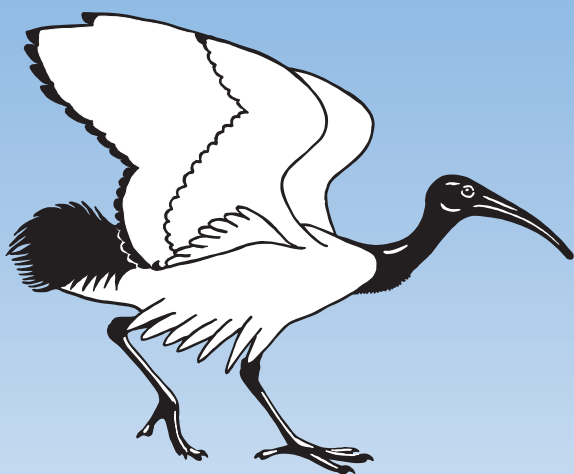


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Volume 146 Number 3, pages 221–326

CONTENTS

Club Announcements	221
MILSOM, T. P. Henry Seebohm (1832–95), subspecies, trinomials and the emergence of avian speciation theory	225
UBAID, F. K., SOUSA, D. S., CAMPOS-CERQUEIRA, M., DE MELO, T. N. & LEITE, G. A. Passive Acoustic Monitoring extends the known distribution of Speckled Spinetail <i>Thripophaga gutturata</i> in eastern Amazonia	244
SMITH, P., GALEANO, S., LESTERHUIS, A. J., MADROÑO, A., OVIEDO-LÖWEN, D. & SMITH, R. L. A compendium of Paraguayan breeding data for nightjars (Caprimulgiformes: Caprimulgidae) and potoos (Nyctibiiformes: Nyctibiidae)	249
RAIMILLA, V., CONTARDO, N., GALLARDO, B., GUTIÉRREZ, P., MELGAREJO, M., MUÑOZ, B., QUINTANILLA, E. & MEDRANO, F. Notes on the breeding biology of Fuegian Snipe <i>Gallinago stricklandii</i> in northern Patagonia	273
MORI, D. & VYAS, R. Notes on breeding by Changeable Hawk-Eagle <i>Nisaetus cirrhatus</i> in Gujarat, India	278
SAGOT-MARTIN, F. & RAMOS, A. F. N. First record of Black-legged Kittiwake <i>Rissa tridactyla</i> in Brazil	291
HALLEY, M. R. A new species of imperial pigeon (Columbidae: <i>Ducula</i>) from Tawi-Tawi, Philippines	295
ANTONELLI, V. R., BREVIGLIERI, E. L., CAVARZERE, V. & FONSECA, R. C. B. Far from home: two narrowly distributed endemic species beyond their known ranges in south-east Brazil	311
COLLAR, N. J. A taxonomic reconsideration of the White-bellied Bustard <i>Eupodotis senegalensis</i>	317

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CLUB ANNOUNCEMENTS

Thanks to Chris Storey, and our new Co-Chairs

Chris Storey's extraordinary 13-year term as Chair of the BOC ended on 30 June. Chris is the second-longest-serving Chair in our history, and his calm, thoughtful and steadfast leadership has guided the Club through significant change. During his tenure, the *Bulletin* moved to an online, open-access format, greatly increasing its accessibility and worldwide reach, with a global readership now in the hundreds of thousands. The Club's YouTube talks have similarly achieved a global audience. His support for the Checklist series and the new biography series, produced with John Beaufoy Publishing, resulted in outstanding volumes on William Yarrell and John Henry Gurney.

Chris leaves a stronger, more influential, and internationally respected Club, and the Trustees and friends of the Club owe him a huge debt of gratitude.

Douglas G. D. Russell and Dr Andy Richford have now become the first Co-Chairs in the Club's history.

Douglas has been a BOC Trustee since 2018. After studying Biological Sciences at Edinburgh Napier University, he began his curatorial career at the Royal Museum of Scotland, working on bird specimens from the 1996 *Sea Empress* oil spill. He subsequently held curatorial roles at the Natural History Museum, London (NHM), and Scarborough Museum before joining the NHM's Bird Group at Tring in 2002. Since 2012, he has been Senior Curator responsible for the internationally renowned bird egg and nest collections. As Co-Chair, Douglas will focus on extending the Club's reach, lowering barriers to participation, and strengthening partnerships with the NHM, conservation charities and research organisations in the UK and internationally. He also aims to expand the BOC's online and in-person programme and foster wider public engagement with ornithology.

Andy has been a BOC Trustee since 2020 and Hon. Secretary since 2023. He studied Ecology and Wildlife Management at the University of Edinburgh before researching Eurasian Jackdaws *Corvus monedula* on Skomer Island for his DPhil. at the Edward Grey Institute, University of Oxford. After working on the *Birds of the Western Palearctic* and becoming Librarian of the Edward Grey Institute library, he moved into scientific publishing, becoming a commissioning editor at Academic Press and Elsevier. He oversaw major ornithological publications, including *Birds of Africa*, the T. & A. D. Poyser list, and books produced with the British Trust for Ornithology and Royal Society for the Protection of Birds, as well as journals including *Animal Behaviour*. Andy shares Douglas's vision for the Club's future and has a lifelong interest in birds, with extensive travels in North America, Africa and Costa Rica. He also has a strong interest in the visual arts, music and cinema.



Douglas G. D. Russell & Dr Andrew Richford
Co-Chairs, British Ornithologists' Club

The 1019th meeting of the Club was held in the upstairs room at the Barley Mow, 104 Horseferry Road, London SW1P 2EE, on 29 June 2026. Eighteen people were present: Ms A. Belman, Mr P. Belman, Mr S. Chapman, Dr R. Cheke, Mr R. Dickey, Ms F. Dobbs, Mr N. Dobbs, Mr A. Jackson, Mr A. Jailumar, Mr N. Perere, Dr R. Prŷs-Jones, Ms B. Pugh, Dr A. Richford, Mr C. W. R. Storey (*Chair*), Mrs J. Sena, Mr G. de Silva Wijeyeratne (*Speaker*), Mrs N. de Silva Wijeyeratne and Ms M. Tibbett.

The author/photographer Gehan de Silva Wijeyeratne is both a Club Trustee and one of the foremost authorities on the natural history of Sri Lanka, having published a wide array of highly successful field

guides on different animal and plant groups. In his richly illustrated talk on *Sri Lanka and its endemic birds*, he began with a consideration of both the factors underlying the island's high biodiversity and an outline of its top birdwatching sites, particularly in relation to its 34 endemic bird species. He then turned to an overview of the individual endemics themselves, comprising a diverse array of bird families ranging from Sri Lanka Spurfowl *Galloperdix bicalcarata* and Sri Lanka Grey Hornbill *Ocyeros gingalensis* to passerines that include both the Endangered montane endemic Sri Lanka Whistling Thrush *Myophonus blighi* and species that thrive much more widely such as Crimson-fronted Barbet *Psilopogon rubricapillus* and Red-backed Flameback *Dinopium psarodes*. By his conclusion, the audience had received a comprehensive and fascinating insight into what makes Sri Lanka ornithologically special.

Robert Prŷs-Jones

Upcoming meetings

The next (1020th) meeting of the Club will be held jointly with the Linnean Society of London at their premises at Burlington House, Piccadilly W1J 0BF, on Thursday 22 October, when Prof. Robert Cheke will speak on *What's new about sunbirds and their allies?* It will start at 18.00 h, and a ticket needs to be purchased in advance—see <https://www.eventbrite.co.uk/e/an-evening-with-the-sunbirds-of-the-world-tickets-1990284594800> or <https://members.linnean.org/events/6a134e4b05f5070008efd458/description>.

Abstract: Sunbirds occur only in the Old World, but they play similar ecological roles to the New World hummingbirds. Together with accounts of the flowerpeckers, spiderhunters and sugarbirds, the sunbirds were described by Robert Cheke and the late Clive Mann in *Sunbirds. A guide to the sunbirds, flowerpeckers, spiderhunters and sugarbirds of the world*, published by Christopher Helm in 2001 with illustrations by Richard Allen. A second edition of the book entitled *Sunbirds of the world. Sunbirds, flowerpeckers, spiderhunters and sugarbirds* appeared in 2025 with updated information and additional illustrations including photographs of all of the 218 species. The talk will describe and discuss recent taxonomic changes in these groups and new research on their breeding behaviour, pollination roles and physiology.

Biography: Robert Cheke is Prof. Emeritus of Tropical Zoology at the Natural Resources Institute of the University of Greenwich and a Visiting Prof. at Imperial College London's Department of Infectious Disease Epidemiology. Before studying zoology at the universities of St. Andrews and Leeds, Robert worked as a field assistant at the British Trust for Ornithology, then based in Tring. His research work has frequently taken him to sub-Saharan Africa, where he has been able to follow his passion for sunbirds, which began during undergraduate expeditions to Ghana and Kenya. His other ornithological interests include the biology and control of Red-billed Quelea birds *Quelea quelea*, West African birds in general (he wrote a BOU Checklist on the Birds of Togo with Frank Walsh), and bird-ringing in the UK. A specialist on the vectors of onchocerciasis ('river blindness'), Robert has also worked extensively on locusts and grasshoppers and mathematical modelling of a variety of biological systems.

The following (1021st) meeting of the Club will be a memorial to our former Chair and Hon. Secretary, Commander Michael Bernard Casement, OBE, RN, who died on 15 May 2026, aged 93 (see Obituary, below). It will be held on Monday 30 November in the upstairs room at the Barley Mow, 104 Horseferry Road, London SW1P 2EE. Doors open at 18.00 h for a 18.30 h start. Lieutenant Commander Philip Boak, Chair of the Royal Naval Birdwatching Society (RNBWS), will focus on *80 years of the Royal Naval Birdwatching Society* since Sir Peter Scott, Captain Roddie Casement and others set up the society. Philip will review the amazing achievements of RNBWS over the decades, and BOC Trustee Stephen Chapman will introduce the meeting with a eulogy for Cdr. Casement.

OBITUARY

Commander Michael B. Casement, RN, OBE (1933–2026)

This year marks the Royal Naval Birdwatching Society's 80th anniversary. It also marks the passing on 15 May at the age of 93 of Michael Casement, who was a member for 75 of those 80 years, and who was for many years the real driving force within the RNBWS. At the BOC, he was Hon Secretary from 1996–2004 and Chairman in 2005–08. He remained closely involved with the Club and was very supportive of all its recent developments.

In early years Michael was already hooked on birds, and he related a talk given by Peter Scott in 1943 at his prep school, a talk illustrated by a beautiful extempore chalk drawing of a Red-breasted Goose *Branta ruficollis* on the blackboard. "Please don't rub it off," pleaded the young Casement, but sadly the board

was wiped clean the next day—no photographic record, no social media comment; just a tragedy for a 12-year-old boy.

Birding continued at Winchester College and then of course in the navy. At Dartmouth he elected for a non-naval subject, to study ornithological evolution and speciation, which involved visiting the Bird Room at South Kensington where Derek Goodwin took him under his wing. Later, his first ship was the battleship HMS *Vanguard*. He came to meet Dr Bill Bourne, and there began a close friendship and professional collaboration. At RNBWS, Bill dealt with seabird reports and Michael with reports of landbirds on board ship, often logged in the Met Reports submitted by ships and Ocean Weather Ships' reports.

For many years Michael was both Chairman of RNBWS and editor of the annual journal *Sea Swallow*. What a task in those days, when there was no e-mail, no affordable colour and no digital photography; instead, it was paper reports, a dependence on the postal service, and hard-copy page proofs. But those old *Sea Swallow* reports are full of interest, full of variety, and most important of all they were very highly regarded by the birding fraternity. Michael was part of that; he had established good contacts with the British Trust for Ornithology and especially with the BOC.

Michael had three ship commands in his naval career: HMS *Shavington*, a coastal minesweeper, and two Tribal Class frigates, HMS *Mohawk* and HMS *Ghurkha*. But Michael's greatest contribution to the navy and indeed to the nation (for which he was awarded the OBE) was in 1982 in an intelligence post on the RN liaison staff in Washington. Michael had special links with the US Pentagon, and throughout the Falklands conflict functioned as a special 'go-between,' often taking secret bits of kit to the UK by special aircraft.

Speaking at the 950th BOC meeting in 2008 (*Bull. Brit. Orn. Cl.* 128: 146) Michael reported on a recent cruise to Antarctica. His aim was to demonstrate the remarkable flexibility of modern digital cameras to record identification details of albatrosses and other seabirds in flight.

Michael was not a twitcher but when invited to Spain in winter 2013 he and David Dobson spent a long weekend birding with Tom Gullick. As David observed, Tom's dedication to the pursuit of birds verged on the obsessive, being the first to observe 9,000 species of birds as long ago as 2012 (*Sea Swallow* 72: 96).

I should emphasise that Michael was more than just a keen birder; he was an excellent observer at sea, meticulous in his approach and record keeping, and when he was Gunnery Officer on the carrier HMS *Centaur* he achieved what is probably a world first—photographs of a radar screen showing flocks of migrating birds as they crossed the Mediterranean (*Ibis* 108: 461–491).

If birds and RNBWS were very important in Michael's life, other forces were even more so. One was his family; he and his wife Christina had three children, 11 grandchildren, and three great-grandchildren. Another was his Christian faith (he was Lay Reader for many years in Harting parish). He died in the house where he had lived for 67 years, Dene Cottage in West Sussex, and wrote a monthly nature report for his parish magazine whenever he was in residence.

Stephen Chapman, Vice Chair, RNBWS



Michael Casement at Pentire Point in Cornwall, in his walking 'uniform' (Casement family)

FRIENDS OF THE BOC

The BOC has since 2017 become an online organisation without a paying membership, but instead one that aspires to a supportive network of Friends who share its vision of ornithology—see: <http://boc-online.org/>.

Anyone wishing to become a Friend of the BOC and support its development should pay UK£25.00 by standing order or online payment to the BOC bank account:

Barclays Bank, 16 High Street, Holt, NR25 6BQ, Norfolk

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Account name: The British Ornithologists' Club

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

The *Bulletin* and other BOC publications

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

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

Henry Seebohm (1832–95), subspecies, trinomials and the emergence of avian speciation theory

by Tim P. Milsom

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<http://zoobank.org/urn:lsid:zoobank.org:pub:DDBF4BEA-902F-4AAE-BEC7-5863E0ED88D1>

SUMMARY.—The acceptance, in the mid-19th century, of geographical variation within species gradually led to the recognition of partially distinct and geographically defined populations (subspecies). The trinomial, in which a third scientific name is appended to the Linnean binomial, was one solution to labelling subspecies. This innovation by European taxonomists lacked traction in Britain. It was overtaken by more assertive support from North America, which later fed back to Europe. In 1884, the American ornithologist, Elliott Coues, visited London in an attempt to overcome British resistance to the trinomial. Henry Seebohm attended the London trinomials meeting as an isolated British promoter of subspecies. His practice of collecting series of specimens while on expeditions across northern Eurasia had previously led him to discern geographical variation within species. This, in turn, led Seebohm to lump taxa previously described as separate species and to employ trinomials to label his newly defined subspecies. He drew inspiration from Temminck and Schlegel's *Fauna Japonica* rather than North American sources. Seebohm's initial trinomial construction and terminology were original, as were subsequent experiments with unorthodox multinomials. He later aligned with North American trinomial constructions for practical purposes. Of greater historical significance were Seebohm's theoretical ideas about subspecies, which set him apart. He grasped that the evolutionary processes proposed by Darwin and Wallace were ongoing and that subspecies were 'species in the process of differentiation'. His perception of subspecies as an active process, as much as a taxonomic category, led onto his pioneering word models of allopatric speciation in birds.

The treatment of species, by avian taxonomists in the 19th century, as narrowly and sharply defined homogenous assemblages of individuals, was gradually replaced by an acceptance of a broader definition. This acknowledged geographical variation in plumage or morphology between local populations within species. However, the continued use of the Linnean binomial to label species did not reflect this shift in thinking. Intra-specific variation remained invisible from a taxonomic perspective. A potential solution was the trinomial, constructed by appending a third scientific name to the Linnean binomial (Haffer 1992, Winker 2010). It was introduced by some avian taxonomists in mainland Europe in the mid-19th century, most notably by Temminck & Schlegel (1844–50). They used the novel construction to label partially distinct and geographically defined populations, now generally known as subspecies, particularly those on islands.

Haffer (1992, 1994, 1997) aimed to trace the genesis of subspecies and their labelling, the routes of their diffusion and to identify the factors that either impeded or promoted the process. He drew on the concept of the taxonomic school; each being defined by shared or inherited views on geographical variation within species and on the taxonomic response. Haffer considered the chronology of his schools, their persistence or transience, and the

communication of ideas between them. He argued that the initial European recognition of geographical variation within species lacked traction and was overtaken by a more assertive campaign in North America for the adoption of trinomials (Haffer 1992). He went on to suggest that the American initiative looped back to Europe, where it acted as a catalyst for a reappraisal of trinomials in the late 19th century. However, an attempt in 1884 by the American ornithologist, Elliott Coues (1842–99), to overcome British resistance to trinomials has been portrayed by some historians as a failure (*inter alia* Stresemann 1975, Haffer 1992, Chansigaud 2009). The activities that preceded it comprise the subject of this review, particularly those of the British ornithologist, Henry Seebohm (1832–95).¹ Seebohm's inclusion in general histories of ornithology has often rested upon his reputation as an isolated supporter of trinomials (*inter alia* Stresemann 1975, Walters 2003, Bircham 2007).

This paper re-assesses the circumstances under which Seebohm acknowledged subspecies and their evolutionary significance and re-identifies the most probable stimulus for his introduction of trinomials. It also considers Seebohm's contact with other avian taxonomists, including with Coues at the 1884 meeting in London. Seebohm's contributions to the establishment of the subspecies concept cannot be assessed in isolation because Haffer (1992, 1997) asserted without any supporting evidence that Seebohm's thinking followed that of North American ornithologists. His innovations have, therefore, been compared and contrasted with contemporaneous efforts by ornithologists associated with Spencer Fullerton Baird (1823–87), particularly members of Haffer's 'Bairdian school'.² Beyond the introductory sections, a chronological approach has been followed, so far as is practicable.

The unsettled history of subspecies and trinomials in ornithology

Trinomial practice emerged at a time when efforts were being made to stabilise biological nomenclature around the Linnean binomial, and it was opposed by defenders of the binomial, particularly in Britain (Allen 1884). Even among supporters of the trinomial, there was no immediate agreement on its construction or, indeed, its purpose. Some promoters in Europe and North America extended the trinomial by inserting a linking term between the specific and subspecific names and, at least one ornithologist, Henry Seebohm, also added authorities for both species and subspecies (Seebohm 1879a). In North America, where trinomials gained greater traction than in Europe during the second half of the 19th century (Haffer 1992, Winker 2010), they were used initially to express taxonomic uncertainty rather than to acknowledge subspecies. In Britain, Henry Seebohm's lone experimentation with trinomials preceded their formal introduction, which was resisted until the early 20th century (Hartert *et al.* 1912, BOU 1915, Bircham 2007). Here, opponents latched onto the underlying problems of defining subspecies that arise from the need to differentiate between statistical variation among populations, which might qualify for subspecific status, and individual variations within populations, which do not. The opponents doubted whether all naming authorities would be cognisant of the difference and feared that it would lead to an unwarranted multiplication of the number of new taxa (Allen 1884). The often ill-defined boundaries (morphological and geographical) between the new taxonomic units also offered scope for undesirable multiplication via the naming of indefinite numbers of subspecies, particularly in the case of species that exhibited clinal

¹ See Milsom (2020), Mearns & Mearns (2022) and Hobson (2025) for recent biographies of Henry Seebohm.

² Baird occupied a key post at the Smithsonian Institution, Washington, DC. His principal associates, who were also involved with the recognition of subspecies, were John Cassin (1813–69), Joel Asaph Allen (1838–1921), Elliott Coues (1842–99) and Robert Ridgway (1850–1929). For a detailed biography of Coues, see Cutright & Brodhead (1981); similarly for Ridgway, see Lewis (2012). Biographical sketches of Baird and Cassin are given in Mearns & Mearns (1992).

variation. In addition, this lack of crisp definition posed practical problems when assigning museum specimens, or individuals observed in the field, to particular subspecies. These matters continue to concern avian taxonomists (Fitzpatrick 2010, Haig & Winker 2010, Remsen 2010, Winker 2010).

Appreciation of the evolutionary significance of subspecies initially lagged behind the development of their labelling but was far more significant. Geographical variation within species emerged as the foundation of the speciation process in birds. A few perceptive ornithologists from the late 19th century deduced that avian subspecies might be 'nascent species' (E. Coues in Baird *et al.* 1874) or 'species in the process of differentiation' (Seebohm 1879b). This realisation provided the key to the theory of allopatric speciation through the geographical isolation of subspecies (Mayr & Diamond 2001). Although the taxonomic validity of subspecies continues to provoke debate, the utility of the subspecies concept to the study of allopatric speciation in birds has contributed to its persistence (Remsen 2010, Winker 2010). Subspecies continue to be widely acknowledged via the application of trinomials (Dickinson & Remsen 2013, Dickinson & Christidis 2014).

The uncertainties surrounding the idea of subspecies and their labelling have extended to the methodology for their historical investigation. Being retrospective constructs, due more to judgement than formal analysis, the details of Haffer's taxonomic schools were open to challenge. Haffer (1997) defended the concept by explaining the processes that lead to the formation of schools and, in the same publication, he added rigour by preparing a cross-tabulated array of avian taxonomists against two defined variables. Nonetheless, the assignment of individuals to particular schools, and the weighting of their contributions, proved problematic and necessitated multiple adjustments. Two examples are particularly relevant. The first concerns Coues, who was distanced from Baird's inner circle, including Allen and Ridgway. Coues was moved closer to Baird's group by Haffer's decision to rename his 'Bairdian school' as the 'Baird-Coues school' (Haffer 1992, Haffer *et al.* 2014). The status of Henry Seebohm, who was perceived initially as a lone actor (Haffer 1992), was dramatically upgraded to that of a joint instigator of a new European taxonomic school, partly through reconsideration of the impact of Ernst Hartert (1859–1933), who was Seebohm's direct intellectual successor (Haffer 1994, 1997). The distinction between Haffer's newly defined 'Seebohm-Hartert school' and its principal North American counterpart, the 'Baird-Coues school', is of immediate interest. However, Haffer (1997) was not able to properly resolve their relationship, because he had only relatively meagre biographical detail about Seebohm to hand. Clarification is offered below.

Early experiments with trinomials by North American ornithologists

Avian taxonomists in North America introduced trinomials *c.*25 years before Seebohm, but their rationale for using them was different and not weighted with evolutionary theory. The earliest known references to trinomials in North American ornithological literature pre-date the commencement of the evolutionary era set in motion by Darwin and Wallace, in 1858. Like Seebohm, his North American contemporaries experimented with the construction of trinomials. Unlike Seebohm, they were initially uncertain as to the purpose of the new nomenclature.

Some doubt surrounds the origin of trinomial use in North America, but it most probably lies with John Cassin. Mengel (1983) drew attention to a comment by Stejneger (1884) about Cassin's *Illustrations of the birds of California, Texas, Oregon, British and Russian America*, which was 'said to contain the first use of trinomials by an American'. Cassin's *Illustrations* was issued in ten fascicles between 1853 and 1856 (Wood 1931). He employed an extended trinomial with the *var.* connecting term when considering the Great Horned

Owl *Bubo virginianus*. The essay on this species appeared in fascicule 6 which, according to Wood (1931), was received by the library of the Philadelphia Academy (where Cassin was based) on 12 September 1854. As Wood noted, 'the dates of receipt by the Academy are probably fairly good as dates of publication, as Cassin doubtless handed in a copy of each part as published, but the dates are not absolute'. Cassin's extended trinomial appears on p. 178 as '*B. virginianus* var., *atlanticus*'. He prefaced his innovation on the previous page, where he observed that the colours and size of the specimens to hand varied considerably, with some evidence of geographical grouping. The crucial sentence follows: 'Though at present, with a large number of specimens before us, we are of the opinion that they are all of one species, it may be that they are distinct'. This wording may be interpreted to mean that Cassin was using the extended trinomial as a hedge against the two contrasting taxonomic possibilities and not as an explicit acknowledgement of subspecies.

Cassin did not indicate whether or not he had drawn inspiration from an external source. One clue may lie in his ornithological report for the US Perry Mission to Japan published about two years later (Cassin 1856). Here, he cited the volume on birds from Siebold's *Fauna Japonica* by Temminck & Schlegel (1844–50), in which trinomials are freely employed to recognise subspecies.³ In his synonymies, Cassin acknowledged the trinomials employed by Temminck & Schlegel for two eastern forms (Common Quail *Coturnix vulgaris japonica* and Great Reed Warbler *Salicaria turdina orientalis*). However, Cassin did not employ trinomials for these taxa himself, and his cognisance of the subspecies concept, at this stage, is uncertain.

Cassin had partially shifted his stance on trinomials when he prepared his text for *The birds of North America* (Baird *et al.* 1860). In his section on birds of prey, he recognised four geographically defined varieties (= subspecies) of *Bubo virginianus*, employing the strict trinomial, as in the case of *Bubo virginianus pacificus*. His wording in the accompanying commentaries conveyed greater confidence in his taxonomic decision than previously. However, Cassin also continued to use the 'var.' connecting term in its previous context. His scientific name for the Dunlin *Tringa alpina* var. *americana* was accompanied by a cautionary note indicating that he was not entirely certain of its taxonomic status. Baird recognised three geographical varieties of Hairy Woodpecker *Picoides villosus*. However, unlike Cassin, he employed the full 'Variety' term ahead of a subspecific name but separate from and below his binomial, *Picus villosus*. But, like Cassin, Baird also employed the full trinomial with 'var.' to signal doubtful taxonomic determination, as when introducing *Herodias egretta* var. *californica* to the nomenclature of Great Egret.^{4,5} The varied styles of labelling and their applications suggest that Baird and his co-authors' thinking on these matters was embryonic at this stage. The evolutionary significance of subspecies was not commented upon.

The diversity of labelling styles and their applications evident in Baird *et al.* (1860) was reduced in Baird's next major statement on the North American avifauna (Baird *et al.* 1874). Many more subspecies appeared in the new work. They were mostly referred to as 'races' but also, not infrequently, as 'varieties'. The strict trinomial used previously by Cassin was abandoned, and the context of the extended trinomial with 'var.' had also changed. In most cases, the latter construction was clearly employed to label races and not to signal taxonomic uncertainty, as it had been previously. More often than not, the extended trinomial, quoted in full, served as a banner for each species or subspecies essay.

³ Cassin enjoyed access to a notably good library (Cassin 1853–56: iv). His frequent page references to Temminck & Schlegel suggest that Cassin had read the original text.

⁴ Baird had similar intent when naming the crow *Corvus americanus* var. *floridanus*.

⁵ Varieties of other taxa are itemised in the List of Species for Baird *et al.* (1860), but their taxonomic treatment in the species' essays is more ambiguous.

The concept of subspecies and the necessity of an associated nomenclature were not addressed in the preliminary sections of Baird *et al.* (1874), either in the Introduction or in Baird's preface. Baird again remained silent on the topic. The only comment on the evolutionary significance of subspecies was in the Glossary, towards the rear of the third and final volume of the first edition of this work. The Glossary was prepared solely by Elliott Coues, who was not one of the principal authors and is not named on the title pages. The comment appeared in an entry for Variety on p. 559. Coues described a 'variety' as 'A nascent species. Practically, the term designates a set of objects incompletely distinguished from others of the same species, by reason of slighness of the difference, or presence of connecting links'. Whereas Coues also defined the terms 'sub-class', 'subfamily' and 'subgenus', 'subspecies' does not appear in his Glossary or, indeed, anywhere else in the book.

The publication of Baird *et al.*'s (1874) work on the landbirds of North America, 20 years on from Cassin's introduction of trinomials, did not signal a consensus about either the labelling of subspecies or their theoretical significance. A lack of agreement about the evolutionary implications of the subspecies concept is suggested by the isolation of any discussion to Coues's appendix. Nor was the manner of labelling subspecies settled. Robert Ridgway, sole author of the descriptions and technical matter for the *Raptors* (owls, hawks, vultures), broke with the convention observed elsewhere in the book by employing two styles of banner for subspecies. One abandoned the trinomial construction.⁶ His underlying thinking was subsequently revealed in Ridgway (1879), where he rejected the extended trinomial, declaring that varieties, as implied by the 'var.' connecting term, were not subspecies, thereby contradicting Coues. He championed the binomial, using a subscript for races.

Ridgway (1881) shifted his stance dramatically when he settled on the strict trinomial: genus, species, subspecies. He may have been encouraged to do this by Joel Asaph Allen (Lewis 2012: 174). Entitled the Nomenclature of North American birds, Ridgway's new statement was sanctioned by Baird, issued on behalf of the United States National Museum and published under the aegis of the US Dept. of the Interior. It carried much greater authority. Whatever previous discussion there may have been about trinomial construction, the sparsest version, genus, species, subspecies, was freely and uniformly employed throughout. More than 150 subspecies were recognised, although the term 'subspecies' is, again, noticeably absent. The phrase 'trinomials for the designation of nascent species' in the preliminary text signalled the necessity of trinomials and the evolutionary significance of subspecies. The strict trinomial that Ridgway had latterly promoted was subsequently adopted by the American Ornithologists' Union in their *Check-list of North American birds*, as in AOU (1889). It had required c.3 decades of experimentation and debate by North American ornithologists to reach this point.

Seebohm's introduction of trinomials

It has been suggested that long series of specimens, which had been amassed during official surveys across North America, often for railroads, and which illustrated

⁶ In some instances, Ridgway followed the style used for banners elsewhere in Baird *et al.* (1874) by employing the extended trinomial, as when labelling the American form of Hen Harrier *Circus cyaneus* var. *hudsonius*. However, in others, he chose the binomial over the trinomial, as with Swainson's Hawk *Buteo swainsoni*, with subspecific names given as subscripts. The former approach was used for species with geographical ranges that extended beyond the boundary of the Nearctic and where only one race (subspecies) was present in North America. The latter appeared to be reserved for North American species comprising two or more subspecies.

geographical variation within species, contributed to the greater readiness by American ornithologists to recognise subspecies (W. Bock *in* Haffer 1992). Sampling at a continental scale was less practicable in Europe, partly because of the geographical division into nation states. Here, national museums often relied upon purchase or exchange of specimens to build up their collections (Allen 1884, Sharpe 1906). The exchanges drew upon stocks of duplicates. Acquisition and retention policies for duplicates in collections in the then British Museum, in London, worked against the assembly of long series (Gunther 1912) where the commoner Palearctic species were under-represented (Allen 1884).

Rather than relying upon institutional collections, Henry Seebohm drew on personal wealth from his steel refining business to build up his own series of specimens of particular taxa. Although some specimens were acquired by purchase and perhaps exchange, Seebohm amassed series while on collecting expeditions across northern Eurasia, which he undertook and funded himself. The development of this practice is evident from his diaries of these expeditions, to northern Norway in 1874 and to the Pechora River valley, in north-eastern Russia, in 1875.⁷ Seebohm's most significant references to series appear in his published reports from the Yenisey River valley, in central Siberia, where he collected in 1877 (Seebohm 1878–80).

Seebohm's awareness of geographical variation within bird species developed in parallel with increases in his sample sizes following each successive expedition. The eastward expansion of his collecting area across northern Eurasia also increased the geographical range of his series of specimens and the scope for detecting geographical variation. His commentaries on geographical variation formed part of his species accounts and were generally referenced against specimens that he had obtained. Their number increased from one to no fewer than six between his reports from the Pechora and Yenisey, as did the level of detail for one species.⁸ In his reports from the Yenisey, Seebohm (1878–80) commented upon recurrent geographical variations in plumage pigmentation within closely related taxa that occupied Siberia.⁹ At first, he made no attempt to revise their classification. However, in the third of his Yenisey reports, Seebohm (1879a) suddenly commenced lumping taxa by reclassifying some as subspecies.¹⁰ His recognition of subspecies was signalled by introduction of the Linnean trinomial, or rather a variant, the extended trinomial, in which a novel linking term was inserted between the second and third scientific names. His decision to include authorities was also atypical.

Seebohm (1879a) applied trinomials to three taxa: Marsh Tit *Poecile palustris*, Siberian Tit *P. cinctus* and Lesser Whitethroat *Curruca curruca*. These took the following form: 'PARUS PALUSTRIS, Linn., subsp. *camtschatkensis*, Bon.', 'PARUS CINCTUS, Bodd., subsp. *griseescens*, Sharpe et Dresser' and 'SYLVIA CURRUCA, Linn., subspecies *affinis*, Blyth'. In

⁷ Seebohm, H. (1874) Ornithological excursion to Norway in company with Robert Collett Esq. of Christiania and Mr. Reuben Webster of Sheffield - June & July 1874. (Unpubl. diary. Zoology Library, Natural History Museum, South Kensington.) Contains register of birds shot, in chronological order. See, for example, the series of Lapland Bunting *Calcarius lapponicus* (then *Emberiza lapponica*), specimen nos.: 120, 127, 146, 151, 170–174, 176, 177, 213, 214, 221–226, 247, 254, 269, 277–279, 297–299, 320, 325, 328–330. Similarly, Shore Lark *Alauda* (now *Eremophila*) *alpestris*, specimen nos.: 121, 122, 128–131, 178, 211, 212, 219, 220, 233, 234, 238, 252, 253, 291–296, 321, 327. Seebohm, H. (1875) Journal of a trip to the Great River Petchora in the land of the Samoyedes, vol. 1. (Unpubl. diary. Dept. of Manuscripts, Cambridge Univ. Library, MS. Add. 4471.) See entry for 16 May 1875, re. collecting series of specimens of Shore Larks. Also see comment on collecting series of Shore Larks by Seebohm and his field companion on the Pechora, Harvie-Brown, in Harvie-Brown (1905).

⁸ Compare the commentary for *Parus cinctus* from the Pechora in Seebohm and Harvie-Brown (1876) with that from the Yenisey in Seebohm (1879a).

⁹ See his commentary on *Sitta europaea* (Seebohm 1878).

¹⁰ See definition of 'lumper' in Campbell & Lack (1985: 331).

the same paper, he suggested that the Arctic form of the Marsh Tit, '*Parus borealis*', might also be treated as a subspecies: '*Parus palustris* subspecies *borealis*.'

