm, tail 88.7 mm, bill length 16.8 mm, bill depth 5.0 mm (Figs. 3–6). Adult male, SAMA B55914, collected by L. Pedler, on Coombra Track c.67 km west-northwest of Yalata, western South Australia (31°23'19"S, 131°20'27"E) on 2 April 2008. Wing 93 mm, tail 85.8 mm, bill length 17.3 mm, bill depth 4.8 mm.

*Diagnosis*.—Distinguished from the most similar and genetically closest subspecies *N. l. novaenoriae* by brighter plumage overall, especially the brighter, yellow olive upperparts and purer (more saturated) yellow breast and belly, slightly longer wing and deeper bill (Table 1), and less complex voice. It is also substantially brighter than subspecies within

the eastern phylogroup, *N. l. leucotis*, *N. l. depauperata* and *N. l. thomasi*, and is further distinguished from them in mtDNA sequence (Dolman & Joseph 2015).

*Etymology*.—Named to honour the foundational work in Australian ornithology of Richard (Dick) Schodde OAM. Particularly, it recognises his identification of distinguishing traits among populations of this and other Australian bird groups that anticipated more recent genetic findings or has facilitated their interpretation. Dr Schodde was foundation Director of CSIRO's Australian National Wildlife Collection 1970–2000, and in 2009 he was awarded the Medal of the Order of Australia for his contribution to the natural sciences, particularly ornithology.

*Distribution*.—The new subspecies is centred on the Eyre Peninsula, South Australia, where it is confined to mallee woodland. It extends west to the limit of mallee near the head of the Great Australian Bight at 31°22'S, 131°20'E and north-west through the Gawler Ranges and Yellabinna at least to Maralinga (30°10'S, 131°34'E). *N. l. schoddei* also ranges east through the Gawler Ranges to the north-east limit of mallee vegetation in the Baxter Range at 32°20'S, 137°17'E.

### Conspectus of subspecies in *Nesoptilotis leucotis*

*N. l. leucotis* (Latham, 1801).—The nominate subspecies of eastern Australian forests, chiefly east of the Great Dividing Range, north to slightly beyond Brisbane, south-east Queensland and through southern Victoria into south-eastern South Australia. A brightly plumaged form, it is larger than other subspecies (Schodde & Mason 1999).

*N. l. depauperata* (Mathews, 1912).—Smaller than nominate *leucotis*, and distributed in south-eastern mallee woodlands, inland of the Great Dividing Range. Its zone of interaction with the nominate subspecies remains incompletely evaluated (Schodde & Mason 1999). Likewise, Lamb *et al.*'s (2018) detection of two subclades within the two eastern subspecies, this and *N. l. leucotis*, warrants further study. This is the palest subspecies and the dullest mainland form.

*N. l. thomasi* (Mathews, 1912).—Restricted to Kangaroo Island, South Australia. Differs from all others in its greyer, more melanised plumage. It occupies both forest and mallee (Baxter 2015). This and the previous two subspecies form an eastern clade.

*N. l. schoddei* Black, 2019.—The subspecies of mallee on the Eyre Peninsula, the Gawler Ranges and Yellabinna region, South Australia. A very brightly plumaged subspecies.

*N. l. novaenorciae* (Milligan, 1904).—The subspecies of Western Australia's mallee and taller semi-arid eucalypt woodlands and scrub (Johnstone & Storr 2004). With *N. l. schoddei* it forms a western clade in *N. leucotis*, but is less brightly plumaged, shorter winged and more slender billed than the Eyre Peninsula form. Its song also contains unique elements.

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# What is known about the enigmatic Gulf of Guinea band-rumped storm petrels *Hydrobates* cf. *castro*?

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**SUMMARY.**—We present what is known about the Gulf of Guinea band-rumped storm petrels *Hydrobates* cf. *castro* to identify priority areas for research and conservation. Addressed are: occurrence in the Gulf of Guinea, including museum specimens, at-sea records, observations on the islands, and potential breeding sites; seasonality, the timing of breeding inferred from condition of trapped birds and birds at sea in primary moult; morphology, including biometrics, structure, plumage aspect; aerial vocalisations at the suspected breeding grounds; and taxonomy. The first photographs and sonograms pertaining to this population to be published are also presented. The evidence indicates that this storm petrel is present in the Gulf of Guinea year-round. It almost certainly breeds on São Tomé during both the wet and long dry seasons, and breeding is probably protracted, possibly seasonal. Morphology indicates a degree of distinctiveness and aerial vocalisations suggest possible taxonomic affinities with Cape Verde Storm Petrel *H. jabejabe*. Our observations are provisional and further research is required. The three most pressing matters for future research are clarifying taxonomy, locating breeding colonies and identifying key threats.

Taxa included in the band-rumped storm petrel complex (*Hydrobates castro*, *sensu lato*) breed in the North Atlantic, South Atlantic and North Pacific Oceans (Brooke 2004, Howell & Zufelt 2019; Fig. 1a). Taxonomic relationships among these cryptic black-and-white taxa are poorly understood, although several species have been recognised in recent years (e.g. Friesen *et al.* 2007, Bolton *et al.* 2008, Deane 2011, Silva *et al.* 2016). Band-rumped storm petrels in the Gulf of Guinea (*Hydrobates* cf. *castro*—hereafter Gulf of Guinea Storm Petrel), in the equatorial east Atlantic, are known from only a small number of museum specimens, and at-sea and over-land records. However, fishermen on São Tomé and Príncipe are familiar with black-and-white storm petrels under the name ‘canimboto’ or ‘caniboto’, suggesting that it is a common bird around the islands. The sole attempt to clarify the general status of the Gulf of Guinea Storm Petrel was published more than 20 years ago and it failed to clarify the taxonomy or to confirm the existence of a breeding population (Monteiro *et al.* 1997, available from the authors). Here we update and expand upon published information to identify priority areas for research and conservation, including data on specimens, at-sea and over-land observations, possible nesting sites, seasonality, and describe this population’s biometrics, structure, plumage aspect and vocalisations, illustrated by the first published photographs and sonograms.

## Occurrence in the Gulf of Guinea

**Study area.**—The Gulf of Guinea (00°20’N, 06°44’S) is located off the Atlantic Ocean coast of Central Africa. It is crossed by a volcanic arc that produced the oceanic islands

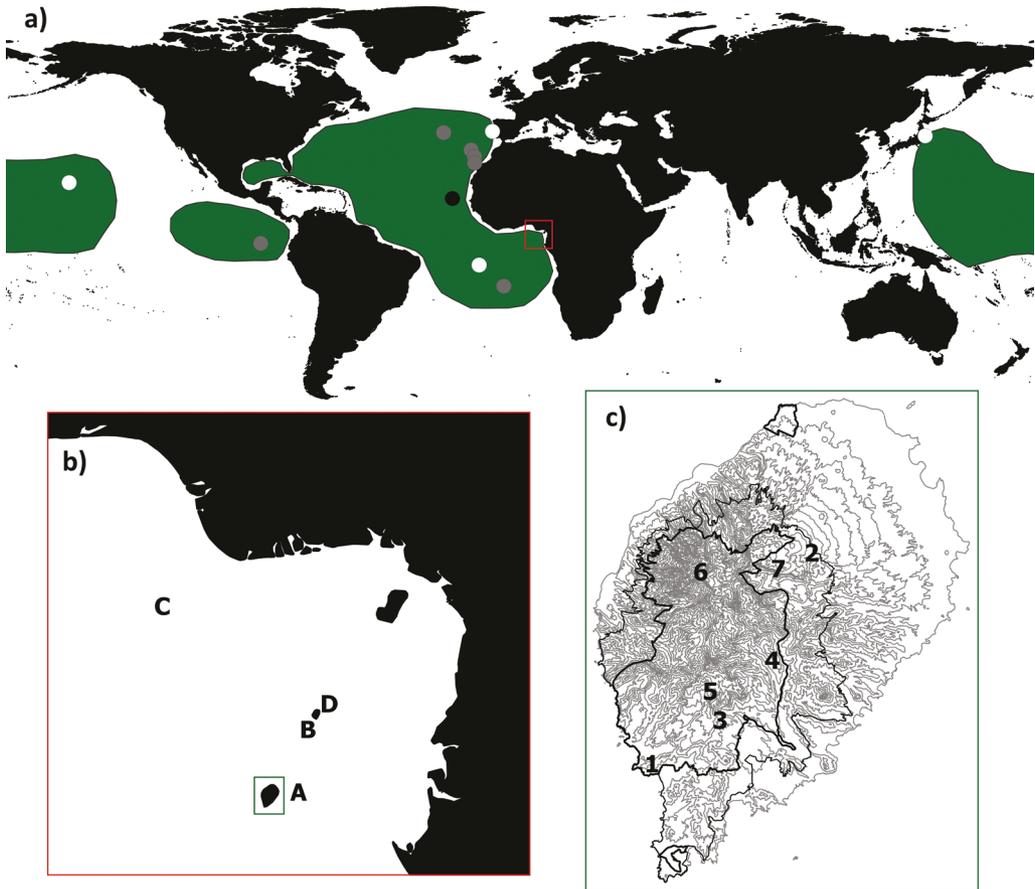


Figure 1. Gulf of Guinea Storm Petrel *Hydrobates cf. castro* distribution maps (background world map: Sandvik 2019). (a) global distribution of Band-rumped Storm Petrel *H. castro*. At-sea distribution shown in green (Howell & Zufelt 2019) and breeding colonies by circular symbols: white—one distinct seasonal population, grey—two distinct seasonal populations, black—protracted breeding season (Friesen *et al.* 2007). The red rectangle indicates the Gulf of Guinea. (b) At-sea observations in the Gulf of Guinea. Letter codes explained in Table 1. The green rectangle indicates São Tomé. (c) Observations on São Tomé. Numeric codes explained in Table 1. Grey lines in the background = 100 m altitudinal isolines; the thick black line = borders of Obô Natural Park; and the thin black line = border of the park's buffer zone.

of Annobón, São Tomé and Príncipe, and the continental island of Bioko (Fig. 1). Max. altitudes are: Annobón 598 m, São Tomé 2,024 m, Príncipe 948 m and Bioko 3,011 m. The mountains are very steep and there are several inland as well as coastal cliffs. The islands' climate at sea level is consistently hot year-round, but the rugged topography gives rise to a strong rainfall gradient and lower temperatures at higher altitudes (Jones *et al.* 1991). There is a long dry season between mid May and early September, a short one between late December and early February, and two wet seasons covering the rest of the year. The mountainous centres of the islands still harbour relatively extensive and well-preserved patches of old-growth forest where most of the native bird species persist (Lima *et al.* 2017).