Seebohm's commentary on PARUS CINCTUS, Bodd., subsp. *griseus*, Sharpe et Dresser, provides a window onto his approach to subspecific determination (Seebohm 1879a: 2):

'I found the Lapp Tit tolerably common in the forests on our arrival on the Arctic circle. It was seldom that I made a round on snow-shoes in the forest without falling in with a small flock of these birds. I did not, however, observe them further north. I brought home a very large series. They agree with skins from Lake Baikal in being much less rusty on the flanks than specimens from Europe usually are. They vary considerably *inter se*; and it would be easy to make a series from the Norwegian bird, through Archangel and Petchora skins, to the eastern Siberian form. My Yen-e-say (*sic*) skins certainly belong to the *Parus griseus* of Sharpe and Dresser; but the authors of that title would, now I believe, scarcely claim specific rank for the bird they described.'

Seebohm examined a large array of specimens, which had been collected by him or his field companions from locations along an arc of c.2,900 km across Eurasia, from northern Norway east to the Yenisey. Sharpe and Dresser had described their *Parus griseus* in 1871, using a single specimen from a series that Jules Verreaux, the Paris zoologist and dealer, had received indirectly from Lake Baikal (Dresser 1871–81). Lake Baikal lies c.1,700 km south-east of Seebohm's collecting area on the Yenisey. Seebohm's reference to 'skins', in the plural, from 'Lake Baikal', implies that he had either had sight of some or all of Verreaux's series or had obtained others from the same geographical source. Seebohm's comparison across the combined series emphasised a gradation in plumage pigmentation without any obvious step changes that might signify species' boundaries. Nonetheless, he discerned some difference to confer subspecific status on *griseus*, which he then grouped with the European form *cinctus*. The alternative, which he did not make but did in contemporaneous instances (e.g. *Phylloscopus seebohmi* Hume 1877, see Milsom 2020: 295), would have been to argue that *griseus* was indistinguishable from *cinctus* and to treat it as a synonym of the older name. Similar reasoning, but with sparser series to hand, lay behind Seebohm's decisions to reclassify two other eastern taxa, *Parus camtschatkensis* Bonaparte and *Sylvia affinis* Blyth, as subspecies of closely related Western Palearctic species. His lumping of *Sylvia affinis* with *S. curruca* entailed morphometric comparison, involving the use of elementary wing formulae. Seebohm's explicit practice of lumping taxa originally described as full species with close relatives, which had been named previously, probably lay behind his unorthodox decision to include authorities for each specific and subspecific name.

Seebohm offered no explanation of his sudden introduction of trinomial nomenclature, which leaves the reader wondering as to its origins. The timing of his abrupt change in practice provides the clue because the explanation lies in another paper, also by Seebohm but on the Japanese ornithological catalogue of Blakiston and Pryer. This followed Seebohm's Siberian paper in the same issue of *Ibis* (Seebohm 1879b; also see Bossoh 2025). Seebohm's recognition of *Parus palustris* subspecies (subsp.) *camtschatkensis* links the two papers; this form being listed in both. Seebohm's Japanese paper yields two significant pieces of information. The first is his declaration that 'I am obliged to admit the use of subspecific names', which implies that he had not used trinomials previously in any context. The references to the volume on birds from Siebold's *Fauna Japonica* (Temminck & Schlegel 1844–50) provide the second clue. Seebohm's comments on the illustrations in

Temminck & Schlegel confirm that he had actually inspected a copy of this rare work.¹¹ Temminck & Schlegel had frequently employed trinomials to recognise geographically defined varieties in the avifauna of Japan. A trinomial for the Common Kestrel, *Falco tinnunculus japonicus*, was introduced in the second of their species' accounts. It was certainly noticed by Seebohm, who cited it, albeit by using a different generic name and his own connecting 'subspecies' term: *Cerchneis tinnunculus*, subspecies *japonicus*. This encounter and Seebohm's response comprised the probable stimulus for Seebohm's wider introduction of his extended trinomial. However, it is doubtful whether his practice of lumping was in imitation of Temminck & Schlegel, whose subspecific names were nearly all new (also see Morioka *et al.* 2005).

Seebohm's commentary on Blakiston and Pryer's catalogue arose from a sudden request by the editors of *Ibis* for Seebohm to identify specimens from two collections with a Japanese provenance (Seebohm 1879b). This paper post-dated Seebohm's purchase, late in 1878, of the reference collection of specimens with Chinese or Japanese associations assembled by Robert Swinhoe (1836–77) (Anon. 1879). The purchase and the editors' request most probably directed Seebohm to Temminck & Schlegel because of its authoritative Japanese content which, in turn, may have determined the timing of Seebohm's introduction of his trinomial. However, exploratory reading by Seebohm, as part of his review of the Siberian avifauna, might also have led him to Temminck & Schlegel via the avifaunal survey of eastern Siberia by Radde (1863).¹²

Notwithstanding the placement and source, it is debatable whether the announcement in Seebohm (1879b) of his decision to employ subspecies' names should be viewed primarily in a Japanese context. It may have simply been the case that the format of Seebohm's 'Contributions to the ornithology of Siberia' (Seebohm 1879a) precluded any explicit announcement there.

Temminck & Schlegel (1844–50) was a source of inspiration for Henry Seebohm, in Britain and, perhaps, also for John Cassin, in the USA. Cassin's encounter with the work considerably pre-dated Seebohm's. However, Seebohm was not directed to Temminck & Schlegel by Cassin, who had died ten years previously. Cassin's report on ornithology of the US Perry Mission to Japan (Cassin 1856) which refers to Temminck & Schlegel, is not cited in either Seebohm's 1879 papers, which may suggest that he was then unaware of it.

Seebohm's initial evolutionary perception of subspecies

Beyond stating, in his Japanese paper, that he was 'obliged to admit the use of subspecific names', Seebohm (1879b) did not discuss their form. Temminck & Schlegel (1844–50) offered two styles to copy: the strict trinomial (genus, species, subspecies), which was employed throughout their main text, and the extended trinomial with the 'var.' term linking the species and subspecific names, which was sometimes used in their index. Seebohm did not follow either, choosing instead to introduce the novel linking term 'subspecies' or its abbreviation, 'subsp'. The term itself was not original to Seebohm. His associate, Richard Bowdler Sharpe (1847–1909), may have been responsible for its introduction. Sharpe did not

¹¹ Seebohm probably owned a copy of Temminck & Schlegel (1844–50). This title is itemised in the catalogue incorporating the posthumous sale of Seebohm's ornithological library, although the bookseller does not confirm its provenance (Item 820, in Sotheran 1896).

¹² Radde (1863) frequently cited Temminck & Schlegel. A reference to Radde, as the naming authority for a taxon listed in Seebohm (1879b), implies an awareness by Seebohm of Radde (1863), which contains the original description, but the evidence is not conclusive. A copy of Radde's work is listed in the sale catalogue that included items from Seebohm's ornithological library, but the bookseller did not confirm its provenance (Item 707, in Sotheran 1896).

accept the routine use of trinomials but had used the term ‘subspecies’ five years previously in the first volume of the *Catalogue of the birds in the British Museum* (Sharpe 1874). However, unlike Sharpe, Seebohm did present subspecies in an evolutionary context, as the following extract from the preface to his Japanese paper illustrates (Seebohm 1879b: 19–20):

‘It would be well for the simplicity of ornithological nomenclature if its complications could stop even here. From the days of Linnaeus to those of Wallace and Darwin most ornithologists were agreed that species were divided by a hard and fast line, and that the difficulty which the student had to surmount was the discovery of the lines of demarcation which nature herself had drawn between the various specially created species. Now that most scientific ornithologists have adopted the theory that these hard and fast lines seldom exist in nature, that species were not specially created but were gradually developed according to certain more or less well known fixed laws, and that consequently there must be at any one period of the world’s history a large number of species in process of differentiation, our difficulties are largely increased. The question naturally arises, What is a species? We must either draw an artificially hard and fast line where nature has drawn none, or we must accept nature as she is, and make the best of the complications which necessarily arise in our nomenclature in attempting to harmonize it with facts which we cannot, as scientific students, ignore. Hence it appears to me to be absolutely necessary for modern ornithologists to recognize the existence of *subspecies*—that is, species in the process of differentiation, incipient species, where the intermediate forms have not yet died out, but where a series gradually leading from one extreme to the other may be obtained. I fully recognise the danger of such a practice. It is easy to imagine the abuses of which it is capable. Inexperienced ornithologists will be tempted to think that differences of age, sex, and season, to say nothing of individual variations, are intermediate forms worthy of the rank of a subspecies; and our nomenclature may run the risk of being still more flooded with names as injurious as the useless synonyms of the elder Brehm. I am, however, of the opinion that these difficulties will have, sooner or later, to be faced. It seems to me that the scientific ornithologist cannot afford any longer to ignore the existence of subspecies in nature, or to attempt to make ornithological nomenclature simpler than the facts of nature which it is intended to discriminate.’

In contrast to the introduction of trinomials in North America, Seebohm’s own was firmly linked to the subspecies concept and its evolutionary significance. His recognition of the biological difference between species and subspecies pre-dated the emergence of his awareness of large-scale geographical variation within species. A commentary incorporated into diary entries for June 1871, in *Henry Seebohm’s ornithological note book, April 1869 to June 1872*, reveals that he had become aware of the significance of reproductive isolation to the definition of species, and the distinction between species and subspecies (Seebohm’s ‘varieties’).¹³ This awareness drew upon his own field observations of varieties of Common Guillemot *Uria aalge*, with some knowledge of the writings of Charles Darwin (Milsom 2020).

As Seebohm’s evolutionary argument was inserted into the preface to his commentary on Blakiston and Pryer’s catalogue (Seebohm 1879b), it was necessarily brief, an announcement more than a fully worked-out theory. The two key elements of his description of subspecies

¹³ *Henry Seebohm’s ornithological note book, April 1869 to June 1872*, MS. Add. 8794, Dept. of Manuscripts, Cambridge Univ. Library. Seebohm’s commentary on the distinction between species and varieties, from his ‘Ornithological note book’, is reproduced in Milsom (2020: 32).

as 'species in the process of differentiation' and 'incipient species, where intermediate forms have not yet died out, but where a series gradually leading from one extreme to the other may be obtained' might, at first sight, be regarded as an example of re-iteration by Seebohm to press home his argument. However, Seebohm may have intended each element to signal a different perspective. The first implies dynamism and regards subspecies as a process. The second is a taxonomic snapshot of a stage in speciation. This distinction is significant and relevant to the subsequent development of Seebohm's thinking on subspecies.

Seebohm's preface also reveals that he was mindful of the practical difficulties of describing subspecies, particularly the taxonomic pitfalls of failing to distinguish between intra- and inter-population variation. Yet, beyond the information given in his commentaries on his newly declared subspecies, set criteria for distinguishing subspecies from full species were lacking (Seebohm 1879b). Two years later, Seebohm did publish some elementary rules in the Introduction to his volume on the warblers and the thrushes for the *Catalogue of the birds in the British Museum* (Seebohm 1881: ix-x):

'Two forms may be very closely allied; but if the difference between them, however small it may be, is constant and not attributable to age, sex, or season, the probabilities are that it is a specific difference. On the other hand, if the two forms are so closely allied that they interbreed and produce fertile offspring, which again interbreed, we may draw two inferences - first, that the difference between the two forms is only subspecific, and, second, that between the two extremes must be an infinite gradation of intermediate forms. If the two forms have different areas of geographical distribution (which is usually the case), the intermediate ones will be found where the two areas overlap.'

This statement combines theory with practice. Seebohm again stressed the significance of interbreeding, as he had in his unpublished manuscript commentary written ten years earlier. The process of differentiation relied solely upon physical evidence from specimens. Seebohm's rules drew upon the contrast between the constancy of differences and gradation in morphology or plumage. The rules facilitated Seebohm's taxonomic lumping but left the practical issue of determining the morphological and geographical boundaries between adjacent subspecies unresolved.

Seebohm's early independence from North American thinking

Seebohm was most probably inspired to introduce trinomials through his reading of Temminck & Schlegel (1844-50), a European text on Japanese ornithology. This connection was overlooked by Haffer when he considered possible external influences on Seebohm's thinking. Haffer (1992) perceived the promotion of trinomials and the subspecies concept by North American ornithologists as dominant in the late 19th century. This view probably lay behind his assertion that 'His [Seebohm's] theoretical views on species, speciation and evolution had been influenced by the publications of C. DARWIN and of the North American ornithologists (BAIRD, COUES, ALLEN, RIDGWAY) during the 1870s' (Haffer 1997). It echoed another made earlier (Haffer 1992), yet no supporting evidence was offered.

There is, however, no evidence for, and much against, any North American influence upon Seebohm's views on species and subspecies during the period leading up to his introduction of trinomials in 1879. Seebohm's independence is evident at each stage of the development of his thinking on these matters. As an ornithologist, Seebohm was isolated in Yorkshire, when he wrote his unpublished commentary, in 1871, on the distinction between

species and subspecies (his varieties) and the significance of reproductive isolation.¹⁴ His interests did not then extend to international ornithology (Milsom 2020: 45). It is, therefore, extremely unlikely that there had been any American influence on his thinking at that time. Seebohm's grasp of geographical variation within species developed primarily from personal observation. As noted previously, his commentaries were made in his species accounts and were often referenced against specimens he had collected. The concept of geographical variation was not introduced by Seebohm in a more general commentary which might have suggested that he had imported the ideas of others. When Seebohm introduced his trinomial, his initial choice of linking term did not follow American practice. Nor did his inclusion of authorities for both nominate and subspecific taxa. Similarly, Seebohm's general use of the term 'subspecies' was not in imitation of American usage. Seebohm's terminology was most probably not a rejection of that employed by others. His choice of the 'subspecies' term followed the example set by Sharpe. The timing of the announcement of Seebohm's intention to use subspecific names (Seebohm 1879b) is also relevant because it pre-dated Ridgway's published commentary on subspecies and trinomials by approximately six months. Ridgway's paper appeared in the July 1879 issue of the *Bulletin of the Nuttall Ornithological Club* (Ridgway 1879). It may have been prompted by Seebohm's publication.

Perhaps the most compelling evidence against Haffer's position is to be found in Ridgway's (1879) trinomial paper. Scrutiny of its contents reveals that the direction of flow of ideas relating to subspecies was in the opposite direction to that suggested by Haffer (1997), being from Seebohm to North America. There was evidence of a vacuum in theoretical thinking that Ridgway aimed to fill by quoting from the passage addressing the concept of subspecies and their recognition in Seebohm's commentary on Blakiston and Pryer's *Catalogue of the birds of Japan* (Seebohm 1879b). Ridgway considered it to be of such significance that he quoted it *verbatim* and in full. It occupied nearly a third of the page space of Ridgway's paper. The wording of Ridgway's introduction ('the following opinion of a writer in a late number of "The Ibis"') implied that Seebohm was then unknown to Ridgway and his immediate circle. It is further evidence of a lack of previous contact between Seebohm and his North American contemporaries.

Beyond the foregoing evidence of independence, the development of Seebohm's thinking on subspecies and trinomials followed a different track from that of his North American contemporaries, with a fundamentally different starting point. For Seebohm, it was the biological distinction between species and subspecies whereas, for Cassin and his successors, it was the problem of classifying taxa exhibiting geographical variation.

Seebohm's shifting stance on labelling subspecies

Apart from the novel connecting term and his inclusion of authorities, Seebohm's initial construction of trinomials was not unusual (Seebohm 1879a). However, later he voiced doubts about the most appropriate form of multinomial and even questioned whether the Linnean construction was the best option when naming subspecies (Seebohm 1882a). The underlying lack of decisiveness in Seebohm's thinking was also evident from the diversity of multinomial constructions in the systematic list that accompanied his discussion. This may have been a product of unconstrained thinking in isolation without the directional influence of debate with other informed taxonomists. Seebohm employed a hyphenated construction when labelling several taxa, to which he added the highly novel *Picus syriacus*-

¹⁴ Seebohm's naturalist circle in Yorkshire, during the 1860s and early 1870s was discussed by Milsom (2020: 13–32, 45) and Hobson (2025: 174–189).

leucopterus vel *P. leptorhynchus* and yet another construction more commonly employed by botanists for labelling hybrids: *Lanius leucopterus* × *excubitor*.

The context of Seebohm's hyphenated construction is clearest in the case of Eurasian goldfinches. He employed *Carduelis major-caniceps* to label intermediate taxa which were referenced against *Carduelis major*, Seebohm's 'Taczanowsky's [*sic*] Goldfinch', and *Carduelis caniceps*, Seebohm's 'Eversmann's Goldfinch' which he treated as extreme forms.¹⁵ This was a fundamental departure from the accepted practice of referencing subspecies against a single nominate taxon based solely upon naming priority. It was unlike any of the subspecific labels then preferred by Seebohm's North American contemporaries, which remained anchored to the Linnean binomial. Seebohm's construction is more reflective of speciation history, which may have been his intention. He had certainly considered the underlying biology. In his accompanying commentary, Seebohm (1882a) noted 'a gradual series of intermediate forms' between *C. major* and *C. caniceps* which was 'probably the result of direct interbreeding of the two extreme forms with other and with hybrids of different degrees, as is the case with the Carrion [*Corvus corone*] and Hooded Crows [*C. cornix*] in the same valley'. These comments coincided with Seebohm's emerging interest in interbreeding between closely related taxa and its significance to speciation (Seebohm 1882b). This had been stimulated by his first-hand observations on Carrion and Hooded Crows and their hybrid offspring, on the Yenisey.¹⁶

Seebohm applied a similar hyphenated construction to his nomenclature of the colour morphs of Gyr Falcon *Falco rusticolus* in pt. I of his *History of British birds* (Seebohm 1883). However, he then abandoned most of his unorthodox multinomial constructions and his 'subspecies' or 'subsp.' connecting terms in his extended trinomials. For practical purposes, the latter were replaced initially by the 'var' term employed in the North American extended trinomial. In pt. II of his *History*, issued no later than May 1883,¹⁷ Seebohm introduced *Regulus cristatus*, var. *japonicus* and *R. cristatus*, var. *azoricus* to name two island forms of Goldcrest (Seebohm 1883).¹⁸ His reference, on p. 17 of pt. I of his *History*, to the use of the 'var' connecting term by Baird *et al.* (1874) to acknowledge varieties of Gyr Falcon, suggests a stimulus for this change in practice.¹⁹ Seebohm continued to employ the new style in his *History* and, with greater frequency, in his papers, particularly in Seebohm (1884a). Seebohm's naming of Wilson's Snipe *Gallinago delicata* as a subspecies, *Scolopax gallinago wilsoni*, in pt. V of the *History*, signalled his conversion to the American strict trinomial, which had been promoted approximately three years earlier by Ridgway (1881) in his *Nomenclature of North American birds*. Pt. V of Seebohm's *History* was published no earlier than 19 December 1884.²⁰

¹⁵ *Carduelis major* = Taxon 111 in Hartert (1903–23: 69); latterly *C. carduelis frigoris* Wolters, 1953, in Dickinson & Christidis (2014: 333, note 15); *Carduelis caniceps* = Taxon 113 in Hartert (1903–23: 70); latterly *C. c. caniceps* Vigors, 1831, in Dickinson & Christidis (2014: 333).

¹⁶ Seebohm, H. (1877) *Journal of a journey to the Yennesie in company with Capt. Wiggins of Sunderland*. Vol. 1. Unpubl. diary. Lodged in the Dept. of Manuscripts, Cambridge Univ. Library, Add, 4474. See entry for 27 May, pp. 110–114.

¹⁷ Seebohm's *History of British birds* was issued in six parts; I and II were published in 1883 and were subsequently bound together to form vol. 1 (Milsom 2020: appendix 3).

¹⁸ *Regulus cristatus* var. *japonicus* is not currently considered valid (Morioka *et al.* 2005: 57); *Regulus cristatus* var. *azoricus* is now treated as *Regulus regulus azoricus* Seebohm, 1883 (Dickinson & Christidis 2014: 549).

¹⁹ This was pre-dated by a published comment by Seebohm dated 1 November 1880, which indicates that he was then aware of American trinomial practice (Seebohm 1881: ix). It signalled Seebohm's qualified approval but not an immediate adoption of American style.

²⁰ For a comment on the date of issue of pt. V of Seebohm's *History of British birds*, see Milsom (2020: 284). Pt. V was later bound with pt. VI to form vol. 3 of the *History* (Seebohm 1885).

Seebohm was certainly aware of Ridgway's *Nomenclature*, having received an inscribed presentation copy. It is recorded in the bookseller's catalogue, part of which itemises the posthumous sale of Seebohm's ornithological library (see Item 731, Sotheran 1896). However, the date of Ridgway's gift is unknown. Seebohm's initial change in practice, in 1883, was to a trinomial style already superseded by Ridgway's promotion of the strict trinomial. This may suggest that Seebohm was then unaware of Ridgway's *Nomenclature*. It is more likely that Seebohm received his copy in person, during his visit to the Smithsonian in September 1884 (Milsom 2020), two months after the trinomials debate in London (*q.v.*). His reading of Ridgway's *Nomenclature*, rather than the defence of trinomialism by Coues at the London meeting, may have convinced Seebohm to adopt the strict trinomial. The wording of Seebohm (1884b), which had been published around the time of the trinomials debate and shortly before his departure to North America, implies that he was then undecided as to the best style of trinomial.²¹

The London trinomials meeting

By the 1880s, encouraged, perhaps, by the emergence of a consensus on the construction of trinomials and their purpose, North American ornithologists had become increasingly critical of British resistance to their adoption. Initial evidence for this comes from private communications between members of Baird's circle identified by Lewis (2012). A request from Coues to Allen was particularly combative.²² However, by summer 1884, the basis of these privately expressed views had become very visible. In a paper in *The Zoologist*, a British natural history journal, Coues defined the trinomial practice followed in America and, by implication the difference between the American and British stances, in overtly nationalistic terms (Coues 1884). Coues styled trinomialism as the 'American School of ornithology' and the 'central idea' [of trinomialism] as the 'American idea of ornithology'. Coues's authority for these claims rested on self-projection as 'one who is largely responsible for the growth and spread of trinomial nomenclature' (Coues 1884). It was against this background of international posturing that Coues travelled to England, in May 1884, to press for the use of trinomials by British taxonomists. Lewis (2012) records that some senior members of the American Ornithologists' Union were critical of Coues's lack of diplomacy and that its committee declined to endorse Coues's visit.

Coues had arrived in London by 4 June 1884. After an interval, a formal discussion about trinomials was arranged by staff from the then British Museum, to which Coues was invited (Cutright & Brodhead 1981). It was set for Tuesday 1 July, as announced by a printed advertisement dated 24 June (Allen 1884). However, the proceedings record that the meeting actually took place in the museum on 2 July (Allen 1884, also see *The Field*, 5 July 1884). Six Fellows of the Royal Society were present, one of whom, Sir William Flower, President of the Zoological Society of London and Director of the British Museum (Natural History), occupied the Chair. The proceedings were published, in detail, as rapidly as was practicable, in North America (Allen 1884), as well as in Britain (Anon. 1884). This and the academic standing of the audience indicate the significance of the meeting, as was perceived at the time.

The advertisement for the meeting referred to only one named speaker, Richard Bowdler Sharpe, who would deliver a talk entitled 'On the expediency, or otherwise, of adopting

²¹ A series of letters from Seebohm to Ridgway, now in the care of the Blacker-Wood Library, McGill Univ., Montreal (E. MacLean *in litt.* 2010), post-dates Seebohm's visit to the Smithsonian, in 1884. None refers to trinomials.

²² Coues to Allen: 'I wish that you would give the truly British stupidity of not seeing our Trinomial ideas a good rap'. (Lewis 2012: 175).

Trinomial Nomenclature in Zoology'. Dr Coues, who was styled as one 'who represents the advanced opinions of American Naturalists', was to be present (Allen 1884). In the event, Coues was not merely present to listen but was an active participant in a meeting that evolved into a debate. There was also an element of surprise in the programming on the day, which may have been a deliberate ploy by the organisers to contain Coues's arguments (Milsom 2020). Seebohm gave a presentation that had not been announced in advance. He spoke after Sharpe but before Coues.

Sharpe's address was cautious and lacked any commitment to immediate reform. He acknowledged subspecies but remained sceptical as to the utility of trinomials. Sharpe set out examples for discussion, using three series of avian taxa to illustrate how trinomials might be applied, or not. He declared that the application of trinomials to his series of *Astur badius* goshawks and *Scops giu* owls conferred little or no advantage. Sharpe was more sympathetic to the use of trinomials to recognise island forms of the Asiatic crows (*Chibia*): 'The use here of trinomial designations he believed conveyed an exact impression of the value of these forms, which are so closely allied as to be almost indistinguishable' (Allen 1884). However, any hint of support was effectively withdrawn by a subsequent remark, reported as follows. 'In regard to the Goshawks, the Scops Owls and the Crows, he was not yet certain whether treating them as subspecies, as he had done in his 'Catalogue,' was not as advantageous as the employment of trinomial nomenclature' (Allen 1884).²³

With his oversight of the bird collections in the British Museum (Natural History), Sharpe was particularly aware of the necessity of series of specimens to the evaluation of specific or subspecific status. He acknowledged that the museum's series of many of the commoner Palearctic species were insufficient, partly because of the difficulties of acquiring specimens from collections in continental Europe via exchange (Allen 1884). Sharpe's concern about sample sizes partially underlay his objection to the adoption of trinomials, which was reported as follows: 'it would open the door to a multiplication of species, or races, founded on insufficient material by authors lacking in experience of the difficulties of the subject' (Allen 1884). This combination of concerns emerged as a dominant theme in the discussion that followed the presentations.

The difficulties of discerning subspecies also underlay Seebohm's presentation. However, Seebohm followed a different line of argument to Sharpe. Whereas Sharpe built up his argument very specifically from personal acquaintance with selected series of specimens, Seebohm presented a broader view of the issues. He prefaced his talk with a commentary on the mismatch between the rigid application of the Linnean binomial and the changing perception of species, particularly the acceptance of intermediate links between species, or 'important local variations which cannot be ignored' (Allen 1884). Seebohm argued that in the light of this development it had become necessary to recognise subspecies as well as species. He then moved on to discuss the labelling of subspecies. However, the report of the meeting did not indicate whether or not Seebohm addressed all the possible options either systematically or in detail. But Seebohm did conclude his commentary by observing that 'the ornithologists of America think that a system of trinomial nomenclature will answer the purpose' (Allen 1884).

²³ Sharpe's 'Catalogue' was the *Catalogue of the birds in the British Museum*, Sharpe being lead author. All species of living bird then known, irrespective of whether they were represented in the museum's collections, were catalogued in its 27 vols. (see Wood 1931: 564). In his treatment of the *Astur badius* group of goshawks, in vol. 1 of this work, Sharpe had labelled each subspecies with a binomial, preceded by the abbreviation Subsp. and followed by a Greek letter in the lower case. As there was a series of subspecies, the leading letter for each binomial followed the order of the Greek alphabet (Sharpe 1874: 109–114). This notation did not originate with Sharpe (Haffer 1992: 126). His labelling sufficed within the confines of his 'Catalogue' but offered no context outside it without supporting text.

Seebohm understood the risks of recognising subspecies but offered qualified support for the American approach nonetheless. He argued against excessive caution by commenting that 'if no paths are to be trodden in which the indiscreet may err, there is an end at once to all progress' (Allen 1884). Unlike Sharpe, who focused on the form of labelling for subspecies, Seebohm addressed the problems of their delineation. He was sceptical about the assumption that 'the judicious ornithologist will be able to select from the infinite number of steps which form the series of intermediate races which lie between two intergrading species, one, two, three or even in some cases more local or climatic races which are worthy of being dignified by a name. ... It credits ornithologists with an amount of discretion which their past history does not justify' (Allen 1884). Seebohm's solution was a 'very slight modification' to the trinomial (Allen 1884).

His modification introduced a hyphenated third scientific name which acknowledged the existence of series of subspecies with ill-defined boundaries, thereby avoiding the undesirable generation of an indefinite series of subspecific taxa. Seebohm presented examples for two groups of subspecies (Allen 1884, Milsom 2020). In the second of these, for White-throated Dipper *Cinclus cinclus*, Seebohm's *Cinclus aquaticus melanogaster-albicollis* acknowledged intermediate taxa between Seebohm's Scandinavian *C. a. melanogaster* and southern European *C. a. albicollis* subspecies, for example.

Seebohm had entered Coues's debating territory and Coues is reported to have prefaced his presentation by stating that he was much gratified at the interest shown in the subject of zoological nomenclature (Allen 1884). Coues introduced his own view of North American trinomial practice by drawing on evolutionary theory, which Seebohm had not addressed explicitly. He alluded to the evolutionary tree to illustrate the relatedness of all life forms and to point out that species could only be defined as discrete taxonomic units once the connections with their progenitors had been severed, these connections being the so-called 'missing links'. Coues then argued that many species still exhibited 'connecting links', which did not sit tidily with the dichotomous classification of the Linnean binomial, thereby echoing Seebohm's comments about intermediate links. He went on to illustrate the practical application of trinomials to these intergrading taxa by drawing upon the nomenclature of the geographical races of Hairy Woodpecker *Picoides villosus*, which had become a well-established North American example (Allen 1884).

An opening response from the floor by Albert Gunther, Keeper of Zoology at the British Museum, was supportive of American trinomial practice. However, this was soon outnumbered by the opinions of another Royal Society Fellow, Philip Lutley Sclater, and other members of the audience, which were increasingly negative. All reported responses focused on the practical aspects of trinomial use (Allen 1884). The perceived vulnerability of the new nomenclature to misuse (as set out in the Introduction) was a repeated concern, to which was added a fear that taxonomic documentation in zoology would be overwhelmed by the introduction of trinomials. Coues responded by emphasising that the use of trinomials addressed geographical or climatic variation between populations of the same species and had nothing to do with individual variation within them (Allen 1884). However, his explanation was not sufficient to retrieve the initial mood for reform.

Drawing on comments by Cutright & Brodhead (1981), Winker (2010) suggested that Coues's visit to Europe was important in the spread of the use of subspecies and trinomial nomenclature. However, there is little, if any, evidence from Britain to suggest that Coues's visit promoted that spread. Approximately 30 years elapsed before Ernst Hartert and Harry Forbes Witherby (1873–1943) presented a successful case for the introduction of trinomials in Britain, with the publication of their *Hand-list of British birds* (Hartert *et al.* 1912). General use of trinomials became official policy in 1915, when they were adopted

by the BOU Records Committee (BOU 1915). Neither Coues nor Seebohm oversaw the introduction, both having died, Coues in 1899, Seebohm in 1895. As Hartert and Witherby had not attended the trinomials meeting, it is unclear what effect, if any, the content of Coues's address might have had on their thinking. However, there is irrefutable evidence that Hartert was persuaded to recognise subspecies by Seebohm's writings (Hartert 1891).

Seebohm had arrived at the meeting as a promoter of trinomials, which was not due to Coues, although he had converted previously to an American style for practical purposes. In these respects, Seebohm's stance remained largely unchanged. His proposed modification to the trinomial was received politely but not adopted (Allen 1884). The published record of the discussions that followed the presentations sheds an objective light upon Seebohm's isolation from nearly all of his British contemporaries (Allen 1884). Seebohm continued, in isolation, to use trinomials quite freely, convinced of their utility to the study of subspecies and speciation.²⁴

Seebohm's and North American stances on the evolutionary significance of subspecies

Although the focus of the trinomials meeting had been on the nomenclature of subspecies, both Seebohm and Coues had previously grasped their evolutionary significance. In his *Glossary*, Coues characterised subspecies as 'nascent species' (E. Coues in Baird *et al.* 1874), which was the essence of a more elaborate explanation he had set out three years earlier (Coues 1871). Here Coues likened the speciation process to the development of stolons in plants. 'Species' he argued, 'like some plants, are *stoloniferous*; they produce offsets that finally separate from their parent stock and appear like distinct entities.' Coues went on to argue that 'our *positive* specific forms ... are simply those whose wide divergence has concealed or broken their connections with the original stem, while all debatable forms ... are merely those in visible process of separation.' At the meeting in July 1884, Coues's discussion about species, subspecies and trinomials was again based on the evolutionary tree and the distinction between missing and connecting links. This suggests that Coues had not elaborated upon his earlier views to any great extent. Ridgway did not express any original views on the evolutionary significance of subspecies but quoted extensively from Seebohm and referred to Coues (Ridgway 1879). Ridgway's use of the term 'nascent species' in his *Nomenclature* (Ridgway 1881) simply restated the definition that Coues had employed in his *Glossary* seven years earlier. None of the statements by Coues or Ridgway makes it clear whether subspecies were perceived as relicts from a past and incomplete speciation event or as a stage in an ongoing process.

Seebohm was more explicit on this point. He interpreted the logic of Darwin and Wallace's arguments to mean that evolution was ongoing and that partially differentiated forms, his 'subspecies', were physical evidence of an active process (Seebohm 1879b). Within four years of the statement in his Japanese paper (quoted above), Seebohm had advanced his thinking to emphasise the dynamic nature of subspecies. In two versions of a commentary on the interbreeding of birds (Seebohm 1882b, 1883), he argued that subspecific variations were continually introduced by evolutionary processes, including natural selection, but were vulnerable to dilution or nullification from interbreeding between populations in the absence of protection conferred by geographical isolation. His perception of the process is clear from a passage in Seebohm (1883: xii): 'slight subspecific variations are constantly being produced by various causes, of which natural selection is probably the most important, and are as constantly being lost by interbreeding.' Two other passages

²⁴ See, for example, Seebohm (1888) and commentary in Milsom (2020: 201–203).

from the same source reveal his thinking upon the importance of geographical isolation. The first is unambiguous: ‘the opportunity of interbreeding is taken away by isolation of area of geographical distribution’. The second is inferred: ‘Amongst British birds there are a great many instances of subspecies of which we know ... Most of these are cases where the individuals of each valley occasionally interbreed, and where the range is great enough to make the sum of a series of small differences show a large difference in the extremes, as in the Nuthatch, Marsh-Tit, Grey Shrike &c.’ Seebohm’s process-based perception of subspecies had diverged significantly from that set out by Coues at the trinomials meeting in July 1884 (Allen 1884), which remained taxonomically slanted.

Seebohm’s dynamic view of subspecies, when combined with his grasp of the importance of their geography, laid the foundations for his models of allopatric speciation in birds (Milsom 2020). The first of these was sketched out in the Introduction to his volume for the *Catalogue of the birds in the British Museum* (Seebohm 1881). Haffer and Mayr highlighted its historical significance (Haffer 1997: 15–17, 639). The initiative for exploring the evolutionary significance of subspecies, particularly the distinction between the geographical isolation of subspecies and development of reproductive isolation between emerging species, remained primarily with Seebohm and his direct intellectual successors from the Seebohm-Hartert school: Ernst Hartert, Erwin Stresemann (1889–1972), Bernhard Rensch (1900–90) and Ernst Mayr (1904–2005) (Haffer 1994, 1997, Haffer *et al.* 2014, Milsom 2020).