**Historical records.**—J. V. Barbosa du Bocage acquired what was presumably a Gulf of Guinea Storm Petrel collected 'far offshore' São Tomé by fishermen around 1891 (Salvadori 1903 *in* Amadon 1953, Christy 1996, Jones & Tye 2006). It was held at the Museu Nacional de História Natural e da Ciência da Universidade de Lisboa, but almost certainly was lost in a huge fire in 1978 (J. Alves & R. Figueira *in litt.* 2018). J. G. C. & V. Correia collected four

TABLE 1

Observations of band-rumped storm petrel *Oceanodroma cf. castro* in the Gulf of Guinea. Under Location, the general locality is provided in parentheses: ST = São Tomé, PR = Príncipe, GG = Gulf of Guinea, and the subsequent numbers and letters indicate the codes used in the maps.

Date	Type of encounter	Location	Observations	Source
c.1891	Captured	'far offshore' (ST)	Acquired by J. V. Barbosa du Bocage from Angolar fishermen; presumed lost in 1978, during a fire at the Museu Nacional de História Natural e da Ciência da Univ. de Lisboa	J. Alves & R. Figueira <i>in litt.</i>
15 Nov 1928	House lights (captured)	Roça Jou (ST-1, c.150 m)	Adult female: plumage slightly worn and gonads small	Correia diaries 1928–29
10 Dec 1928	House lights (captured)	Roça Jou (ST-1)	Juvenile male: fresh plumage and gonads small; adult male: plumage slightly worn and gonads swollen	Correia diaries 1928–29
14 Dec 1928	House lights (captured)	Roça Jou (ST-1)	Adult male: plumage slightly worn and gonads large	Correia diaries 1928–29
24 Mar 1997	Chum	8–19 km east of Santana (ST-A)	11	Monteiro <i>et al.</i> (1997)
18 Jul 1997	At sea (visual)	Near Tinhosas (PR-B)	One in flight at 13.30 h	Monteiro <i>et al.</i> (1997)
23 Jul 1997	Chum (visual)	(ST-A)	20—one adult caught and measured (Table 2) had a fully bare brood patch	Monteiro <i>et al.</i> (1997)
29 Jul 1997	Chum (visual)	(ST-A)	Five	Monteiro <i>et al.</i> (1997)
-	House lights	Pousada da Boa Vista (ST-2, c.800 m)		Jones & Tye (2006)
3 Sep 2001	Sight	(PR)	One, between Príncipe and Tinhosas	J. Drummond (eBird)
Apr 2009	Aural	Nova Moka (ST-2, c.800 m)	In flight	RFL
12 Aug 2009	Camp lights (captured)	Monte Carmo camping site (ST-3)	Adult: plumage slightly worn (Figs. 14–15, c.400 m)	N. Borrow <i>et al.</i>
6 Apr 2011	At sea (visual)	(GG- C)	Seen at 14.50 h, 11 m above sea level, from the bridge of the small cruiser MV <i>Prince Albert II</i> (now MV <i>Silver Explorer</i> ). 51 total: 31 not determined, 12 not in moult (Figs. 6, 7, 12), six moulting (see text; Figs. 6, 8–13)	RLF & WHW
13 Sep 2013	Flushed (visual)	Vieira Machado (ST-4, 373 m)	One caught in a liana, in native forest at 12.42 h	RFL & A. Santana
5 Feb 2015	Visual	Cambumbé (ST-5, 861 m)	At least six in native forest, at 18.50 h	A. Santana
1–19 Jun 2015	Aural	Cambumbé (ST-5)	First recording taken on 1 June. Heard multiple times on subsequent nights	MM
21 Sep 2015	Aural	Monte Carmo (ST-3)	Several heard in native forest, flying above the canopy after sunset	RFL (eBird)
11 Dec 2015	Visual	Mesa do Pico (ST-6, c.1,900 m)	One in flight	A. Coelho & G. Oquiongo
28 Mar 2016	Aural	Macambará (ST-7, c.1,300 m)	One vocalising in flight above the canopy of secondary forest	RFL (eBird)
2 Aug 2016	Aural	Monte Carmo camp site (ST-3)	One heard in native forest, flying above the canopy at 19.20 h	RFL (eBird), PV
8–10 Aug 2016	Aural	Cambumbé (ST-5)	Several	PV <i>et al.</i>
10–13 Aug 2016	Aural	Monte Carmo camp site (ST-3)	Several	PV <i>et al.</i>
21 Sep 2016	Aural	Macambará (ST-7)		MM
20 Jan 2017	Chum	(PR)	None recorded	Bollen <i>et al.</i> (2018)
4 Feb 2017	?	(PR-D)	Two	B. Bronkhorst, <i>in</i> Bollen <i>et al.</i> (2018)
5 Aug 2017	Aural	Monte Carmo camp site (ST-3)	25	J. Smith (eBird)



2



4a



4b



3



4c



4d

Figures 2–4. Four specimens of Gulf of Guinea Storm Petrel *Hydrobates* cf. *castro* collected by J. G. C. & V. Correia, at Roça Jou, São Tomé, 15 November–14 December 1928, now at the American Museum of Natural History (AMNH), New York, left to right (above) and top to bottom (right): AMNH 268390, AMNH 268388, AMNH 268387 and AMNH 268389; note prominent buff ulnar bars, relatively small white ‘rump patch’, and the relatively large size and dark plumage of AMNH 268390 (Angus Wilson & Robert L. Flood)

TABLE 2

Gulf of Guinea Storm Petrel *Hydrobates cf. castro* measurements (mm). Measurements of the 1928 birds (Amadon 1953, Harris 1969) were slightly amended following cross-checks with the museum specimens (RLF). Method for measuring the 'rump patch' is described in the text. The 1997 individual had the following additional measurements: head to bill tip 40.1 mm, bill depth at nostrils 6.9 mm and bill depth at gonys 5.5 mm (Monteiro *et al.* 1997).

AMNH reg. no.	Date	Sex / age	Wing	Bill	'Rump patch'
268390	15 Nov 1928	Female	171	16.8	26
268387	10 Dec 1928	Male	156	17.0	24
268388	10 Dec 1928	Male	160	17.3	25
268389	14 Dec 1928	Male	160	15.5	25
n/a	23 Jul 1997	-	165	16.3	-

specimens at Roça Jou, in the south-west of São Tomé in late 1928 (Location 1 in Fig. 1c, Table 1). The birds entered a house at night, during heavy rain and thunderstorms, attracted by lights; the skins are at the American Museum of Natural History, New York (Figs. 2–4).

**At-sea observations.**—In 1997, three chumming sessions east of Santana, São Tomé, recorded Gulf of Guinea Storm Petrel, of which one was caught using a net (Location A in Fig. 1b, Tables 1–2). The same year one was observed in flight near the Tinhosas Islands (Location B in Fig. 1b, Table 1; Monteiro *et al.* 1997). In 2011, 51 Gulf of Guinea Storm Petrels were recorded midway between Príncipe and Benin, at the edge of the continental shelf, including 18 rafting birds (Location C in Fig. 1b, Table 1, Figs. 5–13). In 2017, none was found near Príncipe's 100 m-depth contour during two chumming sessions, but two were seen near Príncipe at the 1,000 m contour (Location D in Fig. 1b, Table 1; Bollen *et al.* 2018).

We add a caveat for records without documentation, as black-and-white storm petrels are notoriously difficult to identify at sea and safe identification requires an experienced eye or good photographs (Flood & Fisher 2013). It is thus possible that Gulf of Guinea Storm Petrel and migrant black-and-white storm petrel species reported in the region have sometimes been confused: Wilson's Storm Petrel *Oceanites oceanicus*, European Storm Petrel *Hydrobates pelagicus*, Leach's Storm Petrel *H. leucorhoa* and Black-bellied Storm Petrel *Fregata tropica* (Christy & Clarke 1998, Jones & Tye 2006, Dowsett *et al.* 2017). It is also possible that representatives from other populations of the band-rumped storm petrel complex visit the region.

## Observations on the islands and potential breeding sites

There are multiple strong indications that band-rumped storm petrels breed in the Gulf of Guinea, but no conclusive proof (Fig. 1, Table 1; Jones & Tye 2006). It had been suggested that Gulf of Guinea Storm Petrel could nest on the islets around São Tomé and Príncipe (Amadon 1953, Harris 1969, Williams 1984, Christy 1996). However, instead of evidence of breeding, surveys found an abundance of predatory land crabs *Johnngarthia weileri* that would pose a threat to nesting storm petrels (Monteiro *et al.* 1997, Valle *et al.* 2016, Bollen *et al.* 2018). Nevertheless, it would be prudent to resurvey all of the islets.

Gulf of Guinea Storm Petrel probably breeds on the main islands, and most evidence points to nesting on São Tomé (Naurois 1983, Monteiro *et al.* 1997). In addition to the Correias' specimens, collected in south-west São Tomé, storm petrels have been attracted to the lights of the hostel Pousada Boa Vista, in the centre of the island (Banko *et al.* 1991, Monteiro *et al.* 1997), and to the lights of the EMOLVE palm oil factory, in the south-east of



Figures 5–13. Gulf of Guinea Storm Petrels *Hydrobates* cf. *castro*, midway between Príncipe and Benin, at the edge of the continental shelf, 6 April 2011. The raft in Figs. 5–6 had 17 birds. Note the narrow white ‘rump patch’. In Fig. 7, note the prominent ulnar bars in what appears to be relatively fresh plumage and the suggestion of a notched tail tip. In Figs. 8–9 note the early stages of primary moult with pp3/4–p10 old, worn plumage evident in the abraded tips to the outer primaries and untidy ulnar bars, thigh patch, and square tail tip. In Figs. 10–11, the dark replaced inner primaries contrast strongly with the old bleached and worn pp6/7–10. In Figs. 12–13, the moulting bird is almost midway through primary moult with pp7–10 old (William H. Wagstaff)

the island (R. Fonseca *in litt.* 2018). Since 2009, further evidence that reaffirms the likelihood of breeding on São Tomé comprises mostly nocturnal aural records near rugged terrain covered by native forest (Fig. 1c, Table 1). In addition, one was trapped and photographed