Henry Seebohm and taxonomic schools

Haffer regarded his Baird-Coues and Seebohm-Hartert schools as ‘evolutionary’, but separated their respective thinking on the grounds that the former was ‘morphological’ and the latter ‘biological’ (Haffer *et al.* 2014: table 1). The contrast between Seebohm’s and Coues’s stances on subspecies described here further validates Haffer’s distinction. Seebohm’s early debt to European ideas on trinomial construction, revealed here for the first time, and his direct influence on Hartert’s thinking, also indicates that the Seebohm-Hartert school was not simply an offshoot of the Baird-Coues school, its roots being largely independent. Further routes of diffusion of trinomial practice and theoretical ideas about subspecies from Temminck & Schlegel through taxonomic communities in continental Europe may yet emerge. At present, however, it seems that Seebohm, Hartert and their successors ultimately achieved the greatest theoretical impact through their preparation of the taxonomic foundations for the Biological Species Concept, as set out by Mayr in his seminal *Systematics and the origin of species* (Mayr 1942, 1992).

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Passive Acoustic Monitoring extends the known distribution of Speckled Spinetail *Thripophaga gutturata* in eastern Amazonia

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SUMMARY.—Speckled Spinetail *Thripophaga gutturata* is a widespread Amazonian furnariid typically associated with riverine and seasonally flooded forests. Despite its broad distribution, the species had not previously been documented in the Belém Centre of Endemism. Here we present the first documented record of the species in this centre of endemism, representing both the species' easternmost confirmed locality and the first verified record for the state of Maranhão, Brazil. Using Passive Acoustic Monitoring (PAM), we detected 194 distinct vocalisation events in Alto Turiaçu Indigenous Land, on the right bank of the Gurupi River. Our findings extend the known distribution of the species c.346 km east and reinforce the importance of systematic voucher documentation for validating species occurrences in poorly sampled regions. Our results also highlight the effectiveness of PAM for detecting species associated with specific and under-sampled habitats.

The genus *Thripophaga* Cabanis, 1847, comprises five species distributed throughout the tropical forests of South America (Winkler *et al.* 2020). Speckled Spinetail *T. gutturata* (d'Orbigny & Lafresnaye, 1838) is a widespread resident of Amazonia, ranging from southern Venezuela south to northern Bolivia (Remsen 2023). Its congeners have a more restricted distribution in Amazonia—Orinoco Softtail *T. cherriei* von Berlepsch & Hartert, 1902; Delta Amacuro Softtail *T. amacurensis* Hilty *et al.*, 2013; and Plain Softtail *Thripophaga fusciceps* P. L. Sclater, 1889—or in the Atlantic Forest—Striated Softtail *T. macroura* (zu Wied, 1821) (Winkler *et al.* 2020).

Speckled Spinetail typically inhabits edges of low-growing moist forests and seasonally flooded evergreen forests, mainly *várzea* and transitional forests, and may also occur locally in poorly drained or riparian *terra firme* (Remsen 2023). The species is frequently associated with riverbank environments, where it is commonly observed in mixed-species flocks foraging in the foliage, inspecting clusters of dead leaves and probing epiphytes. Sometimes placed in *Cranioleuca*, genetic data indicate it belongs in *Thripophaga* (Derryberry *et al.* 2011). The main song is a series of 4–9 high-pitched sibilant notes (at 6–9 kHz) delivered in rapid sequence over c.3 seconds. The known distribution of Speckled Spinetail covers all of the Amazonian centres of endemism, except Marajó and Belém. Here, we present the first documented records of Speckled Spinetail for the Belém Centre of Endemism (Belém CE), the easternmost locality for the species and the first records for the Brazilian state of Maranhão.

This study was conducted in two indigenous lands in the Belém CE: Alto Rio Guamá Indigenous Land (279,897 ha), on the left bank of the Gurupi River, state of Pará; and Alto Turiaçu Indigenous Land (530,524 ha), on the right bank of the same river, in Maranhão. We used Passive Acoustic Monitoring (PAM) to document bird species. A total of 78 Automatic Recording Units (ARUs) (Shonfield & Bayne 2017), model AudioMoth 1.0 (Hill *et al.* 2018)

were installed in Alto Rio Guamá Indigenous Land and six in Alto Turiaçu Indigenous Land between April and May 2021. ARUs were installed along trails used by the indigenous community, alternating between *terra firme* and *várzea* habitats, with a minimum spacing of 250 m between devices. Each unit was programmed to record one minute every five minutes throughout the day, using a sampling rate of 48 kHz. After 30 days of continuous recording, the ARUs were retrieved and the resultant audio files were uploaded to the Arbimon platform (Automated Remote Biodiversity Monitoring Network; <https://arbimon.org/p/temb-reserve-brazil-species/overview>).

GAL & TNM reviewed the recordings in Arbimon. They manually detected and tagged species from two days of recordings (the second and penultimate days) per sampling site to create a preliminary species list. Following identification, the signal with the highest signal-to-noise ratio and no overlap with other species' calls was selected to serve as a template for Pattern Matching analyses. Arbimon's Pattern Matching (PM) tool permits users to choose an acoustic signal template and then search a user-defined playlist of audio recordings to identify signals that match the selected template. The same two authors then validated the PM results for Speckled Spinetail previously identified when creating the preliminary list using filters that checked all sites and also looked for the largest number of presences for the species, to verify the pattern of vocal activity.

We utilised the *suwo* package (Araya-Salas & Elizondo-Calvo 2023) in the R software environment (R Core Team 2025) to access documented records of Speckled Spinetail on the following online repositories: Macaulay Library (ML), WikiAves (WA), Xeno-Canto (XC), GBIF and iNaturalist (IN). The retrieved data were exported in CSV format using the *openxlsx* package (Schauberger & Walker 2025). Subsequently, a distribution map was generated using QGIS version 3.42.2 'Bratislava' (QGIS Development Team 2025). We also consulted online data from the skin collection of the Museu Paraense Emílio Goeldi, Belém (MPEG). Sonograms were generated in R using the package *seewave* (Sueur *et al.* 2008).

A database of 300,000 one-minute recordings was generated from both areas. The PM analysis using the 'score' and '200 top scores per site' filters revealed the presence of Speckled Spinetail at eight sites, all in Maranhão, with a total of 194 vocalisation events. The species was detected at eight of the 78 sampling sites, ranging from a single detection to as many as 93 detections per site. Vocal activity was recorded at all times of day, with greater activity at 06.00 h and a smaller peak at 13.00 h (Fig. 1). One of these recordings is available in Xeno-canto (XC 983492; G. A. Leite).

A total of 778 documented records was compiled from online repositories (Fig. 2), as follows: ML (165 photographs, 64 audio recordings, nine videos); WA (168 photographs, 25 audio recordings); XC (66 audio recordings); GBIF (19 photographs, 198 specimens); IN (36 photographs, five audio recordings); and MPEG (23 specimens).

The vocalisations recorded in the present study (Fig. 3A) were compared with others made in the Juruá region (Fig. 3B), Canaã dos Carajás (Fig. 3C) and Manaus (Fig. 3D), representing geographically distinct localities across Amazonia. All four vocalisations exhibited a highly similar acoustic structure, consisting of sequences of short, high-frequency notes concentrated predominantly at 6–9 kHz and characterised by comparable temporal spacing, note morphology and frequency modulation patterns. In all sonograms, the notes displayed a predominantly descending frequency contour with broad harmonic energy distribution, forming repetitive phrase-like sequences with consistent spectral organisation. The marked similarity in temporal and spectral parameters across localities strongly supports their attribution to the same vocal type.

Our findings extend the geographic distribution of Speckled Spinetail by c.346 km east, provide the first documented records of the species in the Belém CE (Fig. 2), as well

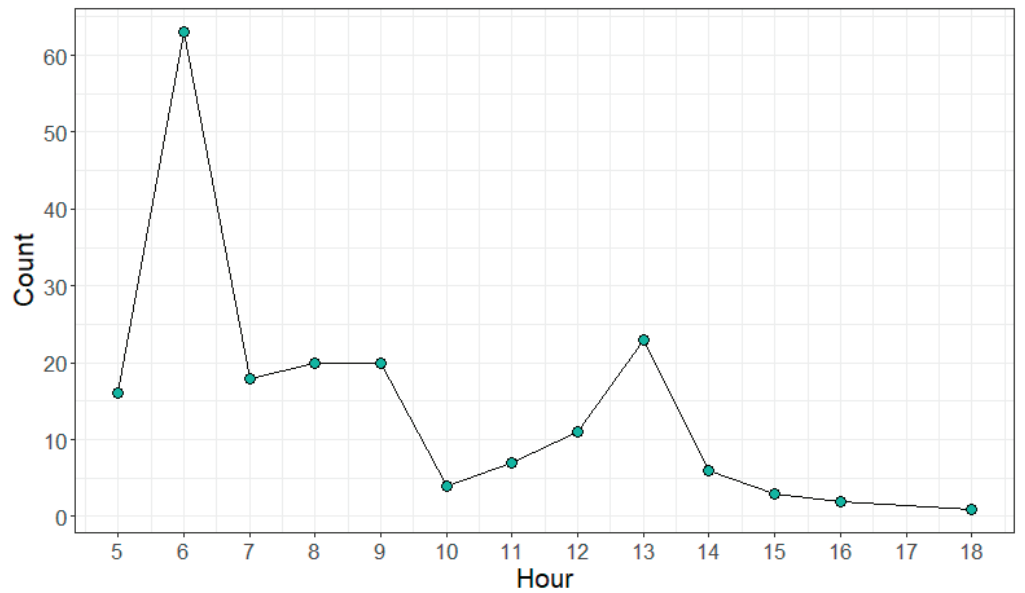


Figure 1. Daily vocal activity of Speckled Spinetail *Thripophaga gutturata* in eastern Amazonian Brazil, as revealed through Passive Acoustic Monitoring.

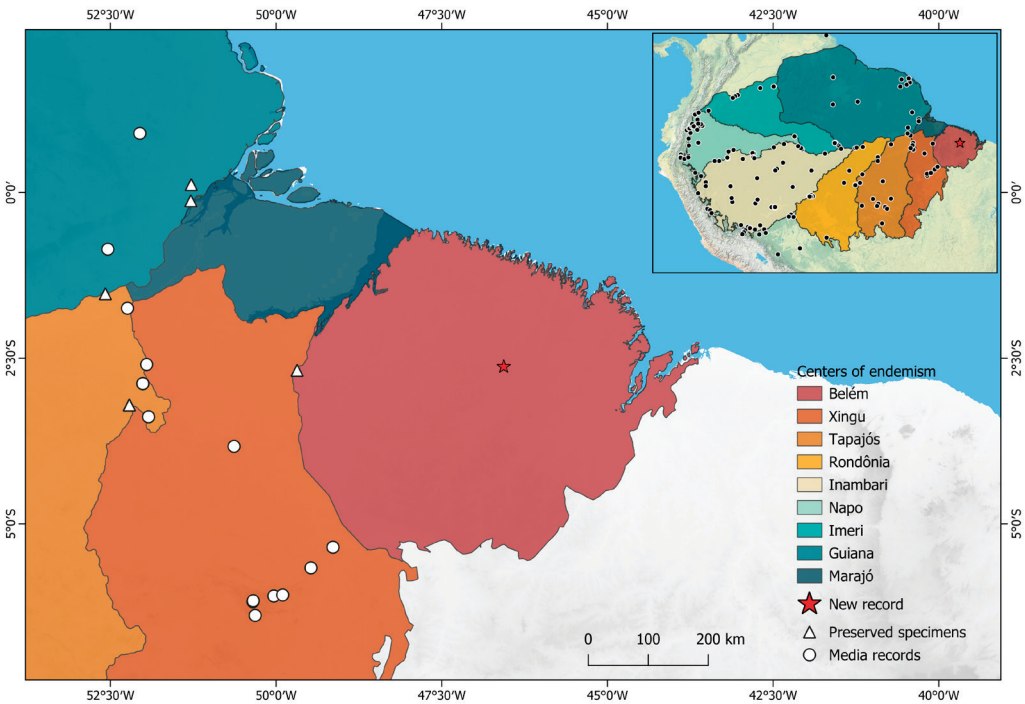


Figure 2. Documented records of Speckled Spinetail *Thripophaga gutturata* across the major interfluvia of the Amazon Basin. The star indicates the first documented occurrence in the Belém Centre of Endemism and Maranhão state. Circles represent media records (photographs, audio recordings or videos), while triangles denote specimens.

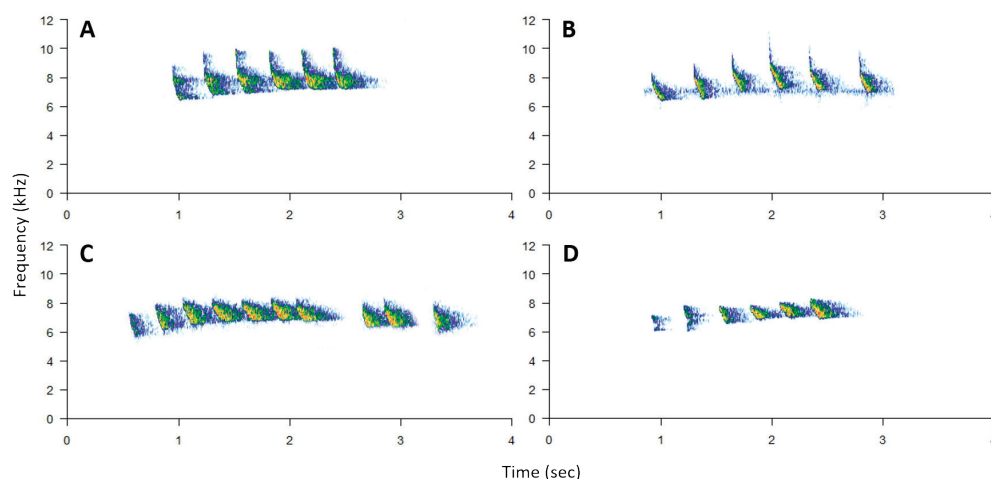


Figure 3. Comparison of sonograms of Speckled Spinetail *Thripophaga gutturata* vocalisations from different localities in Brazil: (A) Alto Turiaçu Indigenous Land, Maranhão (XC 983492; G. A. Leite); (B) Reserva Extrativista Alto Juruá, Acre (XC 95843; J. Minns); (C) Canaã dos Carajás, Pará (XC 711660; F. Arantes); (D) Manaus, Amazonas (XC 345859; J. Honkala), representing distinct localities across Amazonia.

as the first records for Maranhão. The nearest previous record is a male specimen collected by Emilie Snethlage in December 1910 on Pirunum Island, in the Tocantins River, Baião municipality, Pará (Snethlage 1914, Paynter & Taylor 1991). This specimen is at the Museu Paraense Emílio Goeldi (MPEG.OPE 7618).

In a comprehensive review of the avifauna of Maranhão, the potential occurrence of Speckled Spinetail in the state was noted (Silva *et al.* 2021). The only undocumented record in the Belém CE was made during ornithological surveys between 2005 and 2007 at Fazenda Rio Capim, municipality of Tailândia, Pará (Portes *et al.* 2011). The surveyed area encompasses c.150,000 ha, of which 95,000 ha is primary forest. Nevertheless, there is no prior confirmed documentation of the species in the Belém CE, and no voucher material—specimens, photographs or audio recordings—is available to support the Tailândia record.

As emphasised by Lees *et al.* (2012), caution is warranted when considering unverified records in the Belém CE. In this context, the systematic documentation and dissemination of voucher materials represent important practice to validate species occurrences. This is especially relevant in respect of potential range extensions, where the availability of robust evidence is particularly important.

Speckled Spinetail is a small passerine (13–15 cm) with predominantly brown plumage. Due to its inconspicuous behaviour and preference for dense forest, the species is often difficult to detect through direct visual observation (Remsen *et al.* 2023); however, it can be readily identified by its vocalisations.

Given the extensive recent sampling effort devoted to the avifauna of the Belém CE (e.g., Portes *et al.* 2011, Lees *et al.* 2012, Lima *et al.* 2014, Gonsioroski *et al.* 2020), the scarcity of records of this species indicates apparent rarity or extremely local occurrence in this region. Moreover, the present study suggests that its occurrence may be closely associated with structurally intact and well-preserved forests, reinforcing the potential sensitivity of the species to environmental disturbance and habitat degradation. In this context, we underscore the effectiveness of PAM for detecting species associated with specific and under-sampled habitats, as well as its practicality and suitability for field-based biodiversity assessments.

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A compendium of Paraguayan breeding data for nightjars (Caprimulgiformes: Caprimulgidae) and potoos (Nyctibiiformes: Nyctibiidae)

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SUMMARY.—Very few data have been published on the breeding of Paraguayan birds, and those available are typically scattered across relatively low-circulation journals. Here we compile reproductive data from Paraguay for two orders of birds, the Caprimulgiformes and Nyctibiiformes, from published and unpublished sources. Information is provided for eight species of nightjar and three species of potoo. The following species are migratory and are not considered to breed in Paraguay: Lesser Nighthawk *Chordeiles acutipennis*, Common Nighthawk *C. minor* and Band-winged Nightjar *Systellura longirostris bifasciata*. Breeding data for Paraguayan Caprimulgiformes is highly seasonal, being concentrated in late August–January, i.e., the Southern Hemisphere spring and early summer. Additionally, we provide evidence of nest relocation by a Pauraque *Nyctidromus albicollis*.

The Caprimulgiformes and Nyctibiiformes are orders of nocturnal birds, with two families and 40 species occurring in South America (Remsen *et al.* 2025). Despite the diversity of species in the region, their breeding systems, where they are known, tend to be rather conservative and highly seasonal. Among Caprimulgidae most species are ground nesters (some nighthawks are arboreal), typically laying two eggs directly onto the ground with no elaborate nest structure. Eggs may be immaculate to heavily spotted (Cleere & Nurney 1998, Holyoak 2001). Nyctibiidae are arboreal nesters, generally laying a single lightly spotted white egg directly onto a tree branch or post (Cleere & Nurney 1998, Holyoak 2001). Nevertheless, the majority of what is known has been compiled from brief casual observations at scattered locations, and many questions remain to be answered, including whether or not adults are able to transport eggs or young (Cleere & Nurney 1998).

Nineteen species occur in Paraguay—16 species of Caprimulgidae and three species of Nyctibiidae. Published breeding data from the country are available only from scattered records for a small number of species, with most observations being unpublished. Here we aim to summarise available data, supplemented with new observations to build a more complete picture of the breeding behaviour of these species in this under-watched country.

Methods

We collated all Paraguayan breeding records of Caprimulgidae and Nyctibiidae from the published literature, museum specimens, our own field observations and online citizen science platforms (eBird, iNaturalist) with a view to building as complete a picture as possible of reproduction by these families in Paraguay. Breeding records were considered confirmed by the presence of eggs, chicks or incubating adults, and inferred by adults performing distraction displays. Except in a few cases involving poorly known species, we

did not include singing or apparently territorial behaviour in this work as their relevance to breeding is not always clear. Citizen science records were included only if a photograph confirming the species was available. Local naturalists were also contacted and asked to contribute unpublished observations, which were accepted provided verifiable data were available (e.g. a photograph or video). These observations are treated separately and the observers listed by name. Where an observation is by one of the authors, their initials are given in parentheses, unless it is a published record in which case the relevant reference is cited. Museum acronyms used are as follows: MVZ (Museum of Vertebrate Zoology, Berkeley, CA); NHMUK (Natural History Museum, Tring); NRM (Naturhistoriska Riksmuseet, Stockholm).

Following the observations for each species, a series of subheadings summarise the data. Departments: the political departments of Paraguay for which breeding records are available; Extreme dates: summarises the earliest and latest dates for reproductive stages such as incubation, presence of eggs, presence of chicks etc. We include a section on published extralimital reports for published descriptions of breeding data from other countries inhabited by the same subspecies as in Paraguay, although this is not intended to be a complete bibliography. If no subspecies is listed then the species is monotypic. Finally, a comments section places the observations for each species into context and highlights significant reports.

Results

Family Caprimulgidae (nightjars)

NACUNDA NIGHTHAWK *Chordeiles nacunda*

Azara (1805) made the unqualified but accurate statement 'they raise two chicks on the ground'. Two clutches of two eggs and one of a single egg collected by William Foster between 3 and 14 October 1903 at Sapucáí, Paraguari department, at NHMUK (E/1904.7.26.141–144 and E/1904.7.26.306) (Hayes 2014). These are the eggs described by Chubb (1910) as follows: 'One egg...October 3, 1903, is pinkish cream-coloured, mottled with reddish brown and underlying spots of lavender-grey. It measures: axis 1.35 inches; diameter 1.05 [inches] [34.3 × 26.7 mm]'. 'Two eggs...October 14. 1903, are cream-coloured, mottled with brown in greater contrast. Axis 1.35 to 1.45 inches; diameter 0.9 to 0.95 [34.3–36.8 × 22.9–24.1 mm]'. 'Two eggs...October 13, 1903, are pinkish cream-coloured, heavily blotched with brown. Axis 1.45 inches; diameter 1.0 [36.8 × 25.4 mm]'. A female with developed (enlarged) gonads was collected on 9 September 1956, c.65 km south-east of Orloff, Boquerón department, indicating breeding activity (Steinbacher 1962).

One egg, 15 October 2024, on a patch of bare ground in short-grass pasture at Estancia Arrecife, Concepción department (M. Silvera). A nest with two eggs on bare rocky ground on 22 November 2024 at Isla Yacyretá, Itapúa department (27°28'04"S, 56°45'26"W). The



Figure 1. Nest and eggs of Nacunda Nighthawk *Chordeiles nacunda*, Isla Yacyretá, Itapúa department, Paraguay, 22 November 2024 (Sergio Galeano)

eggs were buffy, heavily marked with irregular reddish-brown and dark brown mottling (Fig. 1). They measured $34 \times 24\text{--}25$ mm. When disturbed on the nest the incubating bird did not perform a distraction display, merely flying a short distance (c.2–3 m) and then sitting quietly (SG).

Departments.—Boquerón, Concepción, Itapúa, Paraguari.

Extreme dates.—Enlarged gonads: 9 September; Eggs: 3 October–24 November.

Published extralimital reports.—*C. n. nacunda* Argentina: Barrows (1884), Pereyra (1932), de la Peña (2013), Salvador & Bodrati (2017). Brazil: Euler (1900), Snethlage (1928), Belton (1984). Uruguay: Dalgleish (1881), Aplin (1894), Harrison (1936), Gore & Gepp (1978).

Comments.—Though widespread, the species' status in Paraguay is unclear. Large flocks of up to 300 individuals were observed roosting on sandy beaches in Asuncion Bay ($25^{\circ}15'49''\text{S}$, $57^{\circ}37'47''\text{W}$) in August 2012 (R. Clay & AJL pers. obs.) and although these winter records may suggest residency (at least in the Chaco region), patterns of occurrence are unclear and movements are probably local, complex and perhaps irregular (Salvador & Bodrati 2017).

In his notes Foster reported 'A rare bird throughout central Paraguay. I have only met with two specimens in eight years, but I know of another which was shot at Asuncion'. This would seem to infer that encountering three nests was a particularly unusual occurrence, perhaps indicating opportunistic breeding?

Schönwetter (1966) stated '*fide* Penard' (one of two brothers active in Suriname in the late 19th and early 20th centuries) that clutches of a single egg are typical of the nominate subspecies, but reports here and those in Salvador & Bodrati (2017) from Argentina confirm that the normal clutch is two eggs.

The lower value (22.9 mm) for the width of the eggs collected by Foster on 14 October 1903 is slightly below the range given for this species by Cleere & Nurney (1998) of $33.5\text{--}37.3 \times 23.5\text{--}27.7$ mm.

SHORT-TAILED NIGHTHAWK *Lurocalis semitorquatus*

No reports of breeding in Paraguay.

Vocalisations.—During long-term studies at Reserva Bosque Mbaracayú, Canindeyú department, singing birds were detected from mid-October until late November during 1994, but those observed in January–February 1995 did not sing. Dawn singing was detected again in mid-September 1995, with vocal activity peaking in late November 1995 to early January 1996. Singing commenced once more in the third week of September 1996. This suggests a similar pattern of seasonal breeding as in other caprimulgids, with territories possibly being established shortly after arrival and peak breeding activity potentially during late October–December.

Published extralimital reports.—*L. s. nattereri* Argentina: Straneck *et al.* (1987). Brazil: Simon & Bustamante (1999).

Comments.—This is a migrant caprimulgid (September–April) occurring mainly in forests east of the Paraguay River, with only marginal occurrence on the west bank of the river. An arboreal nester (Straneck *et al.* 1987, Seutin & Letzer 1995), Fiebrig (1921) erred in describing the species a ground nester. A Paraguayan nest of Short-tailed Nighthawk reported by Bertoni (1923) was later doubted by the observer (Bertoni 1926) and, based on the description, it seems certain to be an error.

BAND-TAILED NIGHTHAWK *Nyctiprogne leucopyga*

No reports of breeding in Paraguay.

Published extralimital reports.—*N. l. majuscula* none.

Comments.—A ground nester (Whitney *et al.* 2003). Resident in Paraguay and thus presumably breeds, but restricted to the remote Pantanal ecoregion of northern Alto Paraguay department.

COMMON PAURAUQUE *Nyctidromus albicollis*

Five clutches each of two eggs collected during 1900–08 by William Foster, all between 9 and 22 October at Sapucaí, Paraguari department, held in NHMUK (E/1904.7.26.113–114, E/1904.7.26.120–121, E/1904.7.26.307–308 and E/1905.10.13.583–584) (Hayes 2014). These include the four clutches described by Chubb (1910) as follows: ‘Four clutches of eggs were collected during the month of October 1903. They vary in ground-colour from greyish pink to creamy, spotted and blotched with pinkish brown and underlying marks of lavender-grey. The measurements are: Axis 1.1 to 1.25 inches; diameter 0.85 to 0.9 inches’ [27.9–31.8 × 21.6–22.9 mm]. In his field notes, the collector added: ‘The eggs, two in number, are laid on the bare ground, but the bird will never rise unless almost stepped upon, and its plumage is hard to detect in the lights and shadows of the woods’ (Chubb 1910).

A nest on 15 August 1995 at Lagunita (Arroyo Morotí), Reserva Natural Bosque Mbaracayú, Canindeyú department (AM). A single cream-coloured spotted egg had clearly been laid recently as it was not present the previous day. Two eggs were found in the same nest when it was monitored ten days later on 26 August. A fledgling capable of very limited flight on 25 October 2008 was photographed (Fig. 2) at Lagunita, Reserva Natural Bosque Mbaracayú, Canindeyú department (PS). Nest photographed on 8 October 2012 at Laguna Blanca, San Pedro department, by J. Miller (Fundación Para La Tierra). Unlined depression c.90 mm diameter, bordered by a very slightly raised area (seemingly from displacement of leaves from the depression area, rather than by design) of 150–180 mm diameter. The nest was very exposed in a fairly open area, the nearest tree c.1.5 m away, with sparse vines and dead branches c.1.5 m above it. Two eggs pale pinkish with heavy reddish-brown spotting over the whole surface. Dimensions 28 × 20 mm and 29.0 × 20.5 mm. Images available at http://www.faunaparaguay.com/nyctidromus_albicollis.html.

Nest with two eggs along a trail at Reserva Kanguery, Itapúa department, on 15 September 2014. Eggs were cream-coloured, spotted reddish, but one was distinctly more heavily blotched than the other (AJL; Fig. 3). Nest with two eggs at Jardín Botánico de Asunción, Central department, photographed on 25 October 2014 (A. Caballero). Specimens reported by Foster & Johnson (2017) at Hotel El Tirol, Itapúa department. Two females in January with immature skull and ovaries. Male in January with adult skull and testes 3 × 5 mm. Male in March with non-pneumatized skull and testes 4 × 2 mm.



Figure 2. Fledgling of Common Pauraque *Nyctidromus albicollis*, Lagunita, Reserva Natural Bosque Mbaracayú, Canindeyú department, Paraguay, 25 October 2008 (Paul Smith)



Figure 3. Eggs of Common Pauraque *Nyctidromus albicollis* showing variability of spotting even in a single clutch, Reserva Kanguery, Itapúa department, Paraguay, 15 September 2014 (Arne Lesterhuis)



Figure 4. Nest with two large downy chicks of Common Pauraque *Nyctidromus albicollis*, Puesto Apepu, Parque Nacional Caazapá, Caazapá department, Paraguay, 12 October 2024 (Luis Doldan)

Figure 5. Nest and eggs showing egg covering by Common Pauraque *Nyctidromus albicollis*, Isla Yacyretá, Itapúa department, Paraguay, 10 November 2024 (Paul Smith)

Two recently hatched downy chicks photographed by ‘watarumatsunaga’ on 6 October 2019 at Hohenhau (26°54'32.44"S, 55°53'30.44"W), Itapúa department, (<https://www.inaturalist.org/observations/34006041>). Nest with two eggs photographed by L. Recalde at Parque Nacional Serranía San Luis, Concepción department, on 17 October 2020 (<https://macaulaylibrary.org/asset/272864151>). Nest with two large chicks close to fledging at Salto Suizo, Guairá department, on 17 October 2020 (L. Doldan). Adult performing distraction display at Isla Yacyretá, Itapúa department, on 11 September 2022 but nest was located only on 30 September 2022 containing two cream-coloured eggs spotted red (PS).

Nest with two eggs photographed at Cerro Koi, Aregua, Central department, on 15 October 2022. Eggs were laid directly onto the leaf litter under an *Acrocomia aculeata* palm, close to a ravine and adjacent to some bushes c.2 m in height (DOL). Nest with two eggs, one more heavily blotched than the other, photographed by A. Bowen at Cerro Guy, Mbocayaty, Escobar, Paraguari department, on 16 September 2023, one of which seemed to be starting to hatch. A pair of adults was present nearby (<https://macaulaylibrary.org/asset/609059054>). Nest with one egg and one chick at Reserva Natural del Bosque Mbaracayú, Canindeyú department, on 29 September 2023. The grey-morph male was observed at the nest after dark on 29 September 2023 and a rufous-morph female was brooding at the nest next day (A. Vera).

Nest containing two eggs with similar patterns photographed at Potrero Brachiaría, Concepción department, on 3 November 2023. Approximate dimensions 26 × 19 and 27 × 19 mm (M. Silvera). Nest containing two eggs, one more heavily blotched than the other, photographed by G. Menéndez at Reserva Natural Bosque Mbaracayú, Canindeyú department, on 4 November 2023 (<https://www.inaturalist.org/observations/190515756>). Nest with two eggs, one more heavily blotched than the other, photographed by V. Weber at Jejuí-Mi, Reserva Natural Bosque Mbaracayú, Canindeyú department, on 3 September 2024 (<https://macaulaylibrary.org/asset/623329345>). Nest with two large downy chicks at Puesto Apepu, Parque Nacional Caazapá, on 12 October 2024 (Fig. 4). The attendant female performed a distraction display when the nest was approached (L. Doldan).

Nest containing two pinkish eggs with sparse light reddish-brown blotching was found on 27 October 2024 at Isla Yacyretá, Itapúa department (SG). On 10 November a female was incubating the eggs which had been moved c.40 cm from the original location to the base of a nearby tree. When the bird vacated the nest, it covered one egg completely with a dead leaf, flying quietly away into cover (PS; Fig. 5). On 14 November two small chicks were present, mass 32 and 34 g, respectively, on 15 November (Fig. 6), when they were

c.1.5 m from the original location. On the last date the sitting bird performed a distraction display, gaping widely and flapping both spread wings against the ground as if injured (PS, SG).

Departments.—Caazapá, Canindeyú, Central, Concepción, Guairá, Itapúa, Paraguari, San Pedro.

Extreme dates.—Eggs: 15 August–4 November. Chicks: 29 September–15 November. Fledglings: 25 October. Immatures: January.

Vocalisations.—During long-term studies at Reserva Bosque Mbaracayú, Canindeyú department, greatest vocal activity was recorded from mid-July until the second half of September, followed by a near-total cessation (perhaps corresponding with the nesting period). Nevertheless, the species does vocalise occasionally throughout the year and vocalising is not strictly associated with breeding.

Published extralimital reports.—*N. a. derbyanus* Argentina: Bodrati (2004), Cockle *et al.* (2016), Moresco (2018), de la Peña (2019). Bolivia: Pinto-Ledezma & Aponte Justiniano (2013), Peñaranda Barrios (2023). Brazil: Euler (1900), Ihering (1900), Sneathlge (1928), Mitchell (1957), Salles (1988), Andrade (1996), Alvarenga (1999), Vasconcelos *et al.* (2003), Marini *et al.* (2007, 2012), Luz *et al.* (2011), Mauricio *et al.* (2013), Nacinovic (2018), Studer & Crozariol (2025).

Comments.—Measurements of Paraguayan eggs (26.0–31.8 × 19.0–22.9 mm) are towards the smaller end of the range (27.2–35.1 × 19.0–24.6 mm) for this species given by Cleere & Nurney (1998).



Figure 6. Chick of Common Pauraque *Nyctidromus albicollis*, Isla Yacyretá, Itapúa department, Paraguay, 15 November 2024 (Sergio Galeano)

SICKLE-WINGED NIGHTJAR *Eleothreptus anomalus*

No reports of breeding in Paraguay.

Published extralimital reports.—Argentina: Krauczuk (2013), Fariña *et al.* (2018), Bodrati *et al.* (2019); Brazil: von Pelzeln (1868), Ihering (1902), Lowen (1999), Accordi (2008).

Comments.—A widespread but fairly local resident in Paraguay. Although no concrete breeding data are available for Paraguay, presumed immatures were recorded on Isla Yacyretá, where at least three were trapped in pre-definite plumage in August–September 2007. They had clear barring on the tips of the primaries (similar to immature White-winged Nightjar, see Pople 2003), whereas a female caught in April 2007 had more diffuse barring towards the tip. Females also appear to have white-tipped rectrices (like adult males), which were absent in the presumed immatures. Noteworthy was the mass of the female (67 g), significantly heavier than males trapped at the same time (45.0–53.5 g; $n = 8$) and which may indicate that the female was gravid. However, breeding at this time of year would be unusual.