14



15



16

Figures 14–15. Gulf of Guinea Storm Petrels *Hydrobatas* cf. *castro*, near Monte Carmo, Obô Natural Park, São Tomé, 12 August 2009; note the abraded tail tip in Fig. 14 indicative of wear from time in a burrow; Fig. 15 is the only photograph that shows bill structure of a live bird (Nik Borrow)

Figure 16. Forested gully near Monte Carmo, Obô Natural Park, São Tomé; Gulf of Guinea Storm Petrels *Hydrobatas* cf. *castro* are regularly heard in this forested ravine after dusk (Location 3 in Fig 1c) (Philippe Verbelen)

in native forest near Monte Carmo, in south-central São Tomé, presumably attracted to camp lights (Location 3 in Fig. 1c, Figs. 14–16). Since then, Gulf of Guinea Storm Petrel has been recorded regularly at this location and in the environs (Table 1).

Evidence is scant that Gulf of Guinea Storm Petrel breeds on other islands. Surveys for nocturnal birds on Príncipe found no evidence of it (PV & MM pers. obs.). On Annobón, a 'black bird a little smaller than White-capped Noddy *Anous minutus*' was said to have 'its abode' in the interior (Barrena 1911, Basilio 1957). However, the few ornithological studies

on this small island have found no evidence of breeding storm petrels (Jones & Tye 2006, Sloan 2017). A survey of Bioko is required.

Breeding in mountainous equatorial forests, perhaps on inland cliffs as suggested above, would be quite unique among band-rumped storm petrels. In the Atlantic Ocean, there is some evidence of inland breeding in the Cape Verdes (Hazevoet 1995; V. Bretagnolle *in litt.* 2019), although they typically nest at low elevations in relatively barren rocky and boulder-strewn areas, in crevices, under lava screens, in the remains of walls, and in burrows constructed by White-faced Storm Petrels *Pelagodroma marina* (Hazevoet 1995, Bolton *et al.* 2008; RLF pers. obs.). At several locations, invasive predators restrict breeding to offshore islets and rock stacks. In the Pacific Ocean, breeding occurs in the equatorial Galápagos Islands in crevices and burrows (Swash & Still 2005, Smith & Friesen 2007), and in the tropical Hawaiian Islands in crevices within a cinder cone caldera and sparsely vegetated steep cliffs, with small groups breeding in wetter more vegetated areas (Raine *et al.* 2017, Galase 2019).

## Seasonality

Gulf of Guinea Storm Petrel is present in the region year-round, both at sea and on land (Table 1, Fig. 17). It is present off all oceanic islands and has been observed over the Guinea Rise on which the islands are situated (Fig. 1, Table 1; Robins 1966, Harrison & Steele 1989). Local fishermen report that black-and-white storm petrels are commoner at sea during the long dry season, between mid May and early September (Monteiro *et al.* 1997, Bollen *et al.* 2018). However, research into seasonality is minimal and so we draw upon two indicators of breeding season—nesting condition and primary moult.

**Breeding condition.**—The Gulf of Guinea Storm Petrel captured east of São Tomé on 23 July 1997 had a fully bare brood patch (Monteiro *et al.* 1997). Two of the specimens at Roça Jou on 10 and 14 December 1928 had swollen / enlarged gonads. These observations, together with records year-round (Table 1, Fig. 17), indicate either a protracted breeding season or two distinct nesting seasons: one around December, during the wet season, and the other around July, during the long dry season.

**Primary moult.**—Adult band-rumped storm petrels undertake a complete post-breeding moult that commences at a late stage during chick rearing, while juveniles undertake their first complete moult *c.*10 months post-fledging, approximately two months earlier than adults (Howell 2010, 2012, Flood & Fisher 2013). The ten primaries are replaced sequentially from the innermost to the outermost (from p1 to p10) and grow at a steady rate (Flood & Fisher 2013, Ryan 2014). Six of the 18 birds photographed at sea between Príncipe and Benin on 6 April 2011 were in primary moult (Table 1). Progress of primary moult is staggered—pp3/4–p10 old, pp6/7–p10 old, p7–p10 old, p9–p10 old, and p10 old—and consistent with a protracted breeding season. Primary moult consistent with two distinct nesting seasons would be synchronised. For example, in the Gulf Stream, off North Carolina, in May–June 80–90% of band-rumped storm petrels have just 3–4 old outer primaries, while the other 10–20% are not in primary moult (respectively, cool- and hot-season breeders from Macaronesia) (Howell 2012). We do not know if the primary moult of the 12 non-moulting birds was staggered or synchronised because the photographs are

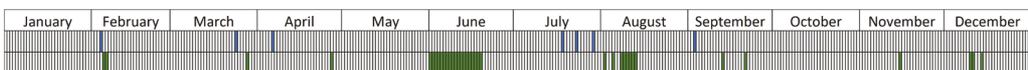


Figure 17. Seasonality of Gulf of Guinea Storm Petrel *Hydrobates cf. castro*; each cell represents one day; a blue cell in the top row represents an at-sea observation, and a green cell in the bottom row an observation on land.

of insufficient quality to assess plumage wear—from fresh to heavily worn—necessary to gauge duration since completing moult.

The end of the breeding season of an adult Gulf of Guinea Storm Petrel can be estimated from its progress in primary moult (Howell 2012, Flood & Fisher 2013). Fifty percent of the primary mass is in the outermost three primaries (p8–p10) meaning that primary moult is *c.*25% complete when it reaches p5, halfway when it reaches p8, and a little over three-quarters by the time it reaches p10. Band-rumped storm petrels might take *c.*24 weeks to complete primary moult based on the timeframe within which entire populations moult (e.g. Bolton *et al.* 2008). Accordingly, when a bird starts moulting p8 it has concluded its breeding *c.*12 weeks earlier.

Based on the above parameters and assuming moulting birds were adults, the range for the end of breeding season for these birds is from late November to late February (6–22 weeks prior to 6 April). If the moulting birds were juveniles, the range for the end of fledging is between late September and late December. Both calculations coincide with the dates of the juvenile collected by the Correias on 10 December. Reasonable adjustments to ‘24 weeks’ do not result in significantly different estimates.

## Morphology

Band-rumped storm petrel populations in the Atlantic Ocean are poorly differentiated morphologically, and the main characters that separate them are depth of the white ‘rump patch’ and thigh patches, the tone of dark feathers not attributable to the ageing process, depth of tail notch / fork, body mass, the length of the bill, tarsus, wing and tail, as well as voice (Bolton *et al.* 2008, Robb *et al.* 2008, Shirihai 2009, Flood & Fisher 2013). Typically, hot-season birds are fork-tailed and tend to have greater body mass, longer and deeper bills, and longer wings (Deane 2011).

Depth of the white ‘rump patch’ is the percentage of the length of the tail that is white, measured along the mid-dorsal line of the tail. The white ‘rump patch’ of specimens collected by the Correias is exceptionally shallow for band-rumped storm petrels, with a mean depth 25% (Figs. 2, 4) vs. 32.3–38.3% in populations globally (Harris 1969). This depth is borne out in birds photographed in the Gulf of Guinea (Figs. 5–14).

Depth of the white ‘thigh patch’ is measured by calculating how far it extends from the fold over of the ‘rump patch’ towards the mid-ventral line of the underparts. Depth of the thigh patch is *c.*50%, similar to Macaronesian band-rumped storm petrels, but much less than the estimated 80% or more in birds breeding in April on Ascension and St Helena (RLF pers. obs.).

Photographs of Gulf of Guinea Storm Petrels mainly show square-ended tails (Figs. 5–14), unlike Atlantic Ocean hot-season taxa (Deane 2011). A photograph from March and another from April suggest a notch in the tail tip, although this could be an effect of angle (Figs. 7, 18).

We have measurements for just five Gulf of Guinea Storm Petrels (Table 2). Mean wing length is 162.4 mm, or 160.25 mm if we exclude the 171 mm of an exceptionally large adult female (AMNH 268390). In either case, the mean wing length for Gulf of Guinea Storm Petrel exceeds that of populations worldwide, whose averages range from 147.2 mm to 156.5 mm (Harris 1969). The long wing of AMNH 268390 (Amadon 1953) exceeds the

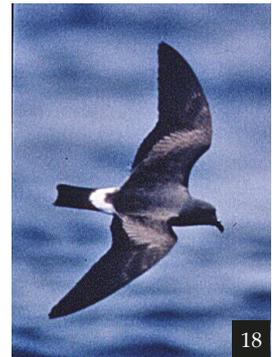


Figure 18. Gulf of Guinea Storm Petrel *Hydrobates cf. castro*, 8–19 km east of Santana, São Tomé, 24 March 1997; note features listed under Figs. 5–13 and the suggestion of a notched tail, and that this individual appears to have uniformly fresh plumage like a recently fledged juvenile (Martim Melo)

longest-winged individuals from the Azores cool-season (166 mm,  $n = 129$ ), Azores hot-season (169 mm,  $n = 209$ ), and Cape Verde populations captured in June (165 mm,  $n = 52$ ), and it is equalled only by the longest Cape Verde bird trapped in November ( $n = 85$ ) (Bolton *et al.* 2008, Deane 2011). AMNH 268390 is also darker in plumage than the other specimens (Figs. 2–3). The mean bill length of Gulf of Guinea Storm Petrel is 16.6 mm, also exceeding that of populations worldwide presented by Harris (1969), whose averages range from 14.4 to 15.5 mm, while V. Bretagnolle (in *litt.* 2019) reports that bill length of Gulf of Guinea Storm Petrel lies within the upper range of 660 specimens of band-rumped storm petrels he has measured.

## Vocalisations

Study of the vocalisations of band-rumped storm petrels has contributed to our understanding of the taxonomic relationships between distinct populations in the Atlantic (Robb *et al.* 2008). On São Tomé, most aerial vocalisation was noted in June–September after