WHITE-WINGED NIGHTJAR *Eleothreptus candicans*

Nest, eggs and chicks illustrated and described by Clay *et al.* (2014) from Aguara Ñu, Reserva Natural Bosque Mbaracayú, Canindeyú department. Nest a patch of bare earth c.300 mm in diameter largely exposed from above but partially obscured from the side by a *Mimosa dolens* (Fabaceae) shrub. Surrounding vegetation was 30–50 cm tall, with



Figure 7. Eggs of White-winged Nightjar *Eleothreptus candicans*, Aguara Ñu, Reserva Natural Bosque Mbaracayú, Canindeyú department, Paraguay (Rob Pople)

Figure 8. Nestlings of White-winged Nightjar *Eleothreptus candicans* showing size asymmetry, Aguara Ñu, Reserva Natural Bosque Mbaracayú, Canindeyú department, Paraguay (Rob Pople)

Figure 9. Fledglings of White-winged Nightjar *Eleothreptus candicans*, Estancia Laguna Blanca, San Pedro department, Paraguay, 10 November 2005 (Paul Smith)

Campomanesia adamantium (Myrtaceae) among the dominant species. Two eggs (28.7–28.9 × 21.3–21.4 mm, mass 7.5–7.6 g) present from at least 22–29 November 1997, and one hatched on 10 December. Eggs were pale creamy brown, with a fairly uniform light covering of darker brown and some greyer speckling. A recently fledged juvenile was observed in early January. Distraction displays were observed when eggs were in the nest.

In a detailed study of breeding biology, Pople (2003, 2014) noted males displaying at leks sporadically during the full moon in August, but this became more prominent from September to December. Incubation period 17–19 days, and two nesting attempts documented during a single season, the first in late September/October and then October/December. Eggs pale cream-beige, with variable dark brown and mauve-grey speckling and blotching. Difference in pattern within each clutch, with one more densely marked than the other. Measurements 26.7–29.9 × 19.8–21.7 mm, mass 5.8–7.5 g ($n = 14$) (Fig. 7). Hatching success 86% and chick growth was often asymmetrical, with the smaller often dying (Fig. 8). Parental care by female alone.

Two fledglings photographed (illustrated and described) on termite mounds on 10 November 2005 at Estancia Laguna Blanca, San Pedro department (Fig. 9; Smith *et al.* 2006). Guest *et al.* (2020) described distraction displays by females at Agroforestal Río Verde, San Pedro department on 27 September 2014 (nest or chicks not located) and on 27 October 2015 when a known nest was approached.

Departments.—Canindeyú, San Pedro.

Extreme dates.—Courtship display: late August–December. Eggs: 25 September–29 November. Chicks: 14 October–17 December. Fledglings: 10 November–early January.

Published extralimital reports.—None.

Comments.—A very local Cerrado endemic resident in Paraguay. The species' display was described by Clay *et al.* (2000).

LITTLE NIGHTJAR *Setopagis parvula*

Two nests each with two eggs on 12 October and 18 November collected during 1900–08 at Sapucái, Paraguari department, by William Foster and housed at NHMUK (E/1904.7.26.219–220 and E/1904.7.26.299–300) (Hayes 2014). These were described by Chubb (1910) as follows: 'Two eggs were obtained on the same date and another clutch on October 12, 1903. They are pale cream-coloured, blotched with brown and zigzag markings of the same colour, and with underlying blotches of lavender-grey. The measurements are: Axis 1.05 to 1.1 inches; diameter 0.8 [inches] [26.7–27.9 × 20.3 mm].' A female with developed (enlarged) gonads was collected on 18 October 1955 at 50 km south of Orloff, Boquerón department, indicating breeding activity (Steinbacher 1962).

Photograph of an egg and a chick on 23 October 1996 at Parque Nacional Serranía San Luis, Concepción department, by M. Robbins (Fig. 10). From the scale provided in the picture the egg was $c.27 \times 20$ mm and was very similar in colour to that described by Chubb (1910). Downy chick greyish, with irregular darker scrawls and apparently blackish bare skin. This is presumed to be the nest and young referred to in Robbins *et al.* (1999). Female specimen (NRM 947259) with brood patch collected at Estancia Apami, Amambay department, on 9 October 1994 (Ericsson & Sosa 2020). Two large fledglings at Parque Nacional Cerro Corá, Amambay department, on 1 October 2023 (F. Capli). Specimens reported by Foster & Johnson (2017) at Hotel El Tirol, Itapúa department. Testes of males enlarged (12–15 × 5–7 mm) September to December. Female with white shelled egg (25 × 19 mm) in oviduct in September and enlarged oviduct and 7 mm ovum in October. Females in January with smooth or post-breeding ovaries. Mated pair in September.

Nest with two eggs photographed on 5 November 2022 at Asunción Bay, Central department. Eggs were not measured; although there was a noticeable difference in size, their coloration and density of markings were similar (AJL; Fig. 11). Fledglings capable of flight observed at night at Fortín Toledo, Boquerón department, on 8 December 2022 (PS). Fledgling photographed at Cerro Corá National Park, Amambay department, by E. Romero on 29 September 2023 (<https://www.inaturalist.org/observations/191621329>). Fledgling photographed at Reserva Privada Yerba Selecta, Bella Vista Sur, Itapúa department, on 14 October 2024 by J. Pereira (<https://macaulaylibrary.org/asset/615755630>).



Figure 10. Chick and egg of Little Nightjar *Setopagis parvula*, Parque Nacional Serranía San Luis, Concepción department, Paraguay, 23 October 1996 (Mark Robbins)



Figure 11. Nest and eggs of Little Nightjar *Setopagis parvula*, Asuncion Bay, Central department, Paraguay, 5 November 2022 (Arne Lesterhuis)

Departments.—Amambay, Boquerón, Central, Concepción, Itapúa, Paraguari.

Extreme dates.—Enlarged gonads: September–December. Eggs: 9 October–18 November. Chick: 1–23 October. Fledglings: 29 September–8 December.

Published extralimital reports.—Argentina: Friedmann (1927), Smyth (1928), Pereyra (1938), Klimaitis (1975), Baliño (1984), de la Peña (1987, 2005), Di Giacomo (2005), Salvador & Bodrati (2013). Bolivia: Brace & Hornbuckle (1998). Brazil: Fry (1970), Belton (1984), Melo *et al.* (2000), Marini *et al.* (2012). Colombia: Hilty & Brown (1986). Uruguay: Gore & Gepp (1978).

Comments.—Purportedly resident in Paraguay, but numbers vary considerably over the year and poorly understood local movements clearly occur (Smith 2016). The species seems to be less common in winter, suggesting at least partial migration. Measurements of Paraguayan eggs ($25.0\text{--}27.9 \times 19.0\text{--}20.3$ mm) are consistent with the range given for this species ($24.0\text{--}28.8 \times 18.2\text{--}21.0$ mm) by Cleere & Nurney (1998).

LONG-TRAINED NIGHTJAR *Hydropsalis forcipata*

No concrete evidence of breeding, but a male (possibly the same individual) held a territory at the same precise locality, Zanja de Pirapó, Itapúa department, from 23 September 2014 (Hostettler & Smith 2014) until at least 17 August 2024 (A. Vera) and was very responsive to playback. Males are known to be highly faithful to display arenas where they breed in Argentina and Brazil (Olmos & Rodrigues 1990, Bodrati & Cockle 2012). A female was photographed nearby on 11 November 2024 by M. Saldívar.

Departments.—Possibly Itapúa.

Extreme dates.—Territory: 17 August–23 September.

Published extralimital reports.—Argentina: Bodrati & Cockle (2012). Brazil: Santos Morães & Krul (1995), Pichorim (2002).

Comments.—Status in Paraguay uncertain. Generally considered to be resident across its range, but there are very few records from Paraguay, and these are all from the breeding season. Probably under-recorded, the population is undoubtedly small, but species may be expanding its range in Paraguay.

SPOT-TAILED NIGHTJAR *Hydropsalis maculicaudus*

No reports of breeding in Paraguay.

Published extralimital reports.—Brazil: Snethlage (1935), Nacinovic (2018), Studer & Crozariol (2025). Colombia: (Hilty & Brown 1986). French Guiana: Ingles *et al.* (2010). Guyana: Penard & Penard (1910). Mexico: Zimmerman (1957), Binford (1989), Moreno *et al.* (2014). Nicaragua: Howell (1972). Suriname: Haverschmidt (1968, 1972), Haverschmidt & Mees (1994).

Comments.—Known from only a handful of Paraguayan localities in Alto Paraguay (July), Alto Paraná (undated), Amambay (June), Canindeyú (September), Caazapá (September, October), San Pedro (May) and Central departments (December) (Bodrati & Areta 2010). Southern South American populations are typically considered resident, however there is no evidence of the species' regular occurrence in Paraguay, and all reports involve single records at each locality. Indeed, all published breeding reports of the species are from north of the equator. Nevertheless, the presence of displaying and singing birds during the probable breeding season in Canindeyú (17–19 September), Caazapá (6 October) and Central departments (14 December) clearly indicates nesting could occur, but the lack of confirmation suggests the species is a vagrant or perhaps undergoing expansion.



Figure 12. Nest with two trampled eggs of Scissor-tailed Nightjar *Hydropsalis torquata*, Tujukua, Cordillera department, Paraguay, 19 October 2024 (Dominic Oviedo-Löwen)

SCISSOR-TAILED NIGHTJAR *Hydropsalis torquata*

A nest with two eggs amongst rocks at Tujukua, Cordillera department, on 19 October 2024 (Fig. 12). The female was attending the nest and spread its wings in distraction display. It was also observed to cover the eggs with the right wing. The nest was unfortunately trampled by a dog during the observation (DOL).

Departments.—Cordillera.

Extreme dates.—Eggs: 19 October.

Published extralimital reports.—*H. t. furcifer* Argentina: Alonso (1974), Baliño (1984), de la Peña (1987), Pautasso & Cazenave (2002), Quiroga & Navarro (2020). Brazil: Belton (1984), Vasconcelos (1999). Uruguay: Gore & Gepp (1978).

Comments.—For such a common and conspicuous species, surprisingly little is known about breeding. Indeed, the species' status in Paraguay is far from clear. The vast majority of records are during April–October, suggesting the bulk of the population is migratory (or on passage), but small numbers are present in the Chaco and Paraguay River basins during the breeding season and some of these evidently attempt to breed.

OCELLATED POORWILL *Nyctiphrynus ocellatus*

Nest with two uniformly cinnamon chicks photographed at Reserva Natural Tapytá, Caazapá department, on 18 September 2015 (Fig. 13). The attending adult performed a distraction display when the nest was approached, flapping along the ground with wings and tail spread as if injured (Fig. 14), before flying up to a low perch and drooping the wings (L. Pérez de Molas). Nest with two immaculate pinkish-white eggs (25 × 17–18 mm) on 29 September 2024 at Estancia Nueva Gambach, Itapúa department (PS). At the same site a distraction display was



Figure 13. Chicks of Ocellated Poorwill *Nyctiphrynus ocellatus*, Reserva Natural Tapytá, Caazapá department, Paraguay, 18 September 2015 (Lidia Pérez de Molas).



observed on 18 September, which may coincide with the early egg-laying period (RS). On 29 September at c.10.00 h, a rufous-morph female flushed with exaggerated flight, in the same place where the bird had previously flushed. The bird clattered clumsily and conspicuously through the vegetation and landed on a liana in cover c.6 m away (PS). On inspection of the area where it flushed, two white eggs with a pale pinkish tinge were found in leaf litter at the edge of the trail at the base of a tree (Fig. 15). The eggs measured 25×17 and 25×18 mm, respectively, and the flattened area where they were located measured c.120 $\times$ 100 mm in the leaf litter. After nightfall on the same day a male was photographed on the nest at c.21.15 h (A. Vera). On 3 October the female was again present incubating at 11.00 h, but allowed much closer approach, refusing to fly even when the observer was within 1 m for several minutes. It was hypothesised that the eggs may have hatched or been close to hatching, reflected in the increased investment by the sitting female. Females are exceptionally well camouflaged amongst leaf litter by day, with their rufous plumage blending into the background, and spotting helping to break up the outline. The eggs were



Figure 14. Adult female Ocellated Poorwill *Nyctiphrynus ocellatus* performing distraction display, Reserva Natural Tapytá, Caazapá department, Paraguay, 18 September 2015 (Lidia Pérez de Molas)

Figure 15. Nest and eggs of Ocellated Poorwill *Nyctiphrynus ocellatus*, Estancia Nueva Gambach, Itapúa department, Paraguay, 29 September 2024 (Paul Smith)

still present on 6 October at 15.00 h with the female sitting. By 12 October only one egg was present, and on 15 October none was found.

Departments.—Caazapá, Itapúa.

Extreme dates.—Eggs: 18?/29 September–17 October. Chicks: 18 September.

Vocalisations.—During long-term studies at Reserva Bosque Mbaracayú, Canindeyú department, singing began in August (intensifying towards the end of the month) and had ceased by mid-October (approximating to the nesting period). Occasional vocalisations were reported year-round (e.g., June 1995, January, June, July 1996).

Published extralimital reports.—*N. o. ocellatus* Argentina: Bodrati *et al.* (2010), Baigorria & Bodrati (2013). Brazil: Bokermann (1978), Silva *et al.* (2006), Lima *et al.* (2008), Kirwan (2009). Ecuador: Hill & Greeney (2000). Peru: Raine (2007).

Comments.—Resident in Paraguay. Few nests have ever been reported, but data from Paraguay are broadly consistent with observations in neighbouring Argentina and Brazil and support a suggested breeding season south of the equator from September–December, i.e., the warmest and wettest period of the year (Silva *et al.* 2006, Kirwan 2009, Bodrati *et al.* 2010). The clutch of two eggs and propensity to nest close to trails is consistent with previous observations (Anderson 2000, Kirwan 2009), although the latter is probably an artefact of the fact that such nests are more easily found.

The behaviour of a sitting female in Ecuador in response to approaching observers, reported by Hill & Greeney (2000), was remarkably similar to that we observed, with the adult first flushing into cover a short distance away but later becoming 'comfortable' with their presence and permitting extremely close approach. Silva *et al.* (2006) suggested that such increased confidence is shown by the sitting bird as hatching approaches, which is also consistent with our findings.

Egg colour reported by Hill & Greeney (2000)—pale tan with a hint of orange and sparsely blotched with tan at the thicker end—and their estimated size (larger at 32 × 19 mm) differed from those in Paraguay. The egg colour we observed is much closer to that in southern Brazil, described as immaculate yellowish white by Bokermann (1978). However, slightly darker markings were reported on eggs of Brazilian birds by Sick (1997), Silva *et al.* (2006) and Lima *et al.* (2008). The two eggs in the Itapúa department nest (25 × 17–18 mm) were at the lower range of the length previously reported, and slightly narrower than those previously documented at 26.2 mm (25.2–28.0 mm) × 19.8 mm (19.0–20.5 mm) (Schönwetter 1966). Bokermann (1978) reported egg mass as 5.4 and 5.5 g for an August nest in Mato Grosso, Brazil.

Silva *et al.* (2006) mentioned that both sexes incubate the eggs in Espírito Santo, Brazil, with the female present at least during the morning hours (pre-midday) and a single observation of the male incubating after dark, suggesting that the sexes follow different routines. This is consistent with our observations.

Note that the nest report for this species from Canindeyú department by Madroño-Nieto & Esquivel (1997) actually corresponds to *Antrostomus rufus* (Bodrati & Baigorria 2013; see below for additional unpublished data).

SILKY-TAILED NIGHTJAR *Antrostomus sericocaudatus*

Bertoni (1919) reported finding 'several nests with two white eggs' at Puerto Bertoni and 'Ighuasú', Alto Paraná department, but provided no further data. An incubating adult was flushed from a nest on 10 November 2017 and a single downy chick (Fig. 16) estimated at 12–15 days old was present on 5 December 2017 at Estancia Nueva Gambach, Itapúa department (Smith & Smith 2024). The authors hypothesised that laying took place around 1–4 November and hatching around 20–23 November.

Departments.—Alto Paraná, Itapúa.

Extreme dates.—Eggs: 1–10 November? Chicks: 20? November–5 December.

Published extralimital reports.—*A. s. sericocaudatus* Argentina: Partridge (1956), Chebez *et al.* (1988), Krauczuk (2013), Bodrati & Cockle (2018).

Vocalisations.—During long-term studies at Reserva Bosque Mbaracayú, Canindeyú department, vocalisations were detected from mid-July and continued until mid-September. Occasionally also heard in February, March and May.

Comments.—Presumably resident in Paraguay, but the species is difficult to detect when it is not vocalising.



Figure 16. Chick of Silky-tailed Nightjar *Antrostomus sericocaudatus*, Estancia Nueva Gambach, Itapúa department, Paraguay, 5 November 2017 (Rebecca Smith)

RUFOUS NIGHTJAR *Antrostomus rufus*

Distraction display observed by a nesting bird ‘fluttering along on the ground’ at ‘forest edge near a weed field’ at noon near Hotel Tirol, Itapúa department, on 4 November 1981 (Foster & Johnson 2017). Broken eggshell with ‘cream-colored background with irregular light brown markings’ collected (MVZ 13597: <https://arctos.database.museum/guid/MVZ:Egg:13597>) but no chick was found.

Nest with a single egg (undescribed) on 17 October 1997 in a ‘patch of low forest close to flooded forest’ at Reserva Natural Bosque Mbaracayú, Canindeyú department (Madroño-Nieto & Esquivel 1997). Ascribed by the authors to *Nyctiphrynus ocellatus*, but actually corresponds to *Antrostomus rufus* (Bodrati & Baigorria 2013). The egg was ‘white with violaceous spotting.’

Nest with two eggs (not described) located following a distraction display at Reserva Natural Bosque Mbaracayú, in low forest on the Arroyo Morotí trail, 30 September 2015 (Guest *et al.* 2020). Distraction display ‘near a chick’ photographed on 17 October 2020 at Parque Nacional Serranía San Luís, Concepción department by L. Recalde (<https://macaulaylibrary.org/asset/272864071>), and a photograph of the chick is available.

Departments.—Canindeyú, Concepción, Itapúa.

Extreme dates.—Eggs: 30 September–4 November. Chick: 17 October.

Published extralimital reports.—*A. r. rutilus* Argentina: Hartert & Venturi (1909), Ihering (1914), Salvador *et al.* (2014). Brazil: Ihering (1914), Maurício *et al.* (2013).

Vocalisations.—During long-term studies at Reserva Bosque Mbaracayú consistent vocal activity was recorded from mid-August until the second half of November, with greatest activity during the full moon and little or none on moonless nights. The vocal period possibly ends earlier in the Atlantic Forest (late October) than in the Cerrado (second half of November). Calling also ceased during rainy periods. During 1996 singing began earlier, in late June.

Comments.—A widespread and fairly common resident in Paraguay.

Family Nyctibiidae (potoos)

GREAT POTOO *Nyctibius grandis*

The only breeding report in Paraguay was of a nesting bird at Estancia Kamba Akâ, Alto Paraguay department, on 16 September 1997 (Clay *et al.* 1998, Capper *et al.* 2001, Guyra Paraguay 2004). The nest was 7 m above ground in an emergent tree (height 10 m) 2 m higher than the scrub-forest canopy and 5 m from a track. A single large white egg was located in the depression left by a broken branch immediately adjacent to the main trunk. A photograph of the nest taken by C. P. Kennedy appeared in Clay *et al.* (1998). The locality was originally reported erroneously as Estancia Campo Grande (Clay *et al.* 1998, Capper *et al.* 2001) but was corrected in Guyra Paraguay (2004).

Departments.—Alto Paraguay.

Extreme dates.—Eggs: 16 September.

Published extralimital reports.—*N. g. grandis* Brazil: Euler (1900), Sick (1951), Lopes *et al.* (2013), Pérez-Granados & Schuchmann (2020), Studer & Crozariol (2025). Colombia: Hilty & Brown (1986). Ecuador: Cisneros-Heredia (2006). Guyana: Penard & Penard (1908). Suriname: Haverschmidt (1948). Venezuela: Van der Werf (1988), Navarro *et al.* (2011).

Comments.—Presumably resident in Paraguay, but known from only a handful of mostly undocumented records in the extreme northern Chaco of Paraguay, in Alto Paraguay department. Often considered monotypic (Cohn-Haft 1999) but Holyoak (2001) recognised two subspecies. Here we include only breeding reports attributed to the nominate in South America, rather than the geographically more distant *N. g. guatemalensis* in Central America.

LONG-TAILED POTOO *Nyctibius aethereus*

Breeding documented 1.5 km east of Jejuí-Mi, Reserva Natural Bosque Mbaracayú, Canindeyú department, between late August and November 1995 (Madroño-Nieto &



Figure 17. Incubating adult Long-tailed Potoo *Nyctibius aethereus*, 1.5 km east of Jejuí-Mi, Reserva Natural Bosque Mbaracayú, Canindeyú department, Paraguay, August/November 1995 (Alberto Madroño)

Esquivel 1997; Fig. 17). The nest was in the knot of a *Chorisia* sp. tree (Bombacaceae) c.10 m above ground and was first observed on 29 August 1995, when an adult was possibly incubating. A small white chick was visible on 9 October 1995, when feeding was observed and considerable vocal activity was heard in the vicinity (barking calls and typical *Uáaaaauu* song). On 10 October 1995 the eyes of the chick were open and the primary feather sheaths were observed to be long. When unattended by the adults the chick lay flattened against the tree. Both adults took turns to tend the chick, although it was also left unattended for short periods. The chick was still present on 12 October (when it was fairly large and the tail was noted to be of median length) but had left by some point on or prior to 19 October. A month later on 20 November 2025 the fledgling was observed within 30 m of the nest. The tail was not yet full length, and the head was a paler than that of the adults. It was probably still dependent on the adults for food.

Departments: Canindeyú.

Extreme dates: Eggs: late August. Chick: 9–12 October; Fledgling: 19 October–20 November.

Published extralimital reports: *N. a. aethereus* none.

Vocalisations.—During acoustic surveys at Reserva Natural Bosque Mbaracayú vocalisations were heard from 29 August 1995 until mid-January 1996. On 30 August 1995 an individual gave a loud *Uáaaaauu* call four times between 04.14 and 04.54 h (c.20 minutes before sunrise), however the birds did not vocalise close to the nest when the egg was present. On 8 (full moon) and 10 September 1995 two were observed (perhaps a pair?) in possible territorial flights during which they gave multiple barking calls. On 11 September 1995 contact barks were heard at 03.30 h and an individual was observed incubating at 04.30 h. At 05.03 h a *meow* call was heard near the nest and a few minutes later a bird approached in flight giving a barking call, followed by a changeover with the sitting bird. Vocalisations were heard near the nest following hatching.

Comments.—Anti-predator behaviour (elevating the head to point skywards) was observed by incubating adults in the presence of Plush-crested Jay *Cyanocorax chrysops* (29 August 1995) and Swallow-tailed Kite *Elanoides forficatus* (11 September 1995). An individual captured an insect on the ground shortly after finishing its incubation duties at 17.57 h on 9 October 1995.

A photograph of a nesting bird at Zanja Morotí, Concepción department and identified as this species in Laubmann (1940: 16) is in fact a Common Potoo *N. griseus* (see below) based on the relatively short tail, the lack of a white shoulder patch and the clear black moustachial stripe.

A rare resident in the Atlantic Forest of the Oriental region in Paraguay.

COMMON POTOO *Nyctibius griseus*

First breeding report by Padre Blas Nosedá in Azara (1805) who collected a bird on 29 November (year not stated), possibly close to San Ignacio Guazú, Misiones department, where he was the parish priest. The nest had been located two days earlier by an unnamed individual who noted it was sitting on two brown spotted eggs ('pardos salpicados'). The eggs were already broken and had been abandoned when the bird was collected. The eggs were described as sited in a small hollow on a dry branch, a third of the way up the tree, and the nest lacked any material or lining. The female was on the nest and the observer was able to touch her while incubating. The report of two eggs would be highly anomalous and potentially erroneous for a potoo, but this was a secondary account by an untrained observer.



Figure 18. Nest and egg of Common Potoo *Nyctibius griseus*, Coronel Bogado, Itapúa department, Paraguay, 21 November 2012 (Paul Smith)

Figure 19. Nest of Common Potoo *Nyctibius griseus* with a single large chick, Refugio Biológico Mbaracayú, Canindeyú department, Paraguay, 22 February 2021 (Oscar Rodríguez)

Laubmann (1940) illustrated a bird incubating an egg in early December 1931 at Zanja Morotí, Concepción department, which he erroneously identified as a Long-tailed Potoo. The nest was on a fence post but was predated by a flock of Plush-crested Jays *Cyanocorax chrysops* a few days later (Laubmann 1940). A male and female with enlarged gonads were collected on 14 January 1957 at Orloff, Boquerón department, indicating breeding activity (Steinbacher 1962).

A nest with a downy chick and sitting adult at Aguara Ñu, Reserva Natural Bosque Mbaracayú, Canindeyú department on 11 November 2000 (AJL). A nest with a single white egg with irregular pale brownish-purple flecks and blotches in a forest island on the road to Isla Alta, near the town of Coronel Bogado, Itapúa department, on 21 November 2012 (Fig. 18). The nest was in the top part of a rotting fence stump at a height of 175 cm, with the unlined cup measuring 75 × 85 mm. An adult was incubating the egg (dimensions 43 × 29 mm; PS). A nest with a single white egg with darker speckling was photographed at Agroforestral Río Verde, San Pedro department, on 28 December 2016 by J. Dickens (<https://macaulaylibrary.org/asset/46030361>). Three specimens reported by Foster & Johnson (2017) at Hotel El Tirol, Itapúa department, in October. Two males with testes 10 × 8–9 mm. Female with largest ovum yolked and 25 mm diameter, and two unyolked (3.5 mm diameter). Oviduct greatly enlarged. Nest with adult and chick at Refugio Biológico Mbaracayú (Itaipú Reserve), Canindeyú department, on 19 February 2019 by S. D. Ríos. Fledgling photographed at Parque Nacional Ybycuí, Paraguari department, on 12 January 2020 by L. Recalde (<https://macaulaylibrary.org/asset/199111901>) and an adult at a nest with a small chick also there on 14 December 2019, photographed by E. Romero (<https://macaulaylibrary.org/asset/193356841>). Nest with an egg and sitting adult at Aguara Ñu, Reserva Natural Bosque Mbaracayú, Canindeyú department, on 18 October 2020, photographed by O. Rodríguez (<https://macaulaylibrary.org/asset/272582271>). Nest with a single large chick attended by a rufous-morph adult at Refugio Biológico Mbaracayú, Canindeyú department, on 22 February 2021 photographed by O. Rodríguez (Fig. 19). Nest with a single large chick near the lagoon at Estancia Nueva Gambach, Itapúa department, on 6–7 January 2023 (A. Vera).

Departments.—Boquerón, Canindeyú, Concepción, Itapúa, Misiones?, Paraguari, San Pedro.

Extreme dates.—Enlarged gonads: 14 January. Eggs: 17 October–28 December. Chicks: 14 December–22 February. Fledgling: 12 January.

Published extralimital reports: *N. g. griseus* Argentina: Saibene (1987), de la Peña (2011, 2019), Moresco (2019), Quiroga & Llugdar (2019), de Boever *et al.* (2023). Brazil: Goeldi (1896, 1902), Euler (1900), Ihering (1900, 1914), Santos (1942), Pinto (1953), Teixeira *et al.* (1983), Belton (1984), Sick (1993), Lopes & dos Anjos (2005), Mendonca *et al.* (2009), Corbo & Maccarão (2010), Cestari *et al.* (2011, 2018), Sazima (2011), Marini *et al.* (2012), Lopes *et al.* (2013), Maurício *et al.* (2013), Nacinovic (2018), Pérez-Granados & Schuchmann (2020), Studer & Crozarior (2025). Colombia: Friedman & Smith (1950), Borrero (1970), Hilty & Brown (1986). Ecuador: Greeney *et al.* (2008). Suriname: Haverschmidt (1958), Haverschmidt & Mees (1994). Trinidad: Muir & Butler (1925), Belcher & Smooker (1936), Snow & Snow (1964), French (1991). Uruguay: Azpiroz (2001). Venezuela: Tate (1994).

Vocalisations.—During long-term studies at Reserva Bosque Mbaracayú, Canindeyú department, vocal activity began in early to mid-September around full moon (occasionally in late August), continuing until mid-November. Song was also heard occasionally during January to mid-February, but usually only briefly. No vocal activity occurs from May–July.

Comments.—Present year-round, but numbers clearly augmented at times as a result of poorly understood movements (DeGroot *et al.* 2020). The measurement of the only Paraguayan egg for which data are available (43×29 mm) is longer than the range given for the species ($35.9\text{--}41.5 \times 25\text{--}32$ mm) by Cleere & Nurney (1998). Fiebrig (1921) provided some general information about this species' breeding in a Paraguayan context.

Discussion

Breeding data are provided for eight species of nightjar and three species of potoo. Nearly all records are from the Oriental region of Paraguay, with just one in the Chaco region west of the Paraguay River. The following species are migratory and do not breed in the country: Lesser Nighthawk *Chordeiles acutipennis*, Common Nighthawk *C. minor* and Band-winged Nightjar *Systellura longirostris bifasciata*. A statement by Padre Blas Nosedá in Azara (1805) that the Common Nighthawk ('Ybyyau Jaspeado') nests on the ground in Paraguay is clearly a case of mistaken identity. The species is a Nearctic migrant that breeds in the Northern Hemisphere.

No breeding data are available for five species: *Nyctiprogne leucopyga*, *Hydropsalis forcipata*, *H. maculicaudus*, *Eleothreptus anomalus* and *Lurocalis semitorquatus*. Spot-tailed Nightjar may breed, but is known from very few records and it may be a vagrant or a species that is only recently expanding its range into Paraguay. Long-trained Nightjar probably breeds based on the presence of a territory-holding male and observations of a female in the vicinity, but again concrete proof is lacking. The other three species certainly do breed, but documentation is non-existent. The status of Scissor-tailed Nightjar in Paraguay is uncertain. It is common in winter and on passage, but there are few records in the breeding season and it may breed only in small numbers or do so only opportunistically.

Breeding data for Paraguayan Caprimulgiformes is highly seasonal and concentrated between late August and January, corresponding to the Southern Hemisphere spring and early summer. This is the warmest and wettest period of the year, and breeding at this time is expected given the various species' largely insectivorous diets.

Observations of incubation by both sexes in two species (*Nyctidromus albicollis* and *Nyctiphrynus ocellatus*) with grey and rufous morphs raise some interesting questions. In both cases the rufous-morph female was observed incubating by day (when they are well camouflaged against the leaf litter) and the duller grey-morph male was present after

TABLE 1

Comparative egg data for Paraguayan Caprimulgidae and Nyctibiidae that are confirmed to breed or likely to do so. Species omitted as being non-breeders are Lesser Nighthawk *Chordeiles acutipennis*, Common Nighthawk *C. minor* and Band-winged Nightjar *Systellura longirostris bifasciata*. Under ‘egg measurements’ Py = extreme measurements for Paraguayan eggs and is compiled from data provided in the main text. G = extreme measurements globally, from Cleere & Nurney (1998) and Holyoak (2001) unless otherwise stated. * As previously noted by Schönwetter (1966), in comparison to other potoos, the dimensions of this single egg (from French Guiana) appear small for the size of the bird and should perhaps be treated with caution; in any case, this measurement would refer to *N. a. longicaudatus* and the subspecies present in Paraguay is *N. a. aethereus*.

	Eggs	Egg measurements	Departments with breeding records
CAPRIMULGIDAE			
<i>Chordeiles nacunda</i>	Buff-coloured, heavily marked with irregular reddish-brown and dark brown mottling	Py: 34.3–36.8 × 22.9–26.7 mm (<i>n</i> = 7) G: <i>C. n. nacunda</i> 33.5–38.4 × 23.5–27.7 mm (Salvador & Bodrati 2017)	Boquerón, Itapúa, Paraguari
<i>Nyctiprogne leucopyga</i>	Cream or buff with small dark spots and lines (Snethlage 1935)	Py: no information G: subspecies not stated 26.6–27.7 × 19.8–20.3 mm (Schönwetter 1966)	No confirmed breeding records
<i>Lurocalis semitorquatus</i>	Whitish, speckled brown and grey, or pale blue streaked chestnut (Straneck <i>et al.</i> 1987)	Py: no information G: <i>L. s. nattereri</i> no information	No confirmed breeding records
<i>Nyctidromus albicollis</i>	Greyish pink to creamy, spotted and blotched pinkish brown with underlying marks of lavender-grey	Py: 27.9–31.8 × 20.0–22.9 mm (<i>n</i> = 10) G: <i>N. a. derbyanus</i> 27.8–32.7 × 20.3–23.5 mm	Caazapá, Canindeyú, Central, Concepción, Guairá, Itapúa, Paraguari, San Pedro
<i>Hydropsalis forcipata</i>	Pinkish blue, speckled chestnut and buff (Cleere & Nurney 1998)	Py: no information G: 28.4–31.5 × 21.0–22.6 mm	No confirmed breeding records
<i>Hydropsalis maculicaudus</i>	Buff or creamy pink, spotted or flecked reddish brown and pale lilac, markings heavier at blunt end (Cleere & Nurney 1998)	Py: no information G: 23.1–26.1 × 16.5–19.6 mm	No confirmed breeding records
<i>Hydropsalis torquata</i>	Pale brown, creamy white or pinkish buff, scrawled or spotted with darker brown and grey (Belton 1984, de la Peña 1987)	Py: no information G: <i>H. t. furcifer</i> 24.6–30.8 × 17.9–22.6 mm	No confirmed breeding records
<i>Eleothreptus anomalus</i>	Creamy white with reddish-brown patches and spots, and grey patches of variable size over the entire surface (Bodrati <i>et al.</i> 2019)	Py: no information G: 25.8–30.0 × 20–21.9 mm (Bodrati <i>et al.</i> 2019)	No confirmed breeding records
<i>Eleothreptus candicans</i>	Pale cream-beige, with variable dark brown and mauve-grey speckling and blotching (Pople 2014)	Py: 26.7–29.9 × 19.8–21.7 mm (<i>n</i> = 16) G: as above (Pople 2003, 2014, Clay <i>et al.</i> 2014)	Canindeyú, San Pedro
<i>Setopagis parvula</i>	Pale cream-coloured, blotched brown and zigzag markings of the same colour, with underlying blotches of lavender-grey	Py: 26.7–27.9 × 20.0–20.3 mm (<i>n</i> = 4) G: 24–28.8 × 18.2–21.0 mm (Schönwetter 1966)	Amambay, Boquerón, Central, Concepción, Itapúa, Paraguari

	Eggs	Egg measurements	Departments with breeding records
<i>Nyctiphrynus ocellatus</i>	Immaculate pinkish white, sometimes faintly spotted reddish, brownish or grey	Py: 25 × 17–18 mm (<i>n</i> = 2) G: <i>N. o. ocellatus</i> 25.2–28.0 × 19.0–20.5 mm (Schönwetter 1966)	Canindeyú, Itapúa
<i>Anrostomus sericocaudatus</i>	Immaculate white (Bodrati & Cockle 2018)	Py: no information G: <i>A. s. sericocaudatus</i> 26–32 × 18–23 mm (Bodrati & Cockle 2018)	Alto Paraná, Itapúa
<i>Anrostomus rufus</i>	Cream-coloured background with irregular pale brown markings (Salvador <i>et al.</i> 2014)	Py: no information G: <i>A. r. rutilus</i> 32.7 × 23.9 and 32.3 × 24.2 mm (Salvador <i>et al.</i> 2014)	Canindeyú, Concepción, Itapúa
NYCTIBIIDAE			
<i>Nyctibius grandis</i>	White, spotted brown and lilac-grey, markings concentrated at blunt end	Py: no information G: <i>N. g. grandis</i> 52.1–60.0 × 38.3–44.0 mm	Alto Paraguay
<i>Nyctibius aethereus</i>	No information	Py: no information G: <i>N. a. longicaudatus</i> 38.2 × 26 mm*	Canindeyú
<i>Nyctibius griseus</i>	White egg with irregular pale brownish-purple flecks and blotches	Py: 43 × 29 mm (<i>n</i> = 1) G: <i>N. g. griseus</i> 35.9–41.5 × 29–32 mm	Boquerón, Canindeyú, Concepción, Itapúa, Misiones?, Paraguari, San Pedro

dark (when it is perhaps harder to detect?). Nocturnal incubation by males and diurnal incubation by females has been previously reported in *Nyctiphrynus ocellatus*, but in *Nyctidromus albicollis* diurnal incubation by males has been reported. Whether or not these daily cycles are chosen preferentially by pairs with a rufous morph, to reflect the more effective camouflage provided by such birds by day perhaps merits study when more data become available.

We provide evidence of nest relocation by a *Nyctidromus albicollis* at Isla Yacyretá in November 2024. There has been considerable dispute as to whether caprimulgids can relocate their nests, with much of the discussion centring on whether or not the adults are able to transport eggs and chicks (Cleere & Nurney 1998). Cleere & Nurney (1998) stated that ‘nightjars may occasionally move an egg a short distance by pushing it with its bill e.g., if an egg has become dislodged from the nest site.’ We consider that the distance the nest in question was moved constitutes more than mere re-accommodation of dislodged eggs, and can be interpreted as deliberate relocation of a nest subject to disturbance, with the nest being gradually moved into denser cover. Movements took place over several days involving both eggs and hatchlings, until they could no longer be refound by the observers. It is perhaps relevant that these ground-nesting birds rely on crypsis for protection, but when detected they are seriously vulnerable, thus theoretically requiring additional protective measures. Many species perform distraction displays, but if successful these still represent a violation of the initial crypsis tactic as any potential predator could return. Given this, relocation to denser vegetation might be a sensible response. Two factors make this an evolutionarily ‘cheap’ solution: (1) because there is no investment in nest structure, eggs are laid directly onto the ground; and (2) the eggs are distinctly ovaloid rather than pointed towards the tip, so they can be rolled in a straight line. Whether chicks are transported or are merely encouraged to move by calling adults is unknown, but both may be true, with newly hatched chicks requiring transportation and larger chicks able to move of their own accord. The rarity of observations of the former is unsurprising given the semi-precocial

nature of chicks, meaning that they are totally dependent on their parents for only a very brief period post-hatching.

Finally, we highlight the number of Paraguayan nest reports that lack even basic data and we urge field workers and citizen scientists to take full advantage of such finds by collecting as many data as possible (while taking care to mitigate potential disturbance). Measurements of eggs and/or chicks should be taken and nests monitored, with any data published or made publicly available via a citizen science website.

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Notes on the breeding biology of Fuegian Snipe *Gallinago stricklandii* in northern Patagonia

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SUMMARY. — Fuegian Snipe *Gallinago stricklandii* is one of the least-known Neotropical snipes; its breeding biology is almost entirely undescribed. We describe the third nest ever recorded and the first away from Cape Horn, reporting nest dimensions, composition, concealment, and egg morphology, all of which are consistent with historical records. We also report new information on breeding habitat, nest structure, egg characteristics, incubation period and phenology based on a separate nest and brood in Parque La Tapera, the species' northernmost known breeding site. Camera traps revealed an incubation period of at least 25 days and confirmed the presence of both adults near the nest. Chicks were observed earlier than previously reported, suggesting a broader phenology and possible asynchrony within populations. These findings substantially expand our knowledge of the species' breeding biology and provide critical baseline information for conservation, particularly given its Near Threatened status and exposure to invasive predators.

The Neotropical region has eight of the 17 species of the genus *Gallinago* (snipes), many of which are poorly known. For several species only a single nest has been described (e.g., Imperial Snipe *G. imperialis*, Amigo *et al.* 2017; Andean Snipe *G. andina*, Ortiz & Aveldaño 2024). Fuegian Snipe *G. stricklandii* has the southernmost distribution of the Neotropical snipes, inhabiting the most remote areas of Patagonia (Chile and Argentina), including fjords and hard-to-access islands (van Gils *et al.* 2020). In this species, and those previously mentioned, many fundamental aspects of their natural history have yet to be elucidated, with some aspects such as the distribution and migration only recently and partially studied (Kusch & Marín 2010, Raimilla *et al.* 2023, Barroso *et al.* 2024, Michel *et al.* 2026), whilst breeding biology is almost undescribed.

Almost a century ago, on 11 December 1932, Reynolds (1935) found the first nest of Fuegian Snipe, with two eggs on Guffern Island (55°26'S, 68°03'W, Cape Horn), but the nest itself was not described. However, Reynolds provided meagre details of a second nest found on 16 December 1932, on Barnevelt Island (55°49'S, 66°47'W; Hermite Archipelago, Cape Horn), also containing two eggs and located over 'short, sparse rushes and grass on the high ground above the tussock'. The eggs from both nests were described as having 'ground-colour deep olive-buff spotted with cinnamon-brown', measuring 53.5 × 37.0 mm and 51 × 37 mm on Guffern Island and 55.0 × 36.5 mm and 53 × 38 mm on Barnevelt Island (Reynolds 1935).

Records of chicks (which are precocial like all snipes; Pereyra 1934) are also scarce and date from 17 November–23 January (Reynolds 1935, Olrog 1950, Kusch & Marín 2010, Barroso *et al.* 2024; S, Anselmino, <https://ebird.org/checklist/S299040810>), whilst juveniles have been recorded with adults between 19 December and 14 February (Barroso *et al.* 2024; S. Saiter, <https://ebird.org/checklist/S289251228>). Most of these records are from the south

of the species' range (e.g., Cape Horn), whereas almost no information for the north of the distribution exists, aside from the remarks of Raimilla *et al.* (2023), who suggested that incubation ends around early December, based on feathers regrowing over brood patches. Nothing else is known about the species' breeding biology and several basic aspects are unknown, e.g., nest structure, composition, and incubation period.

Considering that the species was recently reassessed as Near Threatened in Chile and that one threat is potential nest predation by the invasive American Mink *Neogale vison* (BirdLife International 2024), a better understanding of this snipe's breeding biology is needed. Here we provide new information on the breeding habitat, nest and egg descriptions, and phenology based on monitoring a nest of Fuegian Snipe in the northernmost known breeding area.

Field work and Methods

Field work was conducted in Parque La Tapera (Fig. 1), at the north end of the southern Patagonia ice field, during 10–13 October 2024. Parque La Tapera is a privately protected area of c.12,425 ha, between 48°07'S and 48°18'S (see Raimilla *et al.* 2023 for a more detailed description). Efforts focused on an area (48°14'S, 73°35'W) with previous records (Raimilla *et al.* 2023) and followed the same search methodology. Eight field ornithologists (the authors) walked in a line to flush birds, advancing in parallel no more than 2–3 m from each other. Our work was designed to capture two individuals with mist-nets, to deploy GPS and thereby gather information on the species' migrations (as part of ongoing research), but incidentally we documented two breeding events: an adult with a chick and an occupied

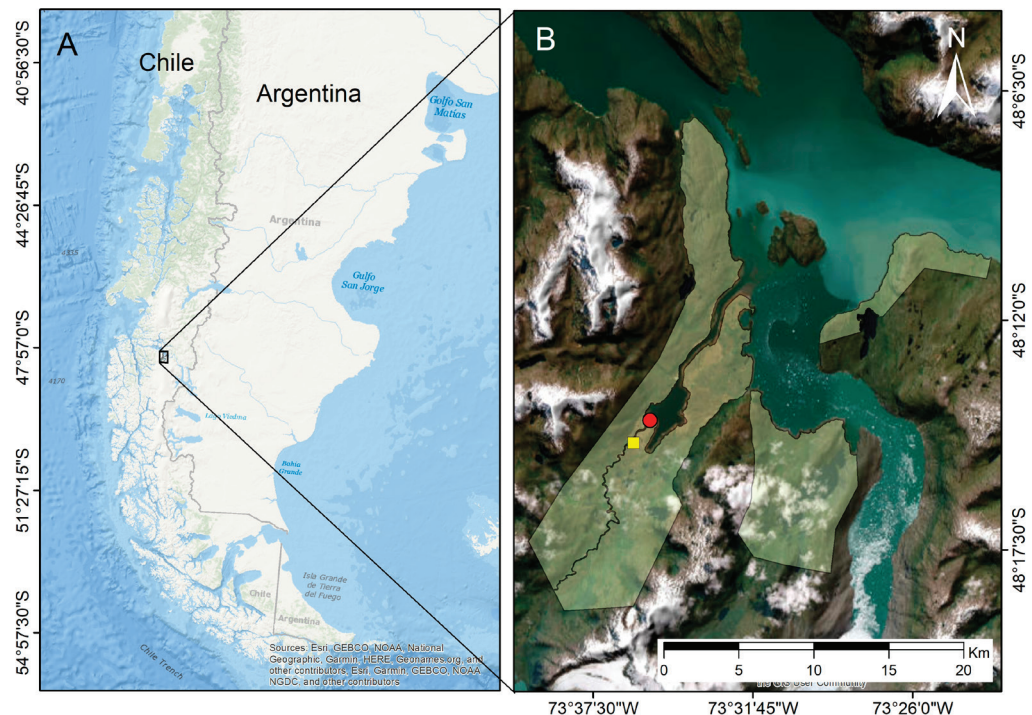


Figure 1. (A) Geographic location of the Jorge Montt fjord, Aysén region, Chile, and (B) location of the two breeding records of Fuegian Snipe *Gallinago stricklandii*: an adult with a single chick (red circle) and two adults attending an active nest (yellow square) in Parque La Tapera (green polygon). Map created using QGIS.

nest, distant from each other by 1.25 km (Fig. 1). We captured one individual from each pair and inspected the brood patch in both birds, but we took morphometrics for only one of them, as in the other case there was heavy rain and we needed to reduce bird-handling time.

Nest structure was assessed according to Simon & Pacheco (2005), thus we measured the dimensions of its internal and external cup, and described the nest's composition. To gauge the volume (V) of the eggs, we applied the formula $V = 0.51 \times (\text{length}) \times (\text{width})^2$ (Hoyt 1979). To describe vegetation surrounding the nest, we measured the height of the surrounding shrub stratum, distance from the nest to the nearest tree/shrub, and degree of nest concealment by estimating the upper vegetation cover within a 25 cm radius, from a perpendicular distance of 1 m above ground (Ralph *et al.* 1996). To estimate the remaining incubation period and periods of activity of the incubating birds around the nest, we installed two trail cameras 3 m from the nest at a height of 40–50 cm above ground. One camera was set to take photos and videos (Bushnell Trophy Cam Aggressor; three photos per event) and the other to take only photos (Browning Dark Ops Pro DCL Dual; five photos per event), deployed on 13 October, checked on 3 November and recovered on 16 December 2024.

Results and Discussion

On 11 October 2024, we captured an adult with a chick (Fig. 2a–b) in a meadow dominated by sparse rushes and grass, outside forest. The chick, of then unknown age, had a bill length of 18.0 mm, tarsus length 25.2 mm, bill–head length 45.0 mm and mass 37.99 g. The adult had a vascularised brood patch with several growing feathers.

On 12 October, we found an adult at a nest containing two eggs (Fig. 3), only the third nest of this species ever found (see Reynolds 1935) and the first in the northernmost breeding area, c.930 km from Cape Horn. The nest was on the ground and its materials did not differ from the vegetation in the surroundings, so we classified it as 'simple/unlined' (Simon & Pacheco 2005). The exterior cup measured 150 × 139 mm, the interior cup 90 × 88 mm, and the nest had a height of 47 mm. The cup comprised peat moss (*Sphagnum* sp.), reeds (*Marsippospermum grandiflorum*), a fern (*Austroblechnum penna-marina*) and an unidentified lichen. The nest was on the west side of the vegetation patch, at the foot of a Prickly heath (*Gaultheria* sp.) 0.56 m tall and a Chilean firetree (*Embothrium coccineum*) of 2.5 m, the latter 0.6 m away. Nest concealment was 65%, with cover provided by *Gaultheria* sp., *Escallonia virgata*, *Embothrium coccineum* and *Marsippospermum grandiflorum*. The two eggs were ovoid, pale brown with yellow undertones, abundant red-brown spots and somewhat fewer cinnamon-coloured spots, both more concentrated at the larger end. One



Figure 2. (a) Adult Fuegian Snipe *Gallinago stricklandii*, Parque La Tapera, Aysén, Chile, 11 October 2024 (Pablo Gutiérrez); (b) chick of Fuegian Snipe, Parque La Tapera, Aysén, Chile, 11 October 2024 (Benjamín Gallardo)



Figure 3. (a) Active brood patch on an incubating adult Fuegian Snipe *Gallinago stricklandii*, 12 October 2024 (Nelson Contardo); (b) nest structure and composition from above; note that the materials do not differ from the vegetational composition in the nest's surroundings, 12 October 2024 (Benjamín Gallardo); (c) eggs of Fuegian Snipe, Parque La Tapera, Aysén, Chile, 12 October 2024 (V́ctor Raimilla); (d) next day, 13 October 2024, an adult that might be incubating (the bird without GPS) was seen near the nest (V́ctor Raimilla)

measured 52×33 mm, volume 28.9 cm^3 and mass 32.24 g , and the other 51.2×34.1 mm, 30.4 cm^3 and 31.88 g . These data coincide with those previously reported by Reynolds (1935) for eggs on Guffern and Barnevelt Islands, Cape Horn.

Incubation at the nest we found spanned at least 25 days, from 12 October to 5 November, on which date two chicks were recorded by the trail cameras in the snow. This is more or less similar to the 19 days suggested for Pantanal Snipe *Gallinago paraguaiiae* (Colombo *et al.* 2021). In the following days, one chick was observed with an adult until 13 November (eight days after hatching). By comparing photographs of the newly hatched chicks to the other adult with a chick found on 11 October, we deduced that this chick was less than one week old. If this assumption is correct, and taking into account the 25-day incubation period, the eggs at the nest were probably laid in early September. The phenology differs from that described in the literature. We found chicks in mid-October, one month earlier than reported on Tierra del Fuego ($54^{\circ}25'S$, $71^{\circ}07'W$; Kusch & Marín 2010) and almost two months earlier than on Horn Island ($55^{\circ}58'S$, $67^{\circ}13'W$; Barroso *et al.* 2024). However, we also found a nest with similar phenology. Consequently, it appears this species does not necessarily nest synchronously at a given locality, and birds might start breeding earlier in Tierra del Fuego and Cape Horn as well. Olrog (1950) also suggested the possibility of second clutches. Further information is needed to understand whether latitude might affect the phenology of this snipe as it does many other species in Patagonia.

Although the relative contribution of each parent during incubation could not be estimated, it was confirmed that both were present or nearby during incubation at the nest with a trail camera, being distinguishable in the photos by the installed GPS antenna and

the ring. Unexpectedly, we found that the bird without a GPS was also ringed, it being one of those trapped 1.5 km away in December 2021 (Raimilla *et al.* 2023). Small territorial shifts have been confirmed for other Patagonian wetland birds, e.g., Austral Rail *Rallus antarcticus* (Galeto *et al.* 2025), as microhabitat features presumably may change between breeding seasons.

Our findings expand our knowledge of breeding phenology, nest structure and composition, and incubation period in *G. stricklandii*, aligning with what is known for other snipes. Use of camera traps could provide further information on this species' reproductive behavior, for example duration of incubation bouts or parental care of chicks, as recently reported for Austral Rail (Galeto *et al.* 2025).

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Notes on breeding by Changeable Hawk-Eagle *Nisaetus cirrhatus* in Gujarat, India

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SUMMARY.—We present new information on breeding by Changeable Hawk-Eagle *Nisaetus cirrhatus* based on a nest monitored using a solar-powered automated surveillance camera and direct observation, for 14 weeks from 20 March to 30 June 2025. The nest was sited in a *Terminalia bellirica* tree in Polo Forest, northern Gujarat, India. The female was incubating when we found the nest; the single egg hatched on 7 April 2025. The nestling period was ten weeks. We recorded 128 prey deliveries over ten weeks (mean 1.82 per day). Food delivered by the male comprised 51 reptiles (three species), 49 mammals (two species), 25 birds (17 species) and three unidentified prey items. The commonest prey species recorded were the lizard *Calotes vultuosus* and the squirrel *Funambulus pennanti*. Both adults tended the young, with the male bringing food to the nest and the female tearing off small pieces to feed the chick. Chick growth and ontogenetic behaviours were described. Additionally, the parents brought 70 sprigs/twigs of *Syzygium cumini* and *Terminalia bellirica* to the nest over 83 days, from incubation ($n = 8$) to the nestling period ($n = 62$). The adults communicated using distinctive vocalisations during the breeding period.

Changeable Hawk-Eagle *Nisaetus cirrhatus* is a diurnal large forest raptor that occurs from the sub-Himalayan region of northern India east to Indonesia and the Philippines (Ali & Ripley 1978, Clark *et al.* 2020). Five subspecies are recognised based on morphology; the nominate is found from the Gangetic plains across all of southern India. Globally, the species' population has been declining in many areas due to habitat loss and human disturbance (Clark *et al.* 2020), although it is considered Least Concern on the IUCN Red List (BirdLife International 2020). Despite being a widely distributed species only limited breeding biology data have been published. Gamauf *et al.* (1998) provided the first evidence of breeding in the Philippines (confirmed by Chan 2019). Senanayake *et al.* (2017) documented breeding by *N. c. ceylanensis* in Sri Lanka. Gunawan *et al.* (2017) studied the species' nesting cycle and nestling development in West Java.

Information on the species' breeding in India is available from southern India on social media, but comprises only evidential images and brief descriptions. Dharmakumarsinhji (1955) mentioned that *N. cirrhatus* breeds in Gir Forest, Saurashtra. Naoroji (1985, 1999) provided a brief account of its breeding in Shoolpaneswar Wildlife Sanctuary and Corbett National Park, India. Here we present new information on the species' breeding behaviour and nestling diet based on a nest we monitored in northern Gujarat, India.

Material and Methods

Study area.—The nest site is in a reserved forest called Polo Forest, near the Vireshwar temple complex in Vijaynagar Taluka, Sabarkantha district, in northern Gujarat. Polo (from the Marwari language, meaning 'gate') Forest is a southern tropical dry deciduous forest, a subtype of dry teak forest (5A/C-1b) according to the classification system of Champion

& Seth (1964). The entire forest covers 400 km² and comprises two blocks, Dholwani and Vijaynagar, in the foothills of the southern Aravalli Mountains, within the catchment of the perennial Harnav River, a small tributary of the Sabarmati River. The forest supports a diverse array of plants and animals, including many bird species (Mori *et al.* 2026).

Methodology.—We monitored a nest of Changeable Hawk-Eagle on the edge of Polo Forest for 14 weeks between 20 March and 30 June 2025, using direct observations and an automated camera. Direct observations were conducted once per week for the entire day from sunrise to sunset, employing DSLR cameras, binoculars and a spotting scope.

Solar-powered 4G live camera surveillance.—To minimise disturbance, we used a fully automated camera to monitor the nesting of a pair of Changeable Hawk-Eagles. We deployed a Godrej ACE Pro 4G Dome Camera system equipped with a 7W solar panel and an integrated 18,000 mAh lithium-ion battery that provides up to 36 hours of autonomous backup under all conditions. The camera was installed on a slender branch in the nest tree, c.9–10 m from the nest. It was positioned at a slightly elevated angle with an uninterrupted view of the nest platform and nearby perches, while minimising disturbance. The device has four infrared LEDs that provide 30-m night vision, ensuring 24-hour visibility under varying light conditions. The camera includes DWDR (Digital Wide Dynamic Range) and an auto electronic shutter for optimised image capture under complex lighting. The Jio 4G SIM card provides reliable, consistent network coverage even in remote areas, making it a convenient choice for uninterrupted data transmission. Manual back-ups to an external drive were made weekly.

Our observations focused on parental care and prey delivery. We spent c.250 hours in the field during the study, concentrated in the early morning and late afternoon, when activity was highest. All observations were conducted from a concealed vantage point c.150 m from the nest using binoculars and a telescope.

We occasionally used DSLR cameras to document visiting raptors or adult eagles for identification. This equipment was used strategically during sensitive periods, like hatching, to minimise disturbance to the adults. We did not visit the nest itself, so we could not measure the eggs and chicks. We ensured that our actions complied with suggested guidelines for such work (Bailey *et al.* 2019, Barve *et al.* 2020).

Study and nest site.—During a raptor survey in Polo Forest, in the second week of February 2025 we observed a pair of Changeable Hawk-Eagles displaying behaviour indicative of early breeding activity. The pair patrolled a well-defined area of semi-deciduous forest, flying low over the canopy and frequently emitting sharp, high-pitched breeding calls often rendered as a series of *kree-kree-kree* or *chee-chee-chee* notes. These vocalisations and coordinated circling flights served to delineate the boundaries of a territory likely centred on a tall tree. We noticed that the pair was mainly restricted to a specific patch of hill forest. Both individuals repeatedly perched on prominent branches of tall trees. They remained vigilant on these elevated perches, continuously scanning the environs, a typical feature of territorial defence during the breeding season. Additionally, we observed the pair aggressively chase an Oriental Honey Buzzard *Pernis ptilorhynchus* and a Bonelli's Eagle *Aquila fasciata* that entered their airspace. The persistent territorial patrols, characteristic breeding calls, aerial displays and active defence against intruders show that this pair had established a breeding territory and was likely preparing to nest.

Results

Nest tree and camera installation.—We found two Changeable Hawk-Eagle nests in a tall *Terminalia bellirica* tree during the third week of March 2025. One nest was larger and had a white egg (Fig. 1). On 25 March 2025, we installed an automated camera and



Figure 1. The red box marks the nest’s position in the *Terminalia bellirica* tree (A) (Devvratsinh Mori), the female Changeable Hawk-Eagle *Nisaetus cirrhatus* repairing the nest (B); and the pair with their egg (C).

solar panels on a branch above this nest to monitor the pair. Both nests were in the upper-middle canopy of the tree. Nest dimensions and other details, such as nest height above ground, tree trunk girth and overall tree height, are presented in Table 1. After the nestling had fledged, we collected measurements and examined the materials used to construct the nest (Table 2), taking care to ensure it was not damaged. All of the nesting materials were available in the area around the nest tree.

Egg and incubation.—When we found the nest on 18 March, it contained a single unmarked white egg. Although we did not measure the egg, it appeared to be twice the size of a domestic fowl’s egg. On the morning of 6 April 2025, at 07.34 h, we observed a small crack in the egg,

TABLE 1
Nest tree and structure details: Changeable Hawk-Eagle *Nisaetus cirrhatus*.

Parameter	Details
Nest type	Stick platform
Study period	March–June 2025
Nest tree species	<i>Terminalia bellirica</i>
Coordinates	23° 56'15.32"N, 73°09'44.08"E
Elevation	264 m
Tree height	32.5 m
Tree girth (circumference at breast height)	4.65 m
Height of the nest above ground	30.5 m
Diameter of the branch supporting the nest	65–68 cm
Diameter of the nest, outer circumference	1.54 m
Depth of the nest cup	36 cm
Nest orientation relative to the tree’s trunk	North-east (built on a strong fork of the secondary branch)

with both adults present at the nest. Next morning, 7 April, the crack had grown slightly and one adult attempted to enlarge it, resulting in the chick hatching at 07.30 h (Fig. 2). Because the female was already incubating when we found the nest, we do not know the incubation period, but we recorded the pair’s behaviour over the last 12 days. Most of the time, the female incubated the egg, but the male took over when she left the nest, e.g., in the morning (probably for only 1–2% of each day), communicating via special calls before switching. The male gave a shrill long *klee... kleeek...* and the female responded with *klee... klee... klee.. kee.. kee...*

kee... kee..klee. The female always incubated at night, while the male roosted on an upper branch of the tree; rarely, both were on the nest at night. The egg was often left unattended for a few minutes (*n* = 18; range 1–22 minutes) during the morning and evening while both adults were foraging. We noted eight instances of the birds bringing green, leafy twigs of *Syzygium cumini* over the 12 days we monitored incubation, i.e., nearly every other day.

Fledgling growth and behaviour.—The changes in plumage colour and growth of the chick, from the day of hatching to the tenth week, were recorded (Table 3, Figs. 2–6). By the end of the tenth week, the chick’s size and colour were similar to those of the adults. We

TABLE 2
List of materials in the nest of Changeable Hawk-Eagle *Nisaetus cirrhatus*.

1	Fresh leaves and twigs of <i>Syzygium cumini</i>
2	Large teak <i>Tectona grandis</i> sticks
3	Sticks of <i>Madhuka longifolia</i>
4	Sticks of <i>Butea monosperma</i>
5	Leaves and twigs of <i>Terminalia bellirica</i>
6	Sticks of unidentified plants

TABLE 3
Summary of the behaviour and growth of a Changeable Hawk Eagle *Nisaetus cirrhatus* nestling from day one to the end of the tenth week.

Age	Chick growth and plumage	Bare-parts colours	Chick behaviour
1st day	All white, with appearance of cotton.	Blackish eyes, a grey-black bill, and pinkish feet and claws.	Hardly capable of raising its head.
1st week	Covered in down.		Raised the head and begged for food.
2nd week	Size had almost doubled since hatching.		When begging for food, the neck was now stable and it more easily seized food from the adult.
3rd week	Body still predominantly white, with a few black and brown feather pins. Wing feather sheaths evident.		Begged for food with low-pitched screams; stretched the feet.
4th week	Many black-brown feathers appeared on wings and tail.		
5th week	Throat, breast, head and belly retain some white.	Claws appeared black.	Capable of swallowing a small lizard whole.
6th week	Small feather buds on the throat and breast still covered in feathers; c.50% of adult size.		Wing-flapping/exercising started; capable of swallowing most prey.
7th week	Entire body covered with brown feathers; c.70% of adult size.	Feet now pale yellowish.	Wing-flapping, jumping and hopping all observed. In response to loud calls from the adult, the chick emits mild whistles.
8th week	Resembled an adult, except overall size, neck colour and short tail.		Jumping behaviour started; chick handled prey for itself.
9th week	Resembled an adult in body colour and size; small crest appears on head.	Feet now completely yellowish.	Hopping behaviour noted; chick capable of tearing prey.
10th week	Very similar to an adult except for the crest.		By end of tenth week, the chick roosts on branch above the nest.



Figure 2 (top left). Pair of Changeable Hawk-Eagles *Nisaetus cirrhatus* with first crack on their egg, 6 April 2025 (A); the crack is enlarged, 7 April (B).

Figure 3 (top right). The chick of Changeable Hawk-Eagle *Nisaetus cirrhatus* hatched on 7 April 2025 (A); the one-week-old chick (B).

Figure 4 (bottom). Chick of Changeable Hawk-Eagle *Nisaetus cirrhatus*, at age two weeks (A), three weeks (B), four weeks (C) and five weeks (D).

observed ontogeny, neonatal development and other developmental stages in the chick. Behaviours such as head-raising and wobbling, food begging, wing-flapping, jumping, hopping and prey-tearing were documented. Overall, the nestling period lasted 70 days.

Feeding and prey delivery.—We observed the pair and prey delivery using the automated camera and visual observations. However, after ten weeks, although both adults continued to bring prey, data collection became difficult because the young often perched on



Figure 5. Chick of Changeable Hawk-Eagle *Nisaetus cirrhatus*, at age six weeks (A), seven weeks (B), eight weeks (C) and nine weeks (D).

branches above or below the nest, thus most activity occurred off-camera. We therefore analysed data only from the first ten weeks, during which the adults delivered 128 prey items, averaging 1.82 deliveries per day; prey delivery per week is visualised in Figs. 7–8. Both adults provisioned the young. The first recorded prey delivery of the day was at 05.32 and the last at 19.02 h. The largest single number of deliveries ($n = 5$) occurred on 7 April 2025, the day the chick hatched. Overall, most prey was delivered in the morning (64%, $n = 82$) and least in the evening (16.4%, $n = 21$).

Diet spectrum and nestling.—The pair delivered a total of 128 prey items to the nest over a ten-week period. Prey fell into three classes of vertebrates: 51 reptiles (Common Garden Lizard *Calotes vultuosus*, Bengal Monitor Lizard *Varanus bengalensis* and Common Bronze-back Tree Snake *Dendrelaphis tristis*: Fig. 9), 49 mammals (Black Rat *Rattus rattus* and Northern Palm Squirrel *Funambulus pennanti*) and 25 birds, excluding three unidentified items (Table 4). Among birds, 22 belonged to 17 species and 13 families, including a single unidentified pipit (*Anthus* sp.). The commonest prey species were *Calotes vultuosus* and *Funambulus pennanti*. The nestling was fed manageable, fleshy morsels, excluding bones, tarsi, feathers and toes, predominantly by the female and, on three occasions, by the male, based on video, images from the automated camera and direct observations.



Figure 6. Ten-week-old chick and adult Changeable Hawk-Eagle *Nisaetus cirrhatus* (A); the young is now capable of tearing prey (B).

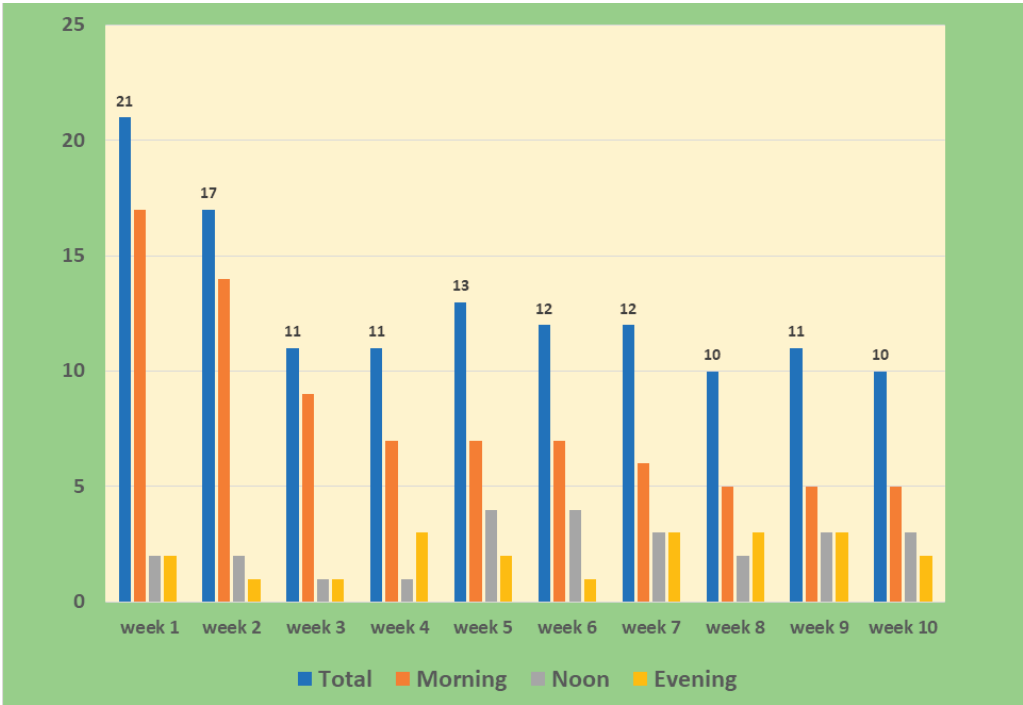


Figure 7 . Bar chart showing weekly prey delivery by the adults to the chick.

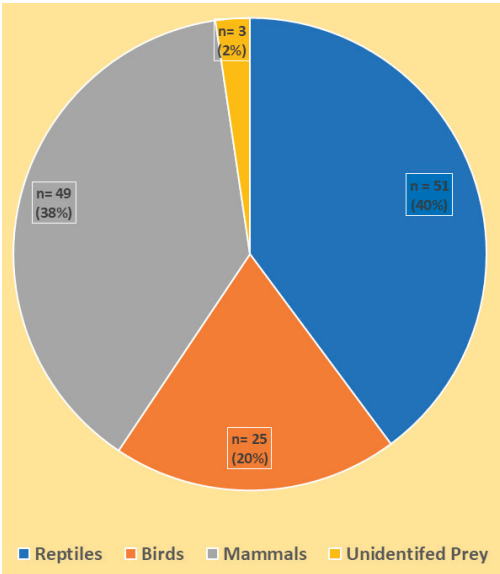


Figure 8. Pie chart showing the percentage distribution of different vertebrate prey fed to the chick over its first ten weeks of life.



Figure 9. Adult male bringing bird prey to the nest (A), and a large Common Bronze-back Tree Snake *Dendrelaphis tristis* being handled by the female (B).

Parental care.—Both adults tended the young, with the male bringing prey (feathered or, sometimes, without large feathers) to the nest, and the female tearing off small pieces to feed the chick. In some cases, after the tenth week, the female also brought prey for the

TABLE 4
List of prey brought by the parent Changeable Hawk Eagle *Nisaetus cirrhatus* for the chick

No.	Class/Family		English and scientific names	No. of prey	% of prey
REPTILES				51	39.84
1	Agamidae	1	Common Garden Lizard <i>Calotes vultuosus</i>	47	36.71
2	Varanidae	2	Bengal Monitor Lizard <i>Varanus bengalensis</i>	3	2.34
3	Colubridae	3	Common Bronze-back Tree Snake <i>Dendrelaphis tristis</i>	1	0.78
MAMMALS				49	38.28
4	Muridae	4	Black Rat <i>Rattus rattus</i>	5	3.90
5	Sciuridae	5	Northern Palm Squirrel <i>Funambulus pennanti</i>	44	34.37
BIRDS				25	19.53
6	Phasianidae	6	Grey Francolin <i>Francolinus pondicerianus</i>	2	1.56
7	Ardeidae	7	Indian Pond Heron <i>Ardeola grayii</i>	1	0.78
8	Accipitridae	8	Shikra <i>Accipiter badius</i>	1	0.78
9	Columbidae	9	Eurasian Collared Dove <i>Streptopelia decaocto</i>	1	0.78
10	Psittacidae	10	Yellow-legged Green Pigeon <i>Treron phoenicopterus</i>	2	1.56
		11	Alexandrine Parakeet <i>Psittacula eupatria</i>	1	0.78
		12	Rose-ringed Parakeet <i>Psittacula krameri</i>	1	0.78
11	Cuculidae	13	Greater Coucal <i>Centropus sinensis</i>	2	1.56
12	Megalaimidae	14	Brown-headed Barbet <i>Psilopogon zeylanicus</i>	1	0.78
		15	Coppersmith Barbet <i>Psilopogon haemacephalus</i>	1	0.78
13	Corvidae	16	House Crow <i>Corvus splendens</i>	1	0.78
14	Timaliidae	17	Jungle Babbler <i>Turdoides striata</i>	3	2.34
15	Sturnidae	18	Rosy Starling <i>Pastor roseus</i>	2	1.56
		19	Brahminy Starling <i>Sturnia pagodarum</i>	1	0.78
16	Passeridae	20	Yellow-throated Sparrow <i>Gymnoris xanthocollis</i>	1	0.78
17	Ploceidae	21	Baya Weaver <i>Ploceus philippinus</i>	1	0.78
18	Motacillidae	22	Unidentified pipit <i>Anthus</i> sp.	1	0.78
		23	Unidentified bird	3	2.34
		24	Unidentified prey	3	2.34
Total				128	

chicks and feeds them. The male typically communicated its arrival with distinct shrill long calls (*kleee... kleee... kleeek...;* up to 8–12 notes), and the female responded with low-pitched short metallic notes, *kleee... klee..kee.. kee...kee...kee.klee*, before accepting the prey. At night, the female stayed with the chick, and the male roosted on a branch immediately above the nest; rarely, both stayed in the nest. At the end of nine weeks, the chick slept alone in the nest, and both adults roosted on the highest branch of the nest tree. On a few occasions, both adults cleaned the nest by removing prey carcasses and repaired it. They also brought green, leafy twigs of *Syzygium cumini* (*n* = 46) and, in some cases, of *Terminalia bellirica* (*n* = 8). Over ten weeks, the adults brought this material (*n* = 54) mainly in the morning (*n* = 48), occasionally in the evening (*n* = 4) and at noon (*n* = 2) to the nest.

Avifauna of the nest area.—The nest site has a diverse avifauna because the forest is well preserved. Within a 1-km radius of the nest, we observed 94 bird species of 46 families, including nine diurnal raptors (Accipitridae, Falconidae) and four species of nocturnal birds. Via the surveillance camera a Common Myna *Acridotheres tristis* was observed at the nest, on 14 April 2025, after the chick had hatched.

Discussion

N. cirrhatus is one of the most widely distributed raptors in the Indian Subcontinent and South-east Asia but its breeding ecology is poorly known (Naoroji 2006, Gunawan *et al.* 2017, Senanayake *et al.* 2017, Clark *et al.* 2020). It is reported to breed in different months across its range: December–May on Sumatra, Borneo, the Malay Peninsula and Sri Lanka; April–August on Java; and late January–June in India (Naoroji 2006, Clark *et al.* 2020). At our nest in northern Gujarat, the season was March–June, consistent with Naoroji's (1985) findings in central Gujarat.

Naoroji (2006) noted nest dimensions of 100–130 cm (diameter) and 28–35 cm (depth). Clark *et al.* (2020) reported diameter as 95–105 cm, but Chan (2019) measured it as 120 cm. Our observations align with descriptions of nests elsewhere, but the nest was even larger—diameter 154 cm and depth 36 cm—perhaps because the pair had nested there regularly for several years and, as a result of renovations, its size had increased incrementally (Naoroji 2006). The nest site was at the forest edge, near human settlements, showing a degree of adaptation to anthropogenic disturbance, whereas previous workers (e.g., Naoroji 1985), reported nests in deep forest far from habitation.

We were unable to determine the incubation period because, when we found the nest, the birds were already incubating. However, we recorded the pair's behaviour over the final 12 days of this period. The female was much more invested in incubation duties than the male, but whenever they swapped roles they communicated vocally. Naoroji (2006) reported on nine tall tree species in the deciduous forest of Rajpipla that were selected for

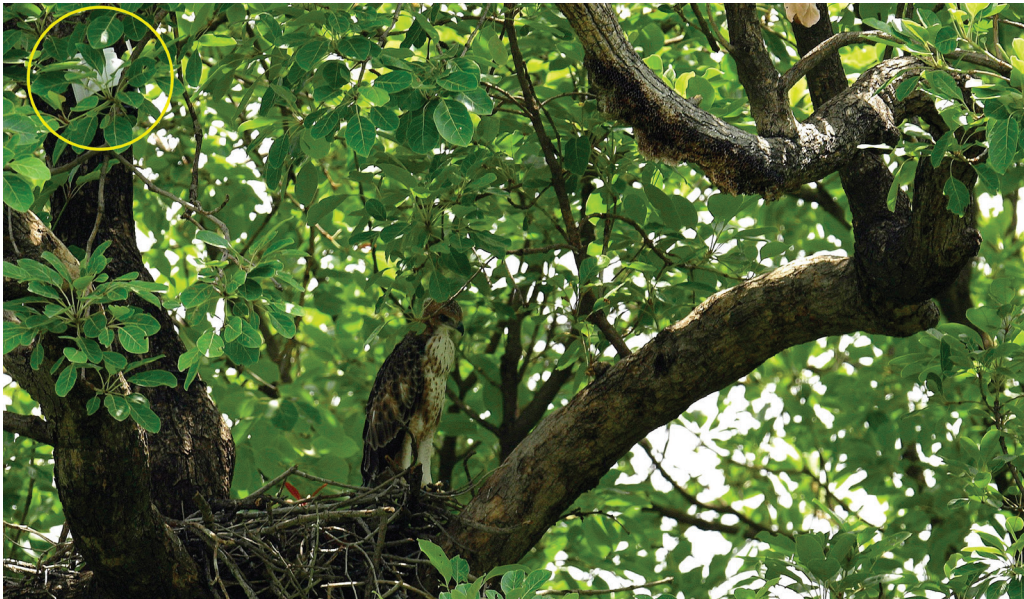


Figure 10. Nine-week-old chick Changeable Hawk-Eagle *Nisaetus cirrhatus*, now almost the same size as an adult, with the surveillance camera top left (Devvratsinh Mori)

breeding. In our study, the nest tree was a *Terminalia bellirica*, which may have been selected because it was the tallest tree in the area and protected from factors such as high winds.

Naoroji (2006) and Gunawan *et al.* (2017) provided an account of chick growth and behaviour based on observations at three nests. We observed a similar 70-day growth period (Figs. 10–11) and comparable chick behaviours. However, we did not collect data such as biometrics (see Material and Methods). Similar growth was observed in the closely related Legge's Hawk-Eagle *Nisaetus kelaarti* (Abhijith & Kumar 2023).

Naoroji (2006) and Clark *et al.* (2020) provided information on the species' diet. This raptor is known for its wide variety of prey—small to large birds, snakes, lizards, frogs and mammals, including hares, monkeys (Clark *et al.* 2020) and even a Nilgai *Boselaphus tragocamelus* (Joshi & Kasambe 2013). It has been reported predating Rhesus Macaque *Macaca mulatta* (Singh *et al.* 2024)



Figure 11. Ten-week-old Changeable Hawk-Eagle *Nisaetus cirrhatus* on the branch it used for roosting above the nest (Devvratsinh Mori)



Figure 12. Adult male Changeable Hawk-Eagle *Nisaetus cirrhatus* with Northern Palm Squirrel *Funambulus pennanti* prey (Niket Chaudhary)



Figure 13. This pair of Changeable Hawk-Eagles *Nisaetus cirrhatus* regularly brought sprigs of *Terminalia bellirica* (A) and *Syzygium cumini* (B) to the nest.

and juvenile Mugger Crocodiles *Crocodylus palustris* (Sharma & Vyas 2024). We recorded a total of 22 vertebrate species in its diet (17 birds, three reptiles and two small mammals), excluding six unidentified items. Main prey species were the lizard *Calotes vultuosus* and the squirrel *Funambulus pennanti* (Fig. 12), which together constituted 71.08% of diet and are probably the most abundant prey in the area. The wide variety of prey indicates this species' foraging capability.

The pair regularly brought sprigs/twigs of *Syzygium cumini* and *Terminalia bellirica* to the nest (Fig. 13), on a total of 70 occasions (16 during incubation, 54 at the nestling stage) over 83 days. Such behaviour has been noted in many eagle species but requires further research (Mori *et al.* 2017, Abhijith & Kumar 2023). However, we are unable to explain

why the birds brought such a large number of leafy twigs to the nest. There are various hypotheses regarding the use of such material in raptor nests (Newton 1979, Petretti 1988, Bakaloudis *et al.* 2000, Mori *et al.* 2017). It may be for the nest's inner lining, or to provide moisture and maintain fitness in the birds (Dimri *et al.* 2025).

Finally, we conclude by noting that our study was based on a single breeding season, within which our observations were limited, primarily using a camera that covered only part of the nest area. As a result, we did not record courtship behaviour, nestbuilding, incubation and other aspects. In addition, many remarks herein are based on single observations and require corroboration via follow-up observations of a single pair across multiple breeding seasons or on other pairs. Therefore, we emphasise the need for further studies of the species' breeding biology to enhance our understanding.

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First record of Black-legged Kittiwake *Rissa tridactyla* in Brazil

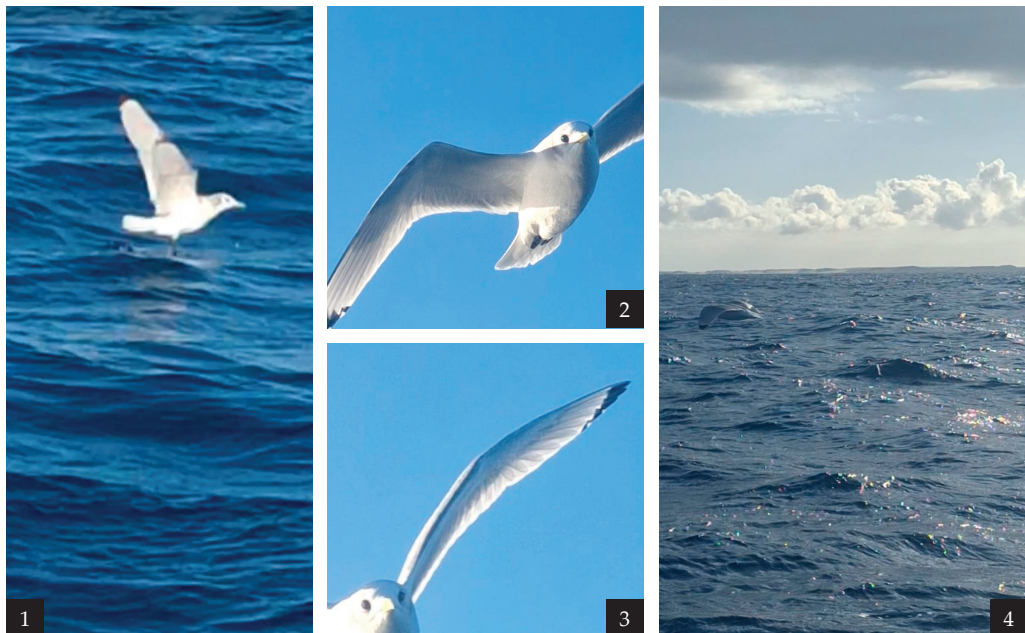
by François Sagot-Martin & André Felipe Nascimento Ramos

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<http://zoobank.org/urn:lsid:zoobank.org:pub9F0135DD-7587-496B-B42D-0CDD30B04A31>

SUMMARY.—The first record of Black-legged Kittiwake *Rissa tridactyla* in Brazil and one of the few documented records in South America and the Southern Hemisphere involved an adult in non-breeding plumage in near-shore waters off the state of Rio Grande do Norte in late December 2025. The identification and possible provenance of the bird are discussed.

During a regular nearshore fishing trip looking for seabirds, an adult Black-legged Kittiwake *Rissa tridactyla* in non-breeding plumage flew close to the boat, c.14 km south-east of Pirangi harbour (06°02'S, 35°00'W; water depth 19 m) off Tabatinga, Nísia Floresta municipality, Rio Grande do Norte, north-east Brazil, at 16.10 h on 27 December 2025. Two smartphone videos by AFNR of the bird were sent to FS-M next day. In one the bird is seen on the water, then taking off, showing the neatly black-tipped wings, black tarsi and grey rear head markings (Fig. 1). In the second, the bird is flying above and towards the boat, enabling a good view of the head, with the all-yellow bill, dark eye and smudge below it, black feet and all-white underwing (Fig. 2), and, when circling, the primary formula and markings (Fig. 3). The bird was apparently healthy, and also



Figures 1–3. Adult Black-legged Kittiwake *Rissa tridactyla*, off Nísia Floresta, Rio Grande do Norte, Brazil, 27 December 2025 (André Felipe Nascimento Ramos)

Figure 4. Adult Black-legged Kittiwake *Rissa tridactyla* with (in the background) the dunes of Tabatinga and Malemba, Nísia Floresta, Rio Grande do Norte, Brazil, 27 December 2025 (André Felipe Nascimento Ramos)

had a pale grey mantle and upperwing (with white trailing edge), all-white underparts including the underwing and undertail-coverts, with the only real contrast being the black feet and wingtips. Tail was slightly rounded when held half-open, and was neither long nor forked. The bill was almost uniform pale to medium-yellow without any dark markings. The primaries (numbered from the innermost, outwards, following Chardine 2002) were all black on pp8–10, whilst pp6–7 had white tips and less black distally. Fig. 4 shows the bird in flight with the dunes of Tabatinga and Malemba, off Nísia Floresta, in the background.

Identification

None of the regularly occurring species of larids in north-east Brazil is similar to the bird observed off Rio Grande do Norte. Comparable in size and bill colour to Black-legged Kittiwake are Red-legged Kittiwake *Rissa brevirostris* and Common Gull *Larus canus*, although neither has been recorded in South America. The all-black tarsi and feet of our bird are generally sufficient to eliminate Red-legged Kittiwake, but the all-white underwing further separates it from Red-legged, which has a darker underwing. Among other features, Red-legged is also clearly smaller than Black-legged, with shorter legs, a shorter bill and darker grey upperparts. Common Gull is distinctive from the second year, when it becomes adult-like, but has more extensive black on the primaries merging with the black primary coverts to form a larger wedge on the outer wing, with on average smaller white spots on the primaries. In autumn and winter it also shows a greater amount of dusky markings on the head and breast. The rectrices usually show some dark markings but vary from primarily dark to all white. Its bill is usually greenish with a blackish tip or other dark marks in autumn and winter, becoming yellowish with indistinct (or no) dusky markings in spring and summer, whereas our bird had an all-yellow bill, in the period when an immature Common Gull should show dark markings on the bill. Our bird was an adult in non-breeding plumage, without dark markings on the primary coverts and alula. Also never recorded in South America, Short-billed (or Mew) Gull *Larus brachyrhynchus* shows only minor differences in morphology from the formerly conspecific Common Gull (Adriaens & Gibbins 2016) and can therefore be discounted by many of the same features.

Discussion

Black-legged Kittiwake winters mainly in coastal waters of the North Atlantic south to the Sargasso Sea, the mid-Atlantic ridge around the Azores, in the North Sea and Bay of Biscay (Olsen & Larsson 2003, Hatch *et al.* 2020). Periodic incursions occur further south, e.g., into the Caribbean Basin in midwinter 1984/85 and early 2009 (Kirwan *et al.* 2009, 2019), with the latter period also seeing large numbers displaced further south in the north-east Atlantic than usual (Hatch *et al.* 2020). The southernmost records anywhere involved vagrants off South Africa (to 28°S), in February 1978, February 1979 and November 1987 (Hockey *et al.* 2005). Vagrants have also reached the Indian Ocean south of the Horn of Africa, c.500 km off Mogadishu (c.02°N), Somalia (GBIF 2026). In the West Atlantic, vagrant records (several of them in 2009) are available from Venezuela, Guyana, and Trinidad & Tobago (c.10°N), with undocumented records in Suriname and French Guiana (c.04°N) (Kirwan *et al.* 2009, Pearman *et al.* 2025), the latter not far from Brazilian waters but still in the Northern Hemisphere. The subspecies *R. t. pollicaris* winters in the North Pacific around Japan, the Korean Peninsula and south-east Alaska south to southern California (Chardine 2002, Hatch *et al.* 2020). In the west, it has occurred in

southern China (Jiang *et al.* 2014). The only other accepted South American record was also in the East Pacific, involving one photographed off Pucusana, Peru (c.12°S) (Haase 1993).

Black-legged Kittiwake is now well known to sometimes follow or associate with fishing boats (Coulson & Macdonald 1962, Hatch *et al.* 2020). Our record, the first in Brazil and one of the apparently few in the Southern Hemisphere (Hockey *et al.* 2005, Pacheco *et al.* 2021, Pearman *et al.* 2025, WikiAves 2026) further illustrates that there would seem to be few limits to larid vagrancy (Lees & Gilroy 2021). The origin of the Brazilian vagrant is a matter of supposition. The amount of black in the wingtip of *R. tridactyla* increases and the amount of white decreases from Arctic Canada/west Greenland counterclockwise around the Arctic to the Pacific, whilst the percentage showing any black on p5 follows the same pattern (Chardine 2002). The primary pattern of the Brazilian bird suggests a North Atlantic origin and the all-white p5 that it originated in the north-west Atlantic (Chardine 2002). Irrespective of the subpopulation involved, this is an extreme case of vagrancy, either an overshooting autumn migrant or a bird displaced from its usual wintering area by storms or other factors. The possibility of ship-assisted passage seems unlikely but cannot be eliminated. *R. tridactyla* becomes the 19th species of vagrant bird to occur in Rio Grande do Norte (Sagot-Martin *et al.* 2020, 2025).

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A new species of imperial pigeon (Columbidae: *Ducula*) from Tawi-Tawi, Philippines

by Matthew R. Halley 

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SUMMARY.—Only three specimens of the Pink-bellied Imperial Pigeon *Ducula poliocephala* (G. R. Gray) are available from the isolated population on Tawi-Tawi Island, in the Sulu Archipelago, Philippines, and all have white (vs. brown) throats—a character shared with the closely related White-bellied Imperial Pigeon *D. forsteni* (Bonaparte). Two adults collected on Tawi-Tawi by the Menage Expedition, in 1891, are preserved in the National Museum of Natural History, Smithsonian Institution, Washington, DC. They bear archival labels with a nomen nudum (*albigularis*) indicating that the collectors initially considered them to be undescribed—because of the white throats—yet did not publish a description. A third white-throated specimen, collected in 1971 and preserved in the Delaware Museum of Nature & Science, Wilmington, confirms the morphological distinctiveness of the Tawi-Tawi population. Audio recordings from the 1990s further reveal that the Tawi-Tawi population is vocally distinct from *D. poliocephala* and *D. forsteni*. Based on its unique morphology and voice, I describe the ‘Tawi-Tawi Imperial Pigeon’ as a new species. It is endemic to the shrinking forests of Tawi-Tawi and faces an imminent risk of extinction.

Modern checklists recognise 42 species in the genus *Ducula* Hodgson, 1836, a clade of large ‘imperial pigeons’ (Columbiformes: Columbidae) that inhabits the Indo-Pacific region (e.g., Clements *et al.* 2025, Gill *et al.* 2025, AviList Core Team 2025). This paper concerns a poorly known group (putative clade) of four species that occurs in the Philippines and Sulawesi, Indonesia, on opposite sides of Wallace’s Line (Goodwin 1960): (1) Pink-bellied Imperial Pigeon *D. poliocephala* (G. R. Gray, 1844),¹ which is wide-ranging in the Philippines (Baptista *et al.* 2020a); (2) White-bellied Imperial Pigeon *D. forsteni* (Bonaparte, 1854), endemic to montane Sulawesi and some satellite islands (Baptista *et al.* 2020b); (3) Mindoro Imperial Pigeon *D. mindorensis* (Whitehead, 1896), endemic to Mindoro Island, Philippines, where it is sympatric with *D. poliocephala* (Baptista *et al.* 2020c); and (4) Grey-headed Imperial Pigeon *D. radiata* (Quoy & Gaimard, 1830), endemic to Sulawesi (Baptista *et al.* 2020d).

These four species—the ‘zone-tailed pigeons’ *sensu* McGregor (1909)—share several plumage characters including rich green upperparts, with variable purplish or bronzy reflections, and long tails with a grey central band. They also have a ‘conspicuous, bright-coloured, fleshy ring round the eyelid, [whereas] true *Carpophaga* [are] feathered right up to the eye’ (Whitehead 1899: 488). Males are slightly larger than females but the sexes are not dichromatic. With a suite of shared characters, the ‘[zone-tailed pigeons form] a more discrete group than any others [in the genus] with the exception of those in the *bicolor* species-group’ (Goodwin 1960: 527), referring to Pied Imperial Pigeon *D. bicolor* (Scopoli,

¹ The second volume of Gray’s *The genera of birds* has the publication year ‘1846’ on its title page. However, the original description and illustration (Pl. 119) of *D. poliocephala* was distributed serially in September 1844 (Bruce 2023: 8). Goodwin (1960: 527) erroneously cited ‘Gray 1884’ [sic].

1786) and its white-plumaged allies. However, as none of the ‘zone-tailed’ species has been included in recent phylogenetic studies of the Columbidae (e.g., Cibois *et al.* 2017), their relationships to each other, and placement within the broader *Ducula* phylogeny, are inferred from phenotypic evidence.

Taxonomic discussions have focused primarily on the two most similar species—*D. poliocephala* (Philippines) and *D. forsteni* (Sulawesi). Both are reportedly monotypic. They differ in body size (*forsteni* is larger), abdomen colour (*forsteni* white; *poliocephala* pink) and throat colour (*forsteni* white; *poliocephala* brown).² However, their songs are said to be similar, both consisting of two low booming ‘hoots’ repeated at intervals: ‘booooouum booooouum’ (Whitehead 1899, Kennedy *et al.* 2000, Baptista *et al.* 2020a,b). Cassin (1855: 231), who examined *D. forsteni* specimens in the Academy of Natural Sciences of Philadelphia (ANSP), which (at that time) lacked Philippine material for comparison, assumed they were conspecific with the birds in Gray’s (1844) plate of *D. poliocephala*, which had been based on a specimen from Luzon (Hachisuka 1931) in what is now the Natural History Museum, Tring: NHMUK 1842.2.15.114 (Warren 1966: 231). The bird in Gray’s (1844) plate was shown in profile and the brown throat patch was rendered as a thin brown line (Fig. 1, left). To readers lacking topotypical specimens or field experience, this figure—like photos in profile (see below)—has the potential to be misleading because the bird appears to have a mostly white throat.



Figure 1. The two earliest depictions of Pink-bellied Imperial Pigeon *Ducula poliocephala*: (left) Gray’s (1844) plate, illustrated by D. W. Mitchell and reproduced with ‘C. Hullmandel’s Patent Lithotint’ (Pl. 119); and (lower right) Hachisuka’s (1931) figure of ‘*D. p. nobilis*’ on a plate produced by ‘John Bale Sons & Danielsson, London.’ These taxa are now considered synonyms. The models for Gray’s and Hachisuka’s figures were collected on Luzon and Negros, respectively (Dickinson *et al.* 1991: 188). The closely related Mindoro Imperial Pigeon *D. mindorensis*, with its grey breast and bluer tail, is also shown on Hachisuka’s plate (upper right).

² Riley (1921) proposed to separate *D. radiata* and *D. mindorensis* in a new genus *Compsoenas* Riley, 1921, based on the shape of the outer primaries, but this was not adopted. Peters (1937: 42) moved all the zone-tailed pigeons to *Ducula*, where they have remained, and listed *Compsoenas* as a junior synonym.

Hachisuka (1931: 398) proposed that there was geographic variation in *D. poliocephala* and applied the trinomial *D. p. nobilis* to a specimen from Negros with iridescent highlights of metallic copper on its nape, back, rump and wing-coverts ('riches reflets métalliques cuivrés'). However, subsequent collecting revealed that dorsal 'coppery reflections' are widespread and individually variable, rendering *D. p. nobilis* a synonym of the apparently monotypic *D. poliocephala* (Dickinson *et al.* 1991). Hachisuka's (1931) figure was also potentially misleading because the bird is shown in right profile and the brown colour was applied so sparingly that the throat appears white (Fig. 1, right); whereas, in his text, Hachisuka (1931: 397) stated that the throat was brownish ('plumes brunâtres à la gorge').

Delacour & Mayr (1945: 107, 1946: 89–90), who lumped *D. poliocephala* and *D. forsteni* as subspecies because of their similar plumage, apparently overlooked or neglected to mention the considerable size difference. Goodwin (1960: 529), following Peters (1937), restored them to species rank, noting that it 'must be a matter of personal opinion whether they should be considered as races of a single species, or as members of a superspecies.' Modern checklists unanimously recognise *D. poliocephala* and *D. forsteni* at species rank (e.g., Gill *et al.* 2025, AviList Core Team 2025).

The Tawi-Tawi Imperial Pigeon

Since the late 19th century, it has been assumed that the isolated population of *D. [poliocephala]* on Tawi-Tawi Island, Sulu Archipelago, Philippines, is phenotypically indistinguishable from other *D. poliocephala* in the Philippines, but this hypothesis has apparently not been examined critically. Only three specimens (all adult males) from Tawi-Tawi are available in databased collections (VertNet.org, iDigBio.org; 17 February 2026). Two of the specimens (Figs. 2–3: USNM 314700, 314701) were collected in October 1891 at 'Tataan' (modern Tarawakan) by Frank S. Bourns (1866–1935) and Dean C. Worcester (1866–1924) of the Menage Expedition (1890–93) and are preserved at the National Museum of Natural History, Smithsonian Institution, Washington, DC (USNM). Worcester (*in* Worcester & Bourns 1898: 596) wrote:

'Tawi Tawi is almost entirely covered with forest. There are several piratical settlements on its southern coast, but its northern side is uninhabited except for a few native huts near the Spanish blockhouse at Tataän ... The first collections ever made on [Tawi-Tawi] were those of Bourns and myself [in 1891].'

It was apparently another 80 years before a third specimen was collected on Tawi-Tawi. That specimen (DMNH 14999), preserved in the Delaware Museum of Nature & Science, Wilmington (DMNH), was the impetus for this study. It is an adult male collected by Dioscoro S. Rabor (1911–96) in December 1971, during an expedition to Tawi-Tawi co-sponsored by DMNH and Mindanao State University (Fig. 4). In the expedition report, duPont & Rabor (1973: 32) wrote:

'*Ducula poliocephala nobilis* [was] more often heard than seen, but it was not rare in the southern half of Tawitawi island, especially in the localities where extensive dipterocarp forests were still found. It was a most difficult bird to locate, even if it called loudly among the dense foliage of the tall fruiting trees that it frequented.'

Rabor's specimen, ever since it was catalogued in 1972, has been identified with the dubious name '*D. p. nobilis*' and stored in a drawer with more typical, brown-throated *D. poliocephala* specimens. The determination was made by John E. duPont (1938–2010),



Figure 2. Historic specimens of the ‘Tawi-Tawi Imperial Pigeon’ collected by Bourns and Worcester at Tataan (modern Tarawaken) during the Menage Expedition and held at the National Museum of Natural History, Smithsonian Institution, Washington, DC: (top left) USNM 314700, 21 October 1891; (bottom left) USNM 314701, 19 October 1891; the pale greenish-grey stains on the chins of these specimens were evidently caused by post-mortem fat migration (Matthew R. Halley; reproduced courtesy of the Bird Division, National Museum of Natural History, Smithsonian Institution, Washington, DC)

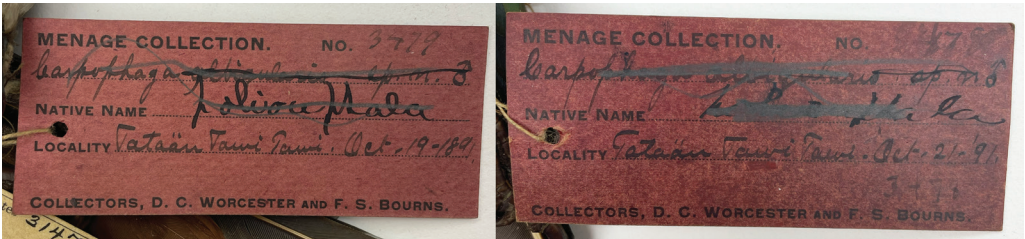


Figure 3. Original labels of USNM 314700 and 314701, each bearing the *nomen nudum* ‘*Carpophaga albicularis* sp. n.’ (struck out); in both cases, the name ‘*poliocephala*’ was written in the ‘Native Name’ field (Matthew R. Halley; reproduced courtesy of the Bird Division, National Museum of Natural History, Smithsonian Institution, Washington, DC)



Figure 4. (left) Three views of DMNH 14999 and (right) its label and entry in the Delaware Museum of Nature & Science, Wilmington, ledger; the specimen was identified (apparently by duPont, see text) as ‘*Ducula poliocephala nobilis*’ when it was catalogued in 1972 (Matthew R. Halley)

who did not accompany Rabor in the field, but who alone claimed ‘[responsibility] for the taxonomic accounts’ in the Tawi-Tawi expedition report (duPont & Rabor 1973: 1). duPont (1971: 129–130) had previously followed Hachisuka (1931) in recognising two subspecies:

a 'northern' *D. p. poliocephala* (Cebu, Luzon, Mindoro, Panay) and a 'southern' *D. p. nobilis* (Basilan, Dinagat, Leyte, Masbate, Mindanao, Negros, Samar, Sibuyan, Tawi-Tawi). As noted above, the southern taxon was supposed to be distinguished by its 'very strong coppery reflections on [the] back and wing-coverts' (duPont 1971: 130).

However, duPont apparently neglected to compare DMNH 14999 to the Menage Expedition specimens at USNM. This is understandable when we consider his diverse commitments and the unique circumstances that befell his collection. Although incorporated in 1957, DMNH did not open its public exhibits until 1972—the same year the Tawi-Tawi material arrived—and duPont was serving as Director of the museum at that time. He hired a full-time curator to work on the collection, David M. Niles (1940–2022), but Niles was preoccupied cataloguing the thousands of specimens arriving annually from South America, Africa, Asia, etc., while building regional collections of his own—there was little time for inter-institutional research.³ No additional material from Tawi-Tawi was added after 1972.

By the early 1980s, the DMNH collection had amassed an impressive geographic series of *D. poliocephala* study skins, capable of revealing the inconsistency of the 'coppery reflections' in Hachisuka's (1931) and duPont's (1971) diagnoses of *D. p. nobilis*, and sufficient (after a brief trip to USNM) to diagnose the novelty of DMNH 14999. However, duPont's interest in ornithology waned as he shifted focus to Olympic wrestling and he practically abandoned the DMNH by the mid-1980s, whilst Niles resigned in c.1988, after which the international research programme languished. For the next three decades, the DMNH Bird Department focused on collections management and monitoring of local bird populations—and the novelty of DMNH 14999 remained unnoticed.

I began full-time work at the DMNH in 2021 and initiated an intensive study of the Philippine material, focusing first on some neglected passerines (e.g., Halley 2022b, 2025). The present study began on 8 December 2025, when I noticed the white throat of DMNH 14999, then visited the USNM on 18 February 2026, to see whether the two Menage Expedition specimens (USNM 314700, 314701) have white throats. I found that they do (did), but both specimens are considerably dirtier (greasier) and more discoloured than the well-preserved and younger DMNH specimen (Figs. 2, 4). Despite a careful examination, I could not find any other plumage character that distinguished the three Tawi-Tawi specimens from typical *D. poliocephala* specimens.

Notably, the original Menage Expedition labels bear an unpublished and struck-out *nomen nudum* ('*Carpophaga albigularis* sp. n.'): primary evidence that Bourns and Worcester initially considered them to be an undescribed species, based on their white throats (Fig. 3). This likely explains why Bourns & Worcester (1894: 30) omitted Tawi-Tawi from the range of *D. poliocephala* in their published report. In any case, they did not publish the name '*Carpophaga albigularis*' nor mention that they had obtained two divergent specimens on Tawi-Tawi.⁴ McGregor & Worcester (1906: 12) later added Tawi-Tawi to the range of *D. poliocephala* without comment, then McGregor (1909: 48) publicly credited the

³ In a similar case, after accessioning specimens of what appeared to be a new species of tanager in August 1976—actually the rare and poorly known Western Hemispingus *Sphenopsis ochracea* (von Berlepsch & Taczanowski, 1884)—it was not until January 1980, that Niles 'finally [got] up to AMNH for a short day, [to run] all of [the DMNH] South American suboscine problems through their collections.' He did not have time to work on the oscines and the tanager problem was left unresolved (Halley 2022a: 215).

⁴ Bonaparte (1854: 1077) stated that George R. Gray (1808–72) had used the name '*Carpophaga albigularis*' in reference to *D. forsteni*, and Bonaparte (1857) stated that Gray had used the name '*albogularis* [sic]'. These names must have been copied from unpublished sources, because neither name appears in Gray's (1844, 1856) major taxonomic works. Whether or not Bourns and Worcester were aware of this unpublished use of the name is doubtful and ultimately irrelevant.

Menage Expedition for being the first to detect *D. poliocephala* on Tawi-Tawi. That Bourns and Worcester initially considered the Tawi-Tawi population to be undescribed was evidently unknown to duPont and later DMNH workers, who alone had the necessary material to test the hypothesis.

Throat colour

I examined a broad geographic sample of *D. [poliocephala]* study skins ($n = 55$) and smaller samples of *D. forsteni* ($n = 6$) and *D. mindorensis* ($n = 2$) in the DMNH and USNM collections. In my sample of adult *D. [poliocephala]* specimens (34 males, 18 females, two unsexed), the brown-throated phenotype was ubiquitous in Luzon, Marinduque, Mindoro, Sibuyan, Cebu, Samar, Leyte, Dinagat and Mindanao—everywhere except Tawi-Tawi (Fig. 5). There is a juvenile female *D. poliocephala* from Mindanao (DMNH 69719) with a white lower throat, but its upper throat and chin are bare (unfeathered) and adults from the same locality are brown-throated. The specimen's immaturity is evidenced by its short wings and tail (WG = 206 mm, TL = 111) and yellow bill tip, an apparent vestige of the egg tooth.

No photos of *D. [poliocephala]* from Tawi-Tawi are available in the Macaulay Library (ML) or eBird.org database (accessed 18 February 2026), but there are 126 photos from other islands in the ML archive. Excluding blurry photos and those where the throat is not clearly visible, 100% of the birds in the remaining sample (93/93, including some duplicates, see below) exhibited brown throats of varying intensity. Of these, *c.*10% (9/93) had 'weak' brown throats, although to some extent this may be an artifact of lighting or pose. For example, C. Borzini and L. Urueña took two photos each of the same individual in eastern Mindanao on 13 November 2024 (eBird checklist S202342352). Each photographer took one photo with the bird's head in left profile, and in both cases the throat appears white or shows a very weak brown 'stripe' (ML 626487071, 629566424). However, in the other two photos, the same bird's head is in right profile and turned toward the cameras, revealing an obvious brown throat patch (ML 626487052, 629566934).



Figure 5. Geographic variation in throat colour in the Pink-bellied Imperial Pigeon *Ducula [poliocephala]* complex, as demonstrated by adult males held in the Delaware Museum of Nature & Science, Wilmington: (A) DMNH 4501: Samar, May 1970; (B) DMNH 66314: Sibuyan, June 1973; (C) DMNH 1701: Mindanao, June 1961; (D) DMNH 14999: Tawi-Tawi, December 1971; (E) DMNH 10576: Mindoro, March 1971; (F) DMNH 66318: Marinduque, April 1972; (G) DMNH 3501: Luzon, March 1969 (Matthew R. Halley)

E. Legaspi photographed a bird with a weak brown patch in Quezon, Luzon, on 21 August 2025 (ML 640677662). It was seen ‘drying off from the rain and feeding on a fruiting tree’ with a second individual, which had a darker brown throat patch (ML 640677663, 640677665). A bird photographed in the same region by J. A. Sta Ana, 8 March 2020, with its head in right profile (ML 214374791), appears to have a white throat, much like the bird in Hachisuka’s (1931) plate. However, a second photo of the same individual, taken by G. So, reveals a weak brown throat patch (ML 214374881). Therefore, available photographic evidence from Luzon, Mindanao, Mindoro, Negros, Panay, Romblon and Samar suggests that the brown throat is a fixed adult character of *D. poliocephala* (excluding Tawi-Tawi), which is often obscured when viewed in profile.

Morphometric divergence

I used a metric wing ruler to measure the flattened length of the right wing of each adult specimen, from the carpal joint to the tip of the longest primary remex (WG); the length of the tail from the insertion point of the central rectrices to the tip of the longest rectrix (TL); and digital callipers to measure the exposed culmen (EC) and bill length from the anterior edge of the nares to the tip (BL). All three taxa for which specimens of both sexes were available (*D. forsteni*, *D. poliocephala*, *D. mindorensis*) exhibited sexual size dimorphism: males were larger than females. I removed one ‘male’ specimen from Mindoro (DMNH 74341) from the analysis on the suspicion it was mis-sexed, based on its measurements. All statistics were performed with R Studio (R Core Team 2020).

The three Tawi-Tawi males were shorter-winged and longer-tailed than male *D. poliocephala* on average (Table 1), but sample sizes were too lopsided for robust statistical analysis. Within the *D. poliocephala* (*sensu stricto*) sample, there were two geographic clusters that warrant further investigation. Males from Mindoro and Sibuyan tended to have longer tails than males from other islands, accounting for the relatively high standard deviation in *D. poliocephala* tail length (Table 1). The larger overall size of *D. forsteni* is also noteworthy, considering it was overlooked by Delacour & Mayr (1946). On average, the wings and tails of male *D. forsteni* (*n* = 5) were respectively 12% and 15% longer than *D. poliocephala sensu stricto* (*n* = 34); and 19% and 7% longer than the Tawi-Tawi sample, respectively.

TABLE 1
Summary statistics (mean ± 1 standard deviation) of sex-specific morphometric variation in White-bellied Imperial Pigeon *D. forsteni*, Pink-bellied Imperial Pigeon *D. poliocephala*, the undescribed taxon from Tawi-Tawi, and Mindoro Imperial Pigeon *D. mindorensis*. Measurements: wing length (WG), tail length (TL), exposed culmen (EC) and bill length from nares to tip (BL). All measurements in mm.

sex	taxon	WG	n	TL	n	EC	n	BL	n
M	<i>D. forsteni</i>	251.8 ± 6.7	5	154.0 ± 6.0	5	24.6 ± 0.4	3	11.8 ± 1.5	3
	<i>D. poliocephala</i>	225.4 ± 6.7	34	133.9 ± 11.0	31	19.5 ± 1.3	33	10.6 ± 0.6	33
	Tawi-Tawi	212.0 ± 7.0	3	143.5 ± 3.3	3	19.2 ± 0.8	3	10.9 ± 0.2	3
	<i>D. mindorensis</i>	245	1	143	1	—	—	—	—
F	<i>D. forsteni</i>	238	1	145	1	22.4	1	10.4	1
	<i>D. poliocephala</i>	220.2 ± 6.1	15	128.0 ± 8.4	15	19.5 ± 1.4	15	10.5 ± 0.5	15
	<i>D. mindorensis</i>	222	1	139	1	21.9	1	9.2	1

Vocal divergence

Song structure develops innately in African Collared Dove *Streptopelia roseogrisea* (Linnaeus, 1758) and is heritable in crosses between vocal breeds of domestic pigeons, and even between the genera *Turtur* Boddaert, 1783, and *Oena* Swainson, 1837 (Nottebohm & Nottebohm 1971, Baptista 1996, Baptista *et al.* 1997). Vocal divergence in the Columbidae is also frequently correlated with species limits; for example, see the *Ramphiculus subgularis* Meyer & Wilesworth, 1896, complex (Rheinhardt *et al.* 2011). D. Allen made recordings of *D. [poliocephala]* on Tawi-Tawi in 1996–99 (Fig. 6, see below) and documented ‘possible geographic differences in voice [which] need further study’ (Allen 2020: 62). Recordings made in three different years, of what appear to be multiple individuals, feature ‘a very different call [than *D. poliocephala*] starting with a dry rattle [or buzz] followed by [a] decelerating series of [5–8] low-pitched hoots’ (Allen 2020: 62). In one of his 1996 recordings, Allen recorded the following voice annotation:

‘That pigeon had a whitish head, kind of buffy or off-white on the sides of the head; [it] seems to be bright green across the breast, followed by white (possibly) followed by a kind of darker color on the undertail coverts ... possibly Pink-bellied Imperial Pigeon; when it bent its head forward, there was no sign of black on the back of the head.’ (ML 312726061)

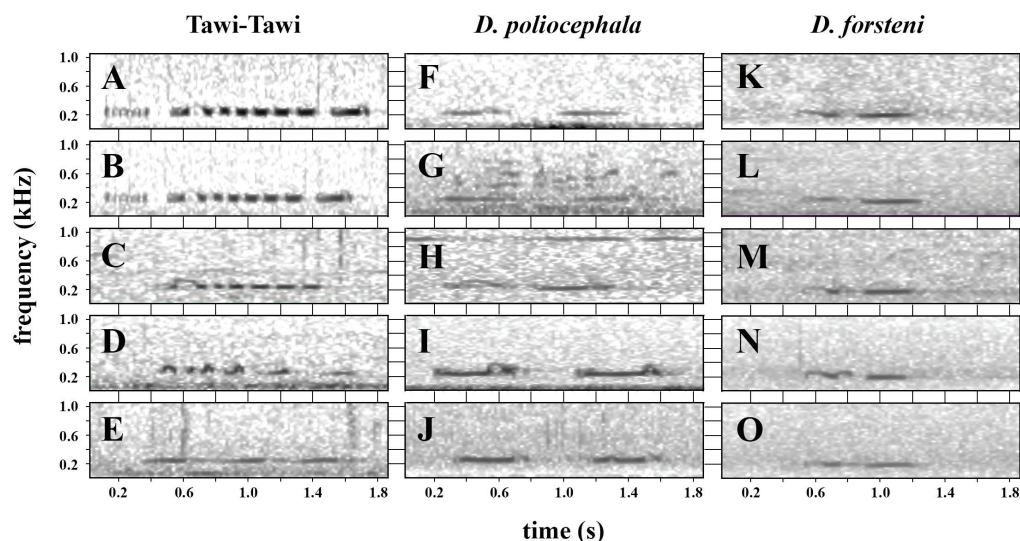


Figure 6. Structural variation in vocalisations of (left) the undescribed taxon from Tawi-Tawi, (centre) Pink-bellied Imperial Pigeon *D. poliocephala* from elsewhere in the Philippines, and (right) White-bellied Imperial Pigeon *D. forsteni* from Sulawesi, Indonesia: **Tawi-Tawi** (A–E): (A) ML 203899211, recorded by D. Allen, 1 January 1996; (B) ML 312726061, recorded by Allen, 2 May 1996; (C) ML 315081131, recorded by Allen, 16 August 1998; (D) ML 319929481, recorded by Allen, 2 March 1999; (E) ML 312725531, recorded by Allen, 2 May 1996; ***D. poliocephala***: (F) ML 636759580, recorded by J. Lindsell on Luzon, 23 May 2025; (G) ML 555871641, recorded by P. Kaestner on Mindoro, 9 April 2023; (H) ML 203997281, recorded by Allen on Panay, 14 August 1997; (I) ML 463664461, recorded by P. Schaffner on Samar, 21 June 2022; (J) ML 609063682, recorded by P. C. Rasmussen on Mindanao, 24 November 2009; ***D. forsteni***: (K) ML 203909321, recorded by J. del Hoyo on Sulawesi, 2 September 2014; (L) ML 551375351, recorded by K. Cheong on Sulawesi, 16 March 2023; (M) ML 597803891, recorded by 志民 蘇 on Sulawesi, 29 June 2023; (N) ML 607433391, recorded by G. Irving on Sulawesi, 26 July 2023; (O) ML 607434671, recorded by Irving on Sulawesi, 27 July 2023.

D. Allen (*in litt.* April 2026) provided some additional context: '[That] was, as far as I can recall, the only time I actually saw the species. It was calling from the canopy from a partially obscured branch, [dis]appearing and reappearing. I can't remember if that was due to the branches moving in the wind or the motion of the bird itself. I think my recordings were all from areas with closed-canopy forest. I never heard the typical [two-note] 'whoomp whomp' call of [*D. poliocephala*] even though I was listening out for it. The bird calling triple low hoots was not seen but I don't think there are any other species present that it could be' (e.g., ML 312725531, 2 May 1996; ML 315058081, 315058271, 15 August 1998).

To investigate Allen's hypothesis of geographic variation, I downloaded his Tawi-Tawi recordings ($n = 7$ unique files) together with all available recordings of *D. forsteni* ($n = 23$) and *D. poliocephala* ($n = 42$) from the Macaulay Library (ML), Cornell University, Ithaca, NY, and xeno-canto.org archive (XC). The sample of *D. poliocephala* recordings was geographically broad, including from Luzon, Mindanao, Mindoro, Negros, Panay and Samar. No recordings were available of *D. mindorensis*, said to have two-note songs (Whitehead 1899: 288), or *D. radiata*, which 'apparently rarely vocalizes [and] only a subdued, monosyllabic "huh" has been described' (Baptista *et al.* 2020d). I used RavenPro 1.6 software (Cornell Lab of Ornithology) to visualise the recordings and calculate spectrographic parameters with the Hann window function. Close inspection revealed that three of Allen's uploaded files from Tawi-Tawi were duplicates (ML 203899211, 609099300, XC 79270) and the introductory buzz had been inadvertently cut off from ML 609099300. After removing duplicates and recordings where it was difficult to distinguish between multiple singers, each row in the truncated dataset reflected the vocal repertoire of a single individual ($n = 68$ recordings).

I defined a 'note' as a continuous trace on the spectrogram and a 'song' as a cluster of 1–8 notes that were preceded and followed by a period of silence that was longer than the song itself. For each song I counted the number of (1) *notes*, and used the selection box feature to calculate the (2) *centre frequency*, equal to the frequency (Hz) that divides the selection into two frequency intervals of equal energy, and (3) *song duration*, equal to the time interval (seconds) containing 90% of the energy in the selection. These 'robust' variables are unaffected by small differences in the size of the selection box. I measured all unmasked songs in each recording and calculated means for each variable. Next, I used selection boxes to measure (4) *singing pace*, equal to the mean time interval (seconds) between songs (i.e., lower values reflect a faster pace). Finally, I calculated (5) *song tempo*, equal to the number of notes per song divided by mean song duration.

A preliminary analysis revealed potential geographic variation in the mean number of notes per song: *D. forsteni* songs were invariably 1–2 notes; *D. poliocephala* songs varied from 1–4 notes, with one exception (see below); and the Tawi-Tawi population varied from 3–8 notes. One recording from Tawi-Tawi (ML 319929481) featured a song that varied between five and six notes, and I conservatively scored it as 'five-note' for the analysis. Similarly, a brief *D. poliocephala* recording from Panay (XC 381614) featured two songs that were identical except the first had four notes and the second had five. Again, I took the lower value and scored this song as 'four-note' in the analysis. Subsequently, I assigned each recording to one of three song classes, based on the average number of notes (1–2, 3–4, 5–8), tested each variable for normality (Anderson-Darling test, $\alpha = 0.05$) and equal variances (Levene's test, $\alpha = 0.05$), then used *t*-tests ($\alpha = 0.05$) to compare taxon-pairs within each song class. When data were not normal or variances were unequal, I compared groups with Mann-Whitney U-tests ($\alpha = 0.05$).

After scoring the two outliers, the 1–2-note class was found only in *D. forsteni* and *D. poliocephala* recordings (not Tawi-Tawi); the 3–4-note class was found in *D. poliocephala* and the Tawi-Tawi sample (not *D. forsteni*); and the 5–8-note class was unique to Tawi-Tawi.

TABLE 2

Statistical variation in three vocal characters based on analysis of audio recordings of White-bellied Imperial Pigeon *D. forsteni*, Pink-bellied Imperial Pigeon *D. poliocephala* and the undescribed taxon from Tawi-Tawi: centre frequency (CF), song pace (PACE) and singing tempo (TEMPO). Song classes were determined by number of notes (see text). Statistical analyses were restricted to comparisons within the same song class. Within each column (variable), taxa that share a superscript letter were significantly different ($\alpha = 0.05$). The songs of the undescribed Tawi-Tawi population had a faster tempo (*) than all other taxa and note classes.

taxon	notes	<i>n</i>	CF (Hz)	<i>n</i>	PACE (s)	<i>n</i>	TEMPO
<i>D. forsteni</i>	1–2	19	191.0 ± 12.5 ^A	17	5.5 ± 1.9 ^A	19	3.2 ± 0.9 ^A
<i>D. poliocephala</i>	1–2	17	245.0 ± 12.6 ^A	16	7.7 ± 3.1 ^A	17	2.3 ± 1.0 ^A
	3–4	6	259.9 ± 17.4 ^B	5	11.0 ± 6.1	6	2.3 ± 0.2 ^B
Tawi-Tawi	3	3	239.7 ± 7.0 ^B	3	6.2 ± 0.7	3	2.8 ± 0.2 ^B
	5–8	4	256.9 ± 29.4	3	9.6 ± 2.3	4	7.5 ± 1.5*

Songs in the 5–8-note class were higher tempo than all other note classes and taxa (Table 2; Mann-Whitney U-test, $W = 0$, $p = 0.001$), but they did not differ in frequency ($W = 52$, $p = 0.171$) or pace (t -test, $t = -1.73$, $df = 3$, $p = 0.193$). In the 3–4-note class, on average, songs from Tawi-Tawi were lower frequency (t -test, $t = 2.47$, $df = 7$, $p = 0.04$) and faster tempo (t -test, $t = -4.05$, $df = 5$, $p = 0.012$) than *D. poliocephala* songs, but did not differ in pace (t -test, $t = 1.711$, $df = 4$, $p = 0.159$). In the 1–2-note class, on average *D. poliocephala* songs were higher frequency ($W = 1$, $p < 0.001$), slower pace (t -test, $t = -2.39$, $df = 25$, $p = 0.025$), and slower tempo (t -test, $t = 2.59$, $df = 32$, $p = 0.014$) than *D. forsteni* songs. This pattern is reminiscent of vocal divergence in *Ptilinopus* Swainson, 1825, a closely related genus that has radiated in parallel across the Indo-Pacific region.⁵ Some *Ptilinopus* species have short advertising songs while others have ‘longer stuttering songs’ (Baptista *et al.* 2009).

However, despite a clear geographic signal, variation in the number of notes may also reflect, to some extent, the internal motivation or stress response of the singer (Zahavi 1982), or may be associated with particular social contexts (e.g., Morejohn 2025). This variation needs to be accounted for in any taxonomic assessment. On 4 October 1981, after recording natural 1–2-note songs of *D. poliocephala* in central Mindanao, R. S. Kennedy conducted a playback experiment that elicited an aggressive territorial display including an extended four-note song (ML 38798). Kennedy stated into the recorder: ‘When I played back the call of the Pink-bellied Imperial Pigeon, it came directly out of the forest, flew toward us, and [did] what I would consider a display—a kind of threat display—it did a U, kind of a U-dive, and splayed the wings and the tail, and it landed about 25 m away’ (ML 38798). Critically, the addition of two more notes to the song during this agonistic encounter doubled the song duration. This reveals an important distinction between the songs of *D. poliocephala* and the Tawi-Tawi population; although the latter have more notes than *D. poliocephala* songs on average, they are not of longer duration. Instead, the notes are compressed into a short time interval, resulting in a significantly higher tempo (Table 2).

Morejohn (2025) described relevant variation in the vocal repertoire of Pacific Imperial Pigeon *D. pacifica* (J. F. Gmelin, 1789), showing that semi-distinct song types (resembling my

⁵ Boyd *et al.* (2022) reconstructed a time-calibrated phylogeny based on sequences from 6,363 nuclear single-copy orthologues, in which samples of three *Ducula* species (none of them ‘zone-tailed’ pigeons) formed a clade sister to Topknot Pigeon *Lopholaimus antarcticus* (Shaw, 1793), in the monotypic genus *Lopholaimus* Gould, 1841, with an estimated age of divergence of c.20 Ma. That clade was reconstructed as sister to the White-bibbed Fruit Dove *Ptilinopus rivoli* (Prévost, 1843), with an estimated age of about 25 Ma. These phylogenetic relationships are supported by a unique lineage of body lice, endemic to the *Ducula* + *Lopholaimus* clade (Sweet *et al.* 2025).

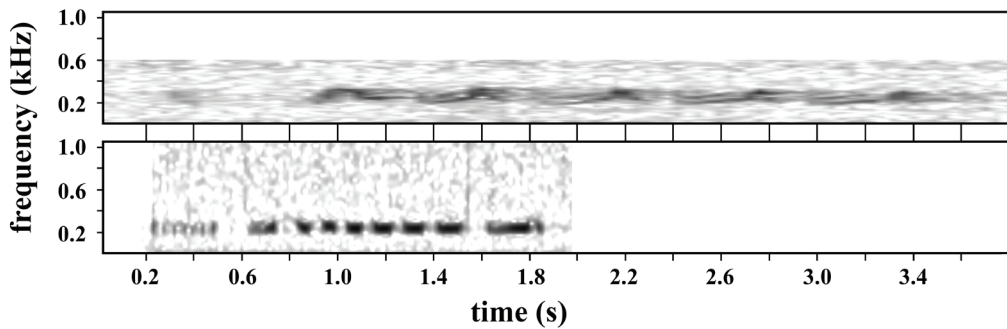


Figure 7. Comparison between (bottom) the high-tempo eight-note song recorded by Allen on Tawi-Tawi on 1 January 1996 (ML 203899211) and (top) a structurally similar five-note song of Pink-bellied Imperial Pigeon *D. poliocephala* recorded on Panay (XC 381614), which was also uttered as a four-note song in the same recording (see text). Both feature a low-amplitude buzz or 'rattle' followed by a brief pause, followed by a series of repeated notes—but the songs differ in tempo and duration.

song classes, see above) are associated with specific social contexts. One such vocalisation ('courtship coo') was longer than typical songs and reminiscent of the 7–8-note songs of the Tawi-Tawi taxon. Morejohn (2025) wrote: 'The *courtship coo* was a series of six to ten progressively shorter *ooohs* with a quick stop between each: *oooh-oooh-oooh-oooh-oh-oh-oh-oh-oh-oh-oh-oh*.' This description is similar to Allen's (2020: 62) description of '[a] decelerating series of [5–8] low-pitched hoots' in the Tawi-Tawi taxon, although 'progressively shorter' suggests that the *D. pacifica* 'courtship coo' sounds like it is accelerating (not decelerating). Furthermore, the common song type in *D. pacifica* consists of 1–3 notes, not unlike the common vocalisations of *D. forsteni*, *D. poliocephala*, and three-note songs recorded on Tawi-Tawi (ML 315058271, 315058081, 312725531).

Therefore, borrowing Morejohn's (2025) nomenclature, it appears that Allen's sample of recordings from the Tawi-Tawi population includes both a 'common' three-note vocalisation (ML 315058271, 315058081, 312725531) and a more complex 'courtship coo' (5–8 notes: ML 203899211, 312726061, 315081131, 319929481).⁶ Allen's recordings of the latter vocalisation feature a quiet 'dry rattle' or buzz followed by a brief pause, before the coos. A similar pattern appears in a recording of *D. poliocephala* recorded by B. Sloan on Panay on 17 March 2021 (XC 381614): a low-amplitude buzz followed by a pause, then a longer-than-usual series of coos (Fig. 7). The similar structure of these vocalisations suggests homology, but the *D. poliocephala* song is more than twice the duration (*c.* 2 seconds), and structurally like the 'agitated' four-note song that Kennedy's playback experiment elicited on Mindanao. In contrast, the songs in the Tawi-Tawi recordings are much briefer (<1 second) with a much higher tempo (Table 2).

Another aspect to consider is the postural display that accompanies the vocalisations. Kennedy described the bowing motions of a singing *D. poliocephala* in Mindanao: 'the bird was calling from a perch about 80 feet [*c.* 25 m] up in a dead tree, and when it called it would bring its head forward and down in front of it' (ML 18633). Morejohn (2025: 199) described similar motions in vocalising *D. pacifica*, especially in association with the 'courtship coo': 'Vocalising birds bobbed their heads with each *oooh*, and occasionally the bobbing caused birds to bounce, particularly when perched on thinner branches.' Vocalising in this way does not merely engage the muscles of the syrinx, but the whole body, and as such likely

⁶ ML 609099300 appears to be a duplicate of ML 203899211, in which the 'rattle' (buzz) preceding the 'coos' was cut off.

encodes honest information about the posture and state of the singer (Zahavi 1982). There is currently no information available about singing posture in the Tawi-Tawi population.

Taxonomy

In a practical sense, taxonomic descriptions are formalised hypotheses as to the diagnosability and/or inferred genetic isolation of populations, which, depending on the species concept used, require data of a certain quality and quantity to reliably test (e.g., de Queiroz 2007, Tobias *et al.* 2010, Cicero *et al.* 2021). Divergence in mating signals is commonly interpreted as evidence of reproductive isolation under applications of the Biological Species Concept in allopatry, with many examples from the Asian avifauna (e.g., Mayr 1940, 1942, Price 2008, Rasmussen *et al.* 2012, Sangster *et al.* 2021, Berryman *et al.* 2025). In lieu of genetic data, I contend that the combination of a fixed plumage difference, distinct vocal structure, and geographic isolation, is sufficient to infer reproductive isolation from the allopatric *D. poliocephala* and *D. forsteni* and warrants species rank for the Tawi-Tawi taxon. Qualitative methods are evidently sufficient to distinguish these field-diagnosable species. Quantitative approaches to species delimitation based on phenotypic data (e.g., Tobias *et al.* 2010) would likewise recognise the new form at species rank; the white throat and divergent song both qualify as ‘major’ characters (i.e., pronounced differences) which distinguish the Tawi-Tawi population from *D. poliocephala*—yielding a score of 8, where 7 is the species-rank threshold (e.g., Collar *et al.* 2026). From the white-throated *D. forsteni*, the Tawi-Tawi population differs in its vocal structure, pink underparts and smaller body size. Genetic data are lacking, but the divergence of both visual and auditory signals associated with mate selection strongly implies underlying genetic differentiation. Therefore, I propose the following name:

***Ducula tawitawi* sp. nov.**
Tawi-Tawi Imperial Pigeon
(Figs. 2, 4, 5D)

Zonophaps poliocephala McGregor & Worcester 1906: 12 (in part); McGregor 1909: 48 (in part).

Ducula poliocephala poliocephala Delacour & Mayr 1945: 89 (in part).

Ducula poliocephala nobilis duPont 1971: 130 (in part); duPont & Rabor 1973.

Ducula poliocephala Cox 1988: 54 (in part); Dickinson *et al.* 1991: 188 (in part); Kennedy *et al.* 2000: 142 (in part); Allen 2020: 62 (in part).

Holotype.—DMNH 14999, adult male collected by D. S. Rabor at Batu-Batu (but see below), Tawi-Tawi, Sulu Archipelago, Philippines, on 2 December 1971.

Diagnosis.—*D. tawitawi* has the pink belly of *D. poliocephala* (unlike *D. forsteni*) but the white throat of *D. forsteni* (unlike *D. poliocephala*). Its courtship or advertising song has a unique acoustic structure consisting of a low-amplitude buzz or ‘rattle’ followed by more notes (5–8) compressed into a shorter time interval, resulting in a higher tempo, than *D. poliocephala* and *D. forsteni*.

Type locality.—D. Allen (*in litt.* April 2026) recalled that in 1995, when he arrived in Tawi-Tawi at Batu-Batu, he ‘was urged to visit the forest of Tarawaken [when enquiring about] better quality forest[,] by travelling a very boggy and nearly impassable road heading north from [Batu-Batu].’ He thinks this was probably the same route taken by Rabor, who ‘most likely travelled by boat to [Batu-Batu;] then they would have walked overland north to the Tarawaken area. So, the type locality of [DMNH 14999] will most

likely be the Tarawaken area in Languyan municipality, accessed from [Batu-Batu] ... Many researchers later visited this area of Tarawaken [by travelling overland] from [Batu-Batu]. This includes trips by Bob Kennedy, Frank Lambert, and Dutson and Brooks ...' (D. Allen *in litt.* April 2026).

Etymology.—The name *tawitawi* is used as a noun in apposition.

Conservation status.—The wide-ranging *D. poliocephala* is uncommon on almost every island it inhabits, and its estimated global population of 5,000–10,000 individuals is inferred to be declining due to forest loss and hunting pressures (BirdLife International 2025b). The size of the *D. tawitawi* population must be far smaller because the species is restricted to a diminishing habitat (dipterocarp forest) on a single island. D. Allen (*in litt.* April 2026) recalled:

'I was fortunate to be able to visit [Tarawaken] several times in the 1990s. There had been a bit of selective felling but it was very moist and parts of it were swampy. It was rich in birds and often cool in the mornings owing to ground fog. I returned in 2008 but it had been heavily degraded and there was little bird life as it was much too hot.'

Deforestation has accelerated on Tawi-Tawi since the 1990s (van de Ven *et al.* 2019), with severe impacts to other endemic columbids including the Critically Endangered and possibly extinct Sulu Bleeding-heart *Gallicolumba menagei* Bourns & Worcester, 1894 (BirdLife International 2021), and the endangered Tawi-Tawi Brown-Dove *Phapitreron cinereiceps* (Bourns & Worcester, 1894), with an estimated population of 500–2,500 adults (BirdLife International 2025a). The situation for other forest endemics is similarly dire including Sulu Hornbill *Anthracoceros montani* (Oustalet, 1880), with fewer than 50 breeding adults (BirdLife International 2020), and Blue-winged Racquet-tail *Prioniturus verticalis* Sharpe, 1883, with a population of about 100–500 adults (BirdLife International 2025c). Given these circumstances, *D. tawitawi* will probably meet the criteria for threatened status.

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This paper is dedicated to the memory of Frederick Jess Thomas (1921–2000), my grandfather, a veteran of World War II, who served on the *USS Dyson* during the Philippine campaign (1944–45). I thank N. J. Collar and D. Allen for constructive feedback during peer review. Christopher Milensky assisted me with specimens in the USNM collection. Audio recordings were collected by Jason Alexander, Desmond Allen, Pritam Baruah, David Bates, Thomas Carlberg, Larry Chen, Po-Wei Chi, Kenneth Cheong, Bram Demeulemeester, David Edwards, Paul Fenwick, Ting-Wei Hung, 志民 蘇, Gregory Irving, He Ji-geng, Peter Kaehtner, Frank Lambert, Jeremy Lindsell, Roger McNeill, Paul Noakes, Pamela Rasmussen, Rose Ann Rowlett, Chi-Hsuan Shao, Brendan Sloan and Philippe Verbelen.

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Appendix 1

The following is a list of study skins and audio recordings examined by the author (MRH) arranged by taxon and geography. Museum acronyms: DMNH = Delaware Museum of Nature & Science, Wilmington; USNM = National Museum of Natural History, Smithsonian Institution, Washington, DC.

Specimens examined

Tawi-Tawi Imperial Pigeon *D. tawitawi*: Philippines (*n* = 3 males): Tawi-Tawi: Languyan, Batu-Batu: DMNH 14999 (male); Tataan: USNM 314700, 314701 (males).

Pink-bellied Imperial Pigeon *D. poliocephala*: Philippines (*n* = 34 males, 18 females, two unsexed): Cebu: unknown locality: USNM 314699 (male); Leyte: Leyte: Burauen, Tambis: USNM 537127 (female); Mahaplag, Mt. Kabalanti-an, Paniniklan: USNM 537126 (male), USNM 537128 (female); Luzon: Laguna: Pakil, Bo. Saray: DMNH 10898–10900 (males), DMNH 10901 (female); Pangil, Bo. Balian: DMNH 1700, 3501, 21746, 21747 (males), DMNH 21748 (female); Los Banos: DMNH 36171 (unsexed); Marinduque: Santa Cruz, Bo. Maculapnit: DMNH 66318, 66319 (males); Mindanao: Bukidnon: Bukidnon Lumber Concession: DMNH 69719 [juvenile], 69720 (females); Davao Oriental: Mati, Umluk: USNM

578457 (female); '*Davao*': locality unknown: DMNH 36172 (unsexed); Lanao del Sur: Lumba-Bayabao, Saronayan: USNM 578452, 578453 (males), USNM 578456 (female); *Misamis Oriental*: Opol, Malibato: USNM 578451 (male), USNM 578455 (female); *Surigao del Norte*: Albor (Libjo), Bo. Plaridel: DMNH 19687 (female); *Surigao del Sur*: Bislig, Rd. 2, Picop Lumber Concession: DMNH 4166, 4167 (males), DMNH 4168 (female); Car-Can-Mad-Lan area: USNM 578538 (female); Lanuza, Sibahay: USNM 578536 (male); '*Zamboanga*': unknown locality: USNM 200851–200853 (males); *Mindoro*: *Mindoro Occidental*: Mamara: DMNH 74341 (male); Abra de Ilog: DMNH 2890 (male); *Mindoro Oriental*: Socorro, Bo. Matungao: DMNH 10577 (male); Victoria, Bo. Alcate: DMNH 10576 (male); *Samar*: *Eastern Samar*: Llorente, Tipawala: DMNH 4501 (male); *Sibuyan*: Magdiwang, Bo. Silum: DMNH 28067, 28069, 28070, 28073 (males), DMNH 28071, 28072 (females); Mt. Guiting-Guiting, north slope: DMNH 28068 (female); Mt. Guiting-Guiting, west slope: DMNH 28066 (male); San Fernando, Bo. Espana: DMNH 66314, 66316, 66317 (males), DMNH 66312, 66313, 66315 (females); unknown locality: USNM 192556 (male).

White-bellied Imperial Pigeon *D. forsteni*: Indonesia ($n = 5$ males, one female): *Sulawesi*: Gimpo: USNM 251701 (male); Menado: USNM 178010 (male); Toemaratas: USNM 249632, 249633 (males); Rano Lindoe: USNM 250776 (male), USNM 250777 (female).

Mindoro Imperial Pigeon *D. mindorensis*: Philippines (one male, one female): *Mindoro*: *Mindoro Oriental*: Calapan, Bo. Arangin: DMNH 2813 (male); Nauhan, Bo. Tarugin: DMNH 37253 (female).

Audio recordings examined

Tawi-Tawi Imperial Pigeon *D. tawitawi*: Philippines ($n = 8$): *Tawi-Tawi*: Lubbuk: ML 319929481; Tarawakan: ML 203899211, 312725531, 315058081, 315058271, 315081131, 312726061; Unknown locality: ML 609099300.

Pink-bellied Imperial Pigeon *D. poliocephala*: Philippines ($n = 38$): *Luzon*: *Bulacan*: Angat Watershed: ML 196898; *Quezon*: Infanta: ML 636759580; *Mindanao*: *Agusan del Sur*: Bunawan: ML 615952651, 617180568, 638970785, XC 39861, 175401, 92701, 987939; Rosario: ML 651672816, 651676037, 651787732, 651787733; *Cotabato*: Magpet, Bo. Amabel: ML 18630, 18632, 18633, 18692; *Davao Oriental*: Aliwagwag: ML 38794, 38798; *Sultan Kudarat*: Senator Ninoy Aquino, Bo. Kuden: ML 509559631; *Surigao del Sur*: Cadanglasan: XC 1083616, 268929, 268931, 268934; Doña Carmen: ML 609063682–609063684; *Mindoro*: *Mindoro Occidental*: Siburan: ML 555871641, 623719644; *Negros*: *Negros Occidental*: Patag: XC 68209–68211; *Panay*: *Aklan*: Sibaliw: ML 203997281, XC 381613, 381614; *Samar*: *Samar*: Ulot River, SINP: ML 463661531, 463664461, XC 616254.

White-bellied Imperial Pigeon *D. forsteni*: Indonesia ($n = 22$): *Sulawesi*: *Sulawesi Utara*: Bitung: ML 640022094; Gunung Ambang: ML 607434671, 609065156; Gunung Mahawu: ML 203909321, 551375351, 607433391, 607459741; Taman Nasional (TN) Bogani Nani Wartabone: ML 218321831, 643125012, 650074670; Tangkoko Batuangas: ML 644447880, 644728236; *Sulawesi Tengah*: Kamarora: ML 33061; Sidaunta: ML 33083; TN Lore Lindu: ML 32760, 32784, 32806, 32815, 593116801, 597803891, 609069699.

Far from home: two narrowly distributed endemic species beyond their known ranges in south-east Brazil

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SUMMARY.—Although disturbed forests are often considered of limited conservation value, recent studies suggest they may still support important avian diversity, including forest-dependent, endemic and threatened species. Here we report two Atlantic Forest endemics—Grey-hooded Attila *Attila rufus* and Black-backed Tanager *Stilpnia peruviana*—more than 100 km beyond their previously known ranges in inland São Paulo, south-east Brazil. The records were obtained during non-systematic field observations in semi-deciduous forests. To assess the significance of these records, we reviewed published information on the species' distributions and habitat preferences, and compiled additional records from citizen science platforms. Our observations may not be isolated events but perhaps indicate a poorly documented dispersal capacity among some Atlantic Forest habitat-specialist birds.

The increasing number of unusual records involving common bird species beyond their known ranges (e.g., Antonelli & Cavarzere 2024, Souza *et al.* 2024) partly reflects the growing integration of citizen science data with bibliographic searches and museum specimen work (Areta & Juhant 2019), as well as targeted field surveys by experienced ornithologists in both remote areas and better-known but poorly monitored locations. Here, we document two range extensions for Atlantic Forest endemics in south-east Brazil—Grey-hooded Attila *Attila rufus* and Black-backed Tanager *Stilpnia peruviana*—whose distributions are limited to a relatively narrow strip of forest along the east Brazilian coast. We compiled all available records of these species to evaluate our unexpected records in the interior of São Paulo state.

Methods

Study areas.—Lageado (LEF) and Edgárdia (EEF) Experimental Farms, properties of the Universidade Estadual Paulista 'Júlio de Mesquita Filho' (UNESP), are in central-west São Paulo state, south-east Brazil (464–800 m; 22°47'–22°50'S, 48°22'–48°26'W), c.10 km beyond the urban perimeter of Botucatu municipality, and encompass 2,140 ha (Fig. 1). LEF contains more urban areas including the UNESP campus and agricultural fields, whereas EEF preserves floodplains, *cerradão* woodland, and seasonal semi-deciduous forests over >65% of its area. The region has transitioned from a humid subtropical (Cfa) to tropical savanna (Aw) classification (Alvares *et al.* 2013), characterised by wet summers (October–March, 1,500 mm annual rainfall) and dry winters (April–August), with a mean annual temperature of 21.3°C (Franco *et al.* 2023).

Bird surveys.—Monthly surveys were conducted during optimal detection periods (05.30–10.00 and 15.00–19.00 h) from May 2018 to April 2019, employing systematic ten-minute point counts (Bibby 2000) spaced ≥200 m apart across seven forest fragments, totalling 648 point counts (108 survey hours). Subsequent intensive sampling at EEF

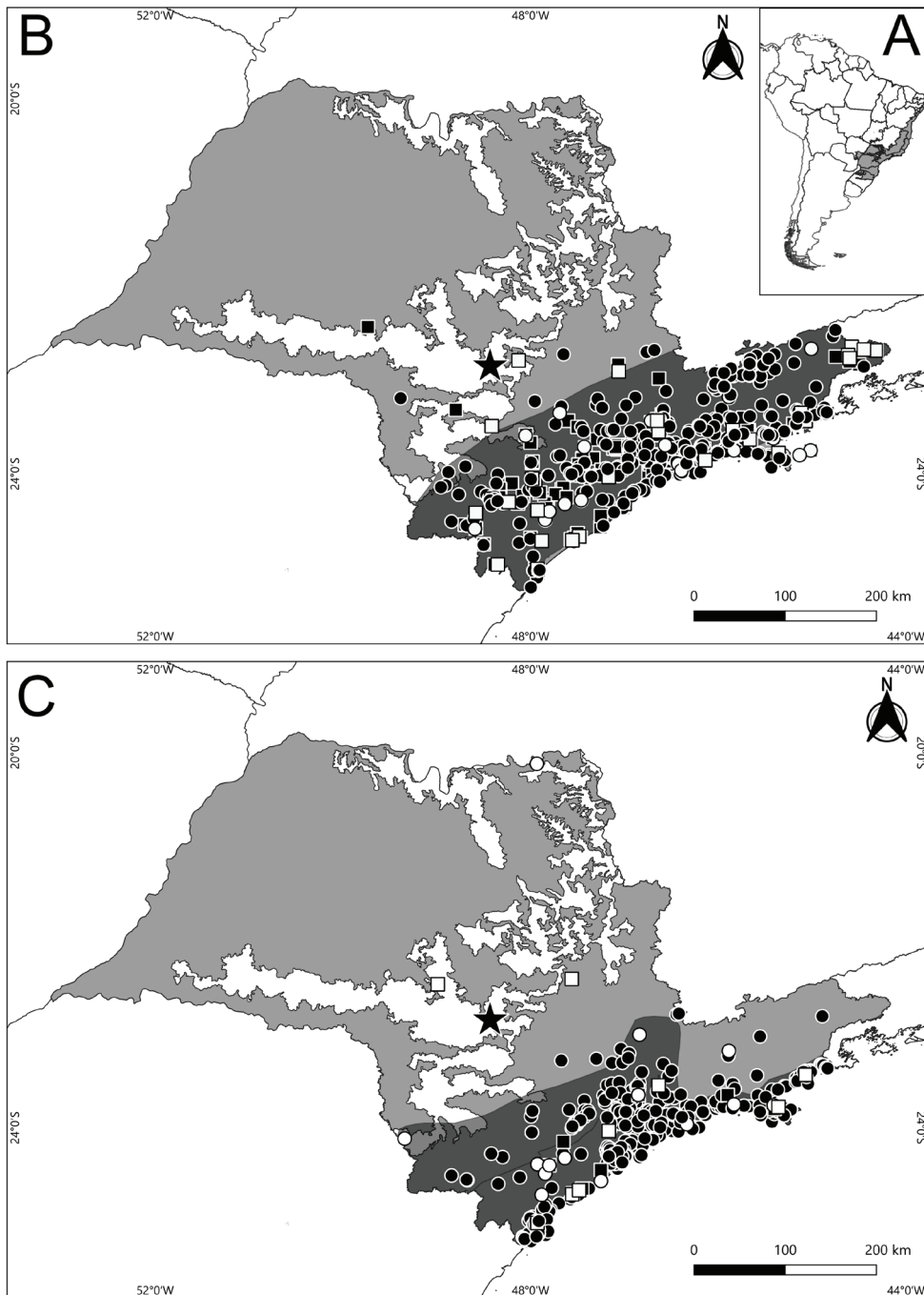


Figure 1. (A) The distribution of two Atlantic Forest endemic bird species based on a literature review and various ornithological platforms. The limits of the Atlantic Forest in South America are shown in pale grey. Dark grey indicates the known range for the species based on major literature sources, and, in the state of São Paulo, the white region is the Cerrado; (B) Grey-hooded Attila *Attila rufus*; (C) Black-backed Tanager *Stilpnia peruviana*. White symbols represent historical records (pre-2000), including museum specimens (circles) and undocumented field or literature records (squares). Black symbols represent recent records (since 2001), including those supported by photographs or sound recordings (circles) and undocumented literature records (squares). The stars represent our inland records in the municipality of Botucatu.

(September 2022–August 2023) incorporated an additional point in each restored area (51 total points), yielding 612 point counts (102 hours) and culminating in 210 total survey hours. We also conducted *ad libitum* observations in other habitats.

Literature review and ornithological platforms.—We searched for records of *Attila rufus* and *Stilpnia peruviana* in São Paulo using Google Scholar (<https://scholar.google.com/>), Scopus (<https://www.scopus.com/>) and Web of Science (<https://www.webofscience.com/wos>). Search strings used included combinations of the species' scientific names, synonyms and Boolean operators: 'Tanagra', 'Tangara' or 'Stilpnia' + 'peruviana' + 'São Paulo', 'Attila' + 'rufus' + 'São Paulo'. Given the large number of results on Google Scholar, we limited our evaluation to studies on the first ten pages for each species. We also searched for records up until 31 December 2024 in eBird (<https://ebird.org/>), iNaturalist (<https://www.inaturalist.org/>), Wikiaves (<https://www.wikiaves.com.br/>) and Xeno-canto (<https://xeno-canto.org/>).

We examined historical records compiled by Willis & Oniki (2003) in museum collections and literature sources, and queried occurrence data available via the Global Biodiversity Information Facility (GBIF, <https://www.gbif.org>). We incorporated records from Hasui *et al.* (2018) and Rodrigues *et al.* (2019), who compiled species occurrence in the Atlantic Forest.

Records obtained before the year 2000 were considered historical because they pre-date the major expansion of ornithological surveys, digital repositories and citizen science initiatives in Brazil, which have greatly increased the quantity and geographic coverage of occurrence data. To evaluate geographic patterns, occurrences were also classified as coastal or inland. Coastal records corresponded to localities within the Atlantic Forest region east of the Cerrado, whereas inland records comprised all occurrences within and/or west of the Cerrado in the interior of São Paulo.

Results

Field records.— *Attila rufus*, a species with few inland records in the state of São Paulo, was documented on 21 June 2024, along a stream in Bexiguento forest fragment at EEF (22°48'39.88"S, 48°24'50.07"W; 520 m). It was seen perched on vines c.10 cm above the stream but flushed when the observers approached. Thereafter, it responded to playback of the species' loudsong, permitting audio (ML 658733729, WA 7707994, XC 1138965) and photographic documentation (ML 658734035, WA 7708012; Fig. 2A).

Stilpnia peruviana is primarily associated with lowland forest. An adult male was recorded on 26 July 2019 on an *Inga laurina* tree at LEF (22°51'2.12"S, 48°25'54.44"W, 786 m) (ML658735802, WA3433603; Fig. 2B). It was seen foraging with a mixed-species flock that included Hooded Tanager *Nemosia pileata*, Tropical Parula *Setophaga pitiayumi*, Burnished-buff Tanager *Stilpnia cayana* and Sayaca Tanager *Thraupis sayaca*. Black-backed Tanager is known to occur in pairs or small groups, but has not been documented in mixed-species flocks (Ridgely & Tudor 1994, Isler & Isler 1999, Hilty & de Juana 2020). Elsewhere, a male and female of the species were seen foraging with other tanagers on a fruiting *Schinus terebinthifolia* at Parque Nacional da Restinga de Jurubatiba, Rio de Janeiro, on 8 June 2022 (eBird checklist S118853268), suggesting that the species may occasionally associate with mixed-species flocks (VRA pers. obs.).

Although part of broader structured bird surveys at LEF and EEF (totalling >200 hours of ten-minute point counts in 2018–19 and 2022–23), neither species was detected during formal sampling.

Literature review and ornithological platforms.—We compiled a total of 30,450 records of *Attila rufus*, predominantly from online platforms (Table 1). Literature records included three (undocumented) inland occurrences in São Paulo state from the 1970s to 1990s, in the



Figure 2. Photographic records of Atlantic Forest endemic bird species in Botucatu, São Paulo state, south-east Brazil. (A) Grey-hooded Attila *Attila rufus*, Edgárdia Experimental Farm, 21 June 2024 (Victor Rodrigues Antonelli); (B) Black-backed Tanager *Stilpnia peruviana*, Lageado Experimental Farm, 26 July 2019 (© Guilherme Notari)

TABLE 1
Number of reports from different sources of two Atlantic Forest endemic bird species—Grey-hooded Attila *Attila rufus* and Black-backed Tanager *Stilpnia peruviana*—in São Paulo state, south-east Brazil.

Species	eBird	Wikiaves	GBIF	iNaturalist	Literature	Xeno-canto	Overall
<i>Attila rufus</i>	14,675	2,333	13,137	122	115	68	30,450
<i>Stilpnia peruviana</i>	3,116	1,615	2,757	124	50	7	7,669

municipalities of Angatuba ($n = 1$), Anhembi ($n = 1$) and Alvinlândia ($n = 1$). Ornithological platforms held two records from Piraju ($n = 1$). For *Stilpnia peruviana*, we obtained 7,669 records, also primarily from online sources (Table 1). Two inland records were documented in literature: one from field observations in Rio Claro during the 1970s to 1980s, and another from *cerradão* in Agudos municipality (Almeida 1979), representing the furthest known occurrence from the species’ distributional centroid. However, this species complex has undergone several taxonomic rearrangements, and there is a possibility that the Agudos bird was the similar but more common and widespread, and formerly conspecific, Chestnut-backed Tanager *S. preciosa*.

Discussion

We documented two Atlantic Forest endemics with no published records from inland São Paulo in the last 50 years. These records are particularly significant because *Stilpnia peruviana* is classified as globally Vulnerable, and the known distributions of both species do not include inland São Paulo.

Although recent records of these species are confined to the Serra do Mar and Planalto Cristalino regions (in easternmost São Paulo), historical literature documents the occurrence of *Attila rufus* and *Stilpnia peruviana* in inland areas prior to extensive deforestation (Almeida 1979, Willis & Oniki 2003). The occurrence in this region of the tanager is unexpected, as it is typically associated with shrubby, often xerophytic vegetation near coasts (Isler & Isler 1999, Sick 1997), raising the possibility that inland records could involve escaped individuals (Senior *et al.* 2022). However, this explanation appears unlikely, given that only two individuals of the species are known among birds confiscated by the Brazilian Institute of Environment and Renewable Natural Resources (IBAMA) during 2003–13 (Vilela 2012, Charity & Ferreira 2020).

Attila rufus, a humid submontane and montane forest species (Ridgely & Tudor 1994, Sick 1997), has never been reported in any avian trade datasets. Additionally, there is a recent undocumented record from Caetetus Ecological Station (Cavarzere *et al.* 2009, Hasui *et al.* 2018).

Attila rufus is resident, but *Stilpnia peruviana* is considered partially migratory (Somenzari *et al.* 2018), with records from Rio de Janeiro and Espírito Santo, south-east Brazil (Hilty 2011, Hilty & de Juana 2020), in the austral winter. Additional occurrences have been documented in coastal Bahia in July 2014 (WA1418349) and July 2022 (WA4917497). We hypothesise that both species may undergo seasonal displacements, potentially driven by fluctuations in resource availability, involving not only elevational but also longitudinal shifts east–west, consistent with their relative prevalence along the Serra do Mar.

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A taxonomic reconsideration of the White-bellied Bustard *Eupodotis senegalensis*

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SUMMARY.—Possibly owing to chronic nomenclatural confusion and/or the difficulty of encountering sufficient museum material in one place, the taxonomy of the White-bellied Bustard *Eupodotis senegalensis* has remained unreviewed in modern times. However, a combination of the holdings at the Natural History Museum, Tring, and the availability of digital images on the Macaulay Library website now provides an opportunity for such work. Four subspecies, nominate *senegalensis* (West Africa to Ethiopia), *canicollis* including synonymised *erlangeri* (Ethiopia to Tanzania), *mackenziei* (Gabon to Zambia) and *barrowii* (essentially South Africa), were measured and scored for diagnostic characters. The eastern form *canicollis* proves to differ in seven characters, five of them distinctive (black subocular line, all-grey neck, upperwing pattern, black axillaries, greater size), and is recommended for species rank ('Grey-necked Bustard'). The other three are largely similar and here retained as one species, but *barrowii* and *mackenziei* together differ from nominate *senegalensis* to the point where, with further study, species rank might prove appropriate.

The nomenclature and taxonomy of the White-bellied Bustard *Eupodotis senegalensis* have an unusually rich history of confusion. The first description of the species, by A. A. H. Lichtenstein in 1793, applying the name *cafra* to a bird of southern African origin, was attributed by his son M. H. C. Lichtenstein to what is now known as Denham's Bustard *Neotis denhami*, an error that went unnoticed for over 150 years until Meise & Stresemann (1950) examined the obscurely published original text. With the support of R. Meinertzhagen, then Chairman of the Standing Committee on Ornithological Nomenclature of the International Ornithological Congress, Stresemann obtained the suppression of *cafra* for the White-bellied Bustard in order to allow the name *senegalensis*, applied to the species since 1820 and based on a specimen from Senegal, the stability of continuing usage. This proscription was, however, ignored in South Africa, seemingly owing to acrimony between senior figures in the ornithological establishment, resulting in the defiant usage there of *cafra* for another 50 years (Allan 2010). Moreover, as soon as South Africa began using *senegalensis* two influential publications there took the view that the southern subspecies of the White-bellied Bustard, for which the name *barrowii* became available following the suppression of *cafra*, constituted a full species, causing new disharmony including, at least initially, inconsistencies in the treatment of the taxon *mackenziei*, then known from Zambia and Angola (Allan 2011). Meanwhile in north-east and East Africa a remarkable degree of muddle over the application of the names *canicollis*, *erlangeri* and *somaliensis*, started by a misunderstanding of a key place name (see, e.g., Friedmann 1930), was finally resolved when it was realised that the latter two were based on a degree of age-related barring, notably on the tertials, and that only the first applied to the populations of the region (Turner 2010). Even now, however, this important correction has been overlooked by world

lists (e.g. Dickinson & Remsen 2013, del Hoyo & Collar 2014, Gill *et al.* 2025, AviList Core Team 2025).

Possibly this protracted fluctuation in the use of names has inhibited researchers from venturing a modern (i.e. post-Peters 1934) consideration of the taxonomy of the White-bellied Bustard. It may also (or alternatively) be that the wide range of the species, from Senegal east to Somaliland, and disjunctly south to South Africa via western Central Africa and East Africa, means that there are very few institutions in which such a consideration of preserved specimens can be undertaken. The best-placed of these for such work is the Natural History Museum in Tring (NHMUK), which houses extensive collections of birds from across Africa (e.g. Snow 1978). Its holdings of *Eupodotis senegalensis* run to more than 60 specimens from all parts of the species' range. However, it is now the case that the availability of photographs of living birds online is substantially reducing the near-total dependency that taxonomic researchers once had on museum material in order to advance our knowledge. In this regard the Macaulay Library (ML, www.macaulaylibrary.org) is a particularly valuable resource, tying all images (as do most museum specimens) to both a place and a date. As at 31 March 2026 the total number of photographs of *E. senegalensis* on ML was 3,592 (albeit many involving repeat shots of the same individual[s]).

This combination of physical material and digital imagery appears sufficiently strong to attempt a fresh consideration of the taxonomy of the species, albeit starting by accepting the well-justified synonymisation of *E. s. erlangeri* and *E. s. somaliensis* with *E. s. canicollis* in East Africa (Turner 2010). With this major adjustment, the taxonomy of world lists resolves into four subspecies:

E. s. senegalensis, Senegal east to north-west Ethiopia and Eritrea, and including northern Nigeria and Cameroon;

E. s. canicollis (with *erlangeri* and *somaliensis* as synonyms), northern Ethiopia and the Horn of Africa south to Uganda, Kenya and Tanzania;

E. s. mackenziei, eastern Gabon and Republic of the Congo south to eastern Angola and western Zambia; and

E. s. barrowii, extreme south-east Botswana, South Africa and eSwatini.

There has been relatively little interest in the study of these taxa to confirm or identify the characters that distinguish them, even though *barrowii* was, briefly, judged a separate species. Perhaps the fullest diagnoses indicated that (a) *barrowii* differs from the nominate by 'tawny-buff' extending up its hindneck, grey from the mid-breast to the white belly, a 'grey-blue spot' below the eye and more heavily marked upperparts; (b) *mackenziei* is like *senegalensis* but the male has the crown mainly grey, the female has upperparts intermediate with *barrowii*, and both sexes show tawny-buff undertail-coverts; and (c) *canicollis* is well marked owing to its thick black facial line, extensive black on throat, all-grey breast, black axillaries and larger size (Collar *et al.* 1986). The Macaulay Library photographs reveal that these descriptions, now 40 years old, are in some respects obsolete. The purpose here then is to scrutinise the taxa more closely and to attempt to re-evaluate the validity and distinctiveness of each.

Methods

The great majority of the material consulted in this study is held at NHMUK, supplemented by holdings at the Museum für Naturkunde, Berlin (ZMB). Specimens of adult males were the focus of investigation, in large part owing to their predominance in the sample but also in consideration of the potential confusion between immature males and females. In NHMUK 45 specimens of male White-bellied Bustard were inspected and measured, consisting of 15 nominate *senegalensis*, 18 *canicollis*, two *mackenziei* (including the

holotype, which Dowsett *et al.* 2008 mistakenly reported as lost) and ten *barrowii*; in ZMB the respective numbers were three, five, zero and one, making a total of 54. Mensural data in mm were gathered using digital callipers sensitive to two decimal places, steel rulers and, where necessary, a metal tape measure; the bill was measured from tip to front of skull, wing curved, tarsus from notch behind the intertarsal joint to base of the middle toe, and tail from tip to point of insertion. A morphometric comparison of taxa was made using principal component analysis (PCA) and visualised by drawing a PCA biplot.

The 3,592 photographs on Macaulay Library were rapidly reviewed, and records compiled of particular images which most effectively and informatively show characters distinguishing each taxon, as determined by the location of the individuals in question. Reference to specific photographs involves citation of a numerical code prefixed by ‘ML’.

For guidance on the issue of taxonomic rank under the Biological Species Concept, use was made of the system of scoring proposed by Tobias *et al.* (2010), in which an exceptional character (radically different coloration, pattern, size or sound) scores 4, a major character (pronounced difference in body part colour or pattern, measurement or sound) 3, medium character (clear difference, e.g., a distinct hue rather than different colour) 2, and minor character (weak difference, e.g., a change in shade) 1. A threshold of 7 is set to allow species status, which cannot be triggered by minor characters alone, and only three plumage characters, two vocal characters, two non-covarying biometric characters—both these and vocal characters assessed for effect size using Cohen’s *d* where 0.2–1.9 is minor (score 1), 2.0–4.9 medium (2), 5.0–9.9 major (3) and 10+ exceptional (4)—and one behavioural or ecological character (allowed 1) may be counted.

Results

The most salient finding of this exercise is that the eastern form *canicollis* merits species rank. Largely consistent with the diagnosis in Collar *et al.* (1986), it has four strong and two relatively weak diagnostic colour characters (see the compilation of photographs, selected for their representativeness and comparability, in Figs. 1–12) and is significantly larger in size than the other three taxa (Table 1, Figs. 13–16), which are all so much alike that for the purposes of comparison with *canicollis* they can be treated as conspecific. These seven distinguishing features are here listed in order of perceived strength, with Tobias criteria scores given in brackets after each, and ‘vs.’ used to introduce the character in the other taxa:

TABLE 1
Morphometric data (in mm) of males of the four subspecies of White-bellied Bustard *Eupodotis senegalensis* showing mean, standard deviation, range and sample size for four standard variables. ¹Sample size = 21; ² = 22; ³ = 27; ⁴ = 29; ⁵ = 28; ⁶ = 15; ⁷ = 17; ⁸ = 16; ⁹ = 10; ¹⁰ = 9; ¹¹ = 8.

taxa\ variables→	<i>n</i>	bill	tarsus	wing	tail
<i>canicollis</i>	23	46.8 ± 1.82 ¹ 44.2–49.3	105.5 ± 4.73 ² 96–113	306.3 ± 9.23 ² 285–322	165.6 ± 6.26 152–178
three taxa below combined	31	41.2 ± 2.61 ³ 35.6–45.6	92.8 ± 3.25 ⁴ 86–98	277.8 ± 10.47 ³ 260–300	146.5 ± 5.03 ⁵ 139–159
<i>senegalensis</i>	18	42.3 ± 2.71 ⁶ 35.6–45.6	92.6 ± 3.66 ⁷ 86–98	271.3 ± 6.09 ⁸ 260–282	144.8 ± 3.81 139–153
<i>mackenziei</i>	2	40.1 38.9–41.2	92.5 88–97	287.5 284–291	145 143–147
<i>barrowii</i>	11	39.8 ± 1.87 ⁹ 36.4–42.7	93.2 ± 2.04 ⁹ 89–96	287.2 ± 8.64 ¹⁰ 276–300	150.8 ± 5.68 ¹¹ 142–159

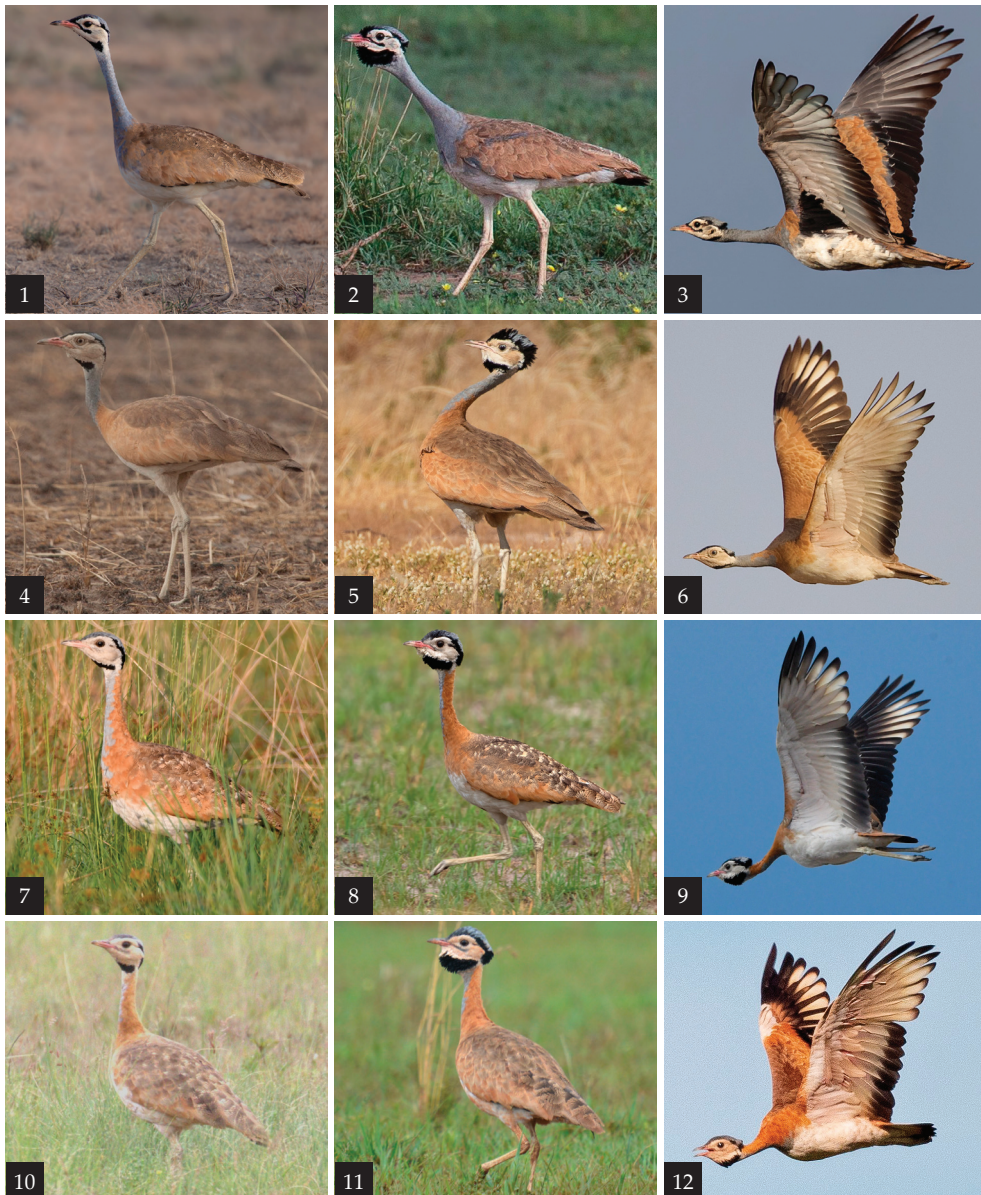


Figure 1. *Eupodotis senegalensis canicollis* male, Amboseli National Park, Kenya, 5 December 2025 (Alain Jacot, ML 648069598); Figure 2. *Eupodotis senegalensis canicollis* male, Alledeghi Wildlife Reserve, Ethiopia, 5 August 2018 (Chris Wood, ML 651099065); Figure 3. *Eupodotis senegalensis canicollis* male, Laikipia, Kenya, 8 September 2011 (Adam Scott Kennedy); Figure 4. *Eupodotis senegalensis senegalensis* male, Waza National Park, Cameroon, 10 March 2009 (Simon Colenutt, ML 262687661; image flipped for comparability); Figure 5. *Eupodotis senegalensis senegalensis* male, Ndiaffate, Senegal, 30 November 2019 (Stéphane Aubert, ML 236136261; image flipped for comparability); Figure 6. *Eupodotis senegalensis senegalensis* male, Ndiaffate, Senegal, 1 February 2026 (Gerard Phillips, ML 652613993); Figure 7. *Eupodotis senegalensis mackenziei* male, North-Western Province, Zambia, 12 November 2021 (Gabriel Jamie, ML 400635281); Figure 8. *Eupodotis senegalensis mackenziei* male, Western Province, Zambia, 8 November 2023 (Per Alström, ML 614337310); Figure 9. *Eupodotis senegalensis mackenziei* male, Western Province, Zambia, 8 November 2023 (Gabriel Jamie, ML 611388525); Figure 10. *Eupodotis senegalensis barrowii* male, Mpumalanga, South Africa, 7 December 2024 (Chris Rasmussen, ML 628893929); Figure 11. *Eupodotis senegalensis barrowii* male, Mpumalanga, South Africa, 6 December 2018 (Simon Tonge, ML 208221991); Figure 12. *Eupodotis senegalensis barrowii* male, Wakkerstroom, South Africa, 13 February 2022 (Dylan Vasapolli, ML 582747041; image flipped for comparability)

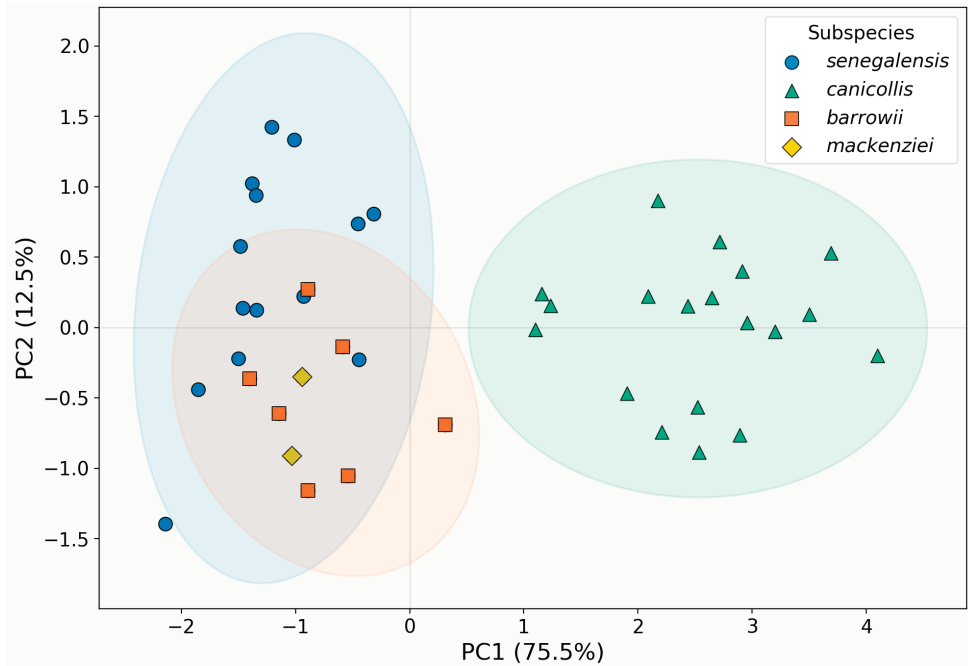


Figure 13. Principal component analysis (PCA) biplot for all measured morphometric parameters showing differences in subspecies of *Eupodotis senegalensis*. Ellipses (none for *mackenziei* as sample too small) represent 95% confidence intervals of the principal component scores for each taxon. Explained variation for each axis is given in parentheses.



Figure 14. Ventral view of male specimens of *Eupodotis senegalensis* in NHMUK. Left two nominate *senegalensis* (NHMUK 1922.12.8.219, 1922.12.19.2); middle two *barrowii* (NHMUK 1903.10.14.224, 1904.7.23.63); right two *canicollis* (NHMUK 1946.5.1534, 1910.4.30.13) (N. J. Collar, © Trustees of the Natural History Museum, London)



Figure 15. Dorsal view of the same specimens as in Fig. 14 (N. J. Collar, © Trustees of the Natural History Museum, London)



Figure 16. Lateral view of the same specimens as in Fig. 14 (N. J. Collar, © Trustees of the Natural History Museum, London)

- i. bold black line under the eye connecting to the forehead across the (frontal part of the) lores, isolating the white of the face from the maxilla (Figs. 1–2) vs. small grey or no patch, with lores all white (Figs. 4–12, 16; score 3);
- ii. wholly grey neck and lower ‘collar’, i.e. upper breast around the shoulders to the mantle (Figs. 1–2, 14–16) vs. much rufous (in nominate, sandy-rufous) on the hindneck, mantle and breast (Figs. 4–12, 14–16, score 3);
- iii. different upperwing pattern, involving whitish-grey vs. white inner webs of primaries (latter with blackish bases), and pale grey vs. sandy-rufous primary coverts and carpal area (so that the outer upperwing shows a large grey patch), plus a triangular pale grey patch on the inner forewing (Figs. 3 & 16 vs. Figs. 6, 9 & 12; score 3);
- iv. black vs. white axillaries—a constant character, as confirmed from Macaulay Library images with clear underwing views (40 *canicollis*, ten *senegalensis*, 18 *barrowii* + *mackenziei*) (compare Fig. 3 with Figs. 6, 9 & 12; score 3);
- v. greater size in all variables measured, with PCA clearly separating *canicollis* from all other taxa along PC1, which explained 75.5% of variance (Table 1, Figs. 13–16), and effect sizes >3 for wing and tail (2);
- vi. inverted black V on the upper throat and neck-sides larger and thicker, and extending onto the chin in a much sharper point (Fig. 14; score 1);
- vii. stronger colours and pattern on the bill (at least in presumed breeders), with