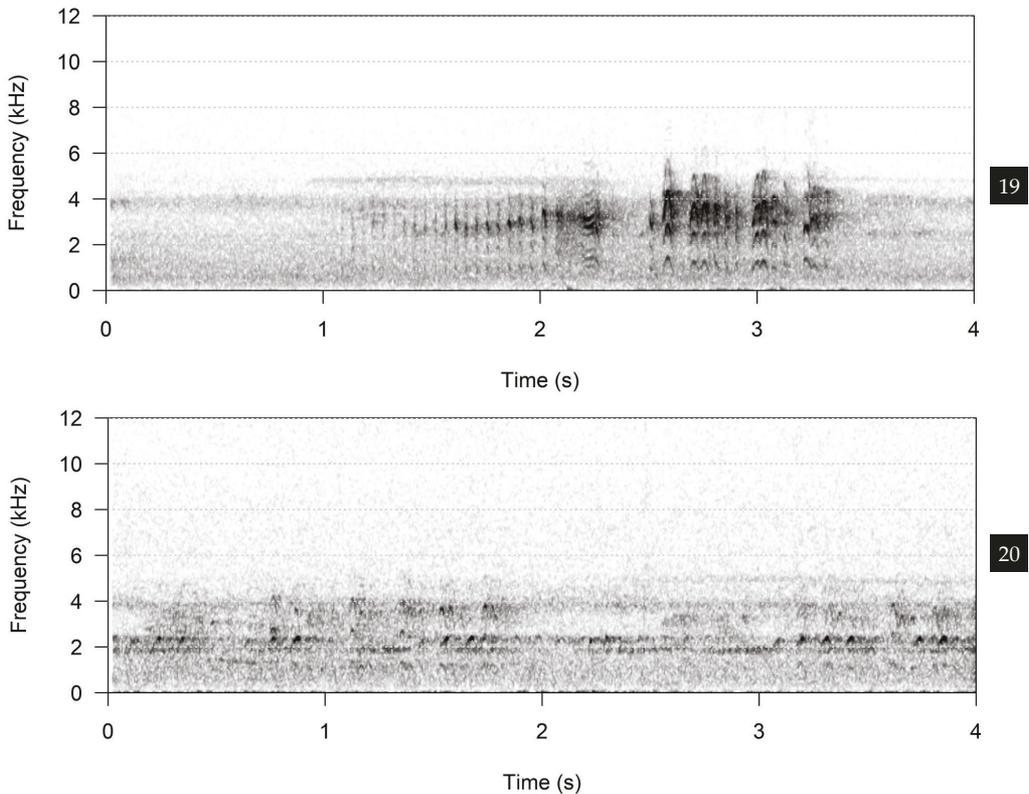


Figure 19. Aerial vocalisation of Gulf of Guinea Storm Petrel *Hydrobates cf. castro*, near Monte Carmo, Obô Natural Park, São Tomé, 9 August 2016 (19.25 h) (Philippe Verbelen). Short purring is visible between seconds 1.0 and 2.0, before the chatter call starts. Reversed 'v' notes are visible in the mid-section between seconds 2.5 and 3.0, and these are similar to the structure of chatter calls of Cape Verde Storm Petrels *H. jabejabe* (cf. Fig. 22). XC473562.

Figure 20. Aerial vocalisation of Gulf of Guinea Storm Petrel *Hydrobates cf. castro*, Ribeira Peixe, Obô Natural Park, São Tomé, 8 August 2016 (19:16 h) (Philippe Verbelen). The large number of notes in a downward spiral at the end of the chatter call is similar to Cape Verde Storm Petrel *H. jabejabe* (M. Robb in *litt.* 2016). XC473563.

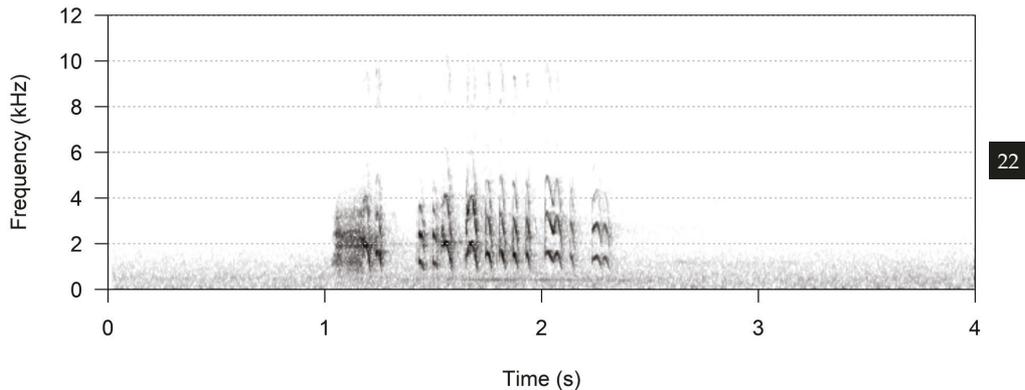
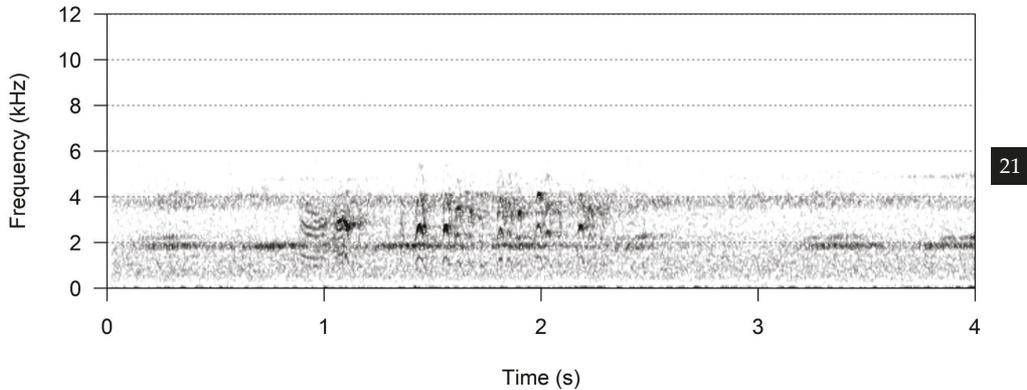


Figure 21. Aerial vocalisation of Gulf of Guinea Storm Petrel *Hydrobates cf. castro*, Ribeira Peixe, Obô Natural Park, São Tomé, 9 August 2016 (19.37 h) (Philippe Verbelen). Typical flight call with purring in the opening part, long middle section of chatters, ending with a short flourish. XC473564

Figure 22. Aerial vocalisation of a Cape Verde Storm Petrel *Hydrobates jabejabe*, Raso, Cape Verde Islands, 22 March 2007 (19.49 h) (Robb *et al.* 2008). The three parts of the call are clearly visible: the opening part, a long middle section of chatters, ending with a short flourish (CD2:60, Robb *et al.* 2008).

nightfall, from around 18.15 h onwards and peaking at *c.*19.00 h. The birds were probably flying to nesting sites.

On 8–13 August 2016, we employed directional microphones in combination with headphones to sound-record flight calls and to locate potential nest sites. Storm petrels were heard calling intensively in the vicinity of Monte Carmo just above the canopy, along forested ravines, and within forested gullies where breeding is suspected (Fig. 16).

The aerial vocalisation of Gulf of Guinea Storm Petrels (Figs. 19–21) has three parts: the opening purr, a long middle section of chatters, and ends with a short flourish. However, there is considerable variation in aerial calls and only a few recordings capture aerial purring or the concluding flourish. Background noise made detailed interpretation of sonograms difficult. Nevertheless, an important observation is the notable similarity with the aerial vocalisation of Cape Verde Storm Petrel (Fig. 22).

Vocalisations of Cape Verde Storm Petrel include many more chatter notes than those published for other populations of band-rumped storm petrel (Robb *et al.* 2008). Also, the climax of pitch and intensity in Cape Verde Storm Petrel usually is reached during the long middle section, while the calls of other band-rumped storm petrels become louder at the end (Robb *et al.* 2008). Gulf of Guinea Storm Petrel vocalisations appear to share the distinct

features of Cape Verde Storm Petrel. Purring calls recorded at burrow nest sites have proven important when comparing vocalisations of band-rumped storm petrels (Robb *et al.* 2008), but no nest of Gulf of Guinea Storm Petrel has been found. A selection of our Gulf of Guinea Storm Petrel sound-recordings are available on [www.xeno-canto.org](http://www.xeno-canto.org).

## Taxonomy

Band-rumped storm petrels were treated as monotypic for many years (Cramp & Simmons 1977, Warham 1990, Brooke 2004). Recently, significant genetic structure and restricted gene flow have been recorded in Atlantic populations (Friesen *et al.* 2007). Gulf of Guinea Storm Petrel might represent an unnamed taxon (Jones & Tye 1988). The differences in the principal morphological characters from those of other band-rumped storm petrel populations support this hypothesis (Harris 1969). Similarities between the aerial vocalisations of Gulf of Guinea Storm Petrel and Cape Verde Storm Petrel suggest some taxonomic affinity. Several island groups in the Atlantic hold taxonomically distinct allochronous populations (Friesen *et al.* 2007, Silva *et al.* 2016), and we do not discard this possibility for Gulf of Guinea Storm Petrel, especially given evidence of a prolonged breeding season. Proof that Gulf of Guinea Storm Petrel represents a different taxon requires additional evidence from morphology, vocalisations and genetics.

## Conclusion

The Gulf of Guinea oceanic islands are relatively small, but support an exceptionally large number of endemic bird species (Stattersfield *et al.* 1998). Like so many other oceanic islands, their biodiversity faces a variety of threats, including habitat loss, over-exploitation, and introduced invasive and predatory species (Jones *et al.* 1991, Ndong'ang'a *et al.* 2014). Add to this the tiny potential breeding range and Gulf of Guinea Storm Petrel, if classified taxonomically, will almost certainly qualify as threatened (Gascoigne 1995).

The most concerning threat to the storm petrel is the large number of non-native mammals (Dutton 1994). Predatory Black Rats *Rattus rattus* and feral cats *Felis catus* are well known for their devastating impact on seabird colonies (e.g. Zino *et al.* 2001, Madeiros 2005, Pinet *et al.* 2009). Other introduced mammals—such as African Civet *Civettictis civetta*, feral pigs *Sus scrofa* and Mona Monkey *Cercopithecus mona*—are also likely to negatively impact the storm petrel. The problem is exacerbated by the presence of these species in the remote and mountainous terrain of potential breeding colonies, where conservation efforts will be challenging. Furthermore, legal protection given to the best-preserved forest under the Obô Natural Park remains largely ineffective (Lima *et al.* 2017).

The three most pressing issues for future work on Gulf of Guinea Storm Petrel are clarifying its taxonomy, locating breeding colonies and establishing the threats to those sites. Additionally, it is important to gain a better understanding of phenology and ecology, both at sea and on land, including dispersive and migratory behaviour, and to assess population size and conservation status.

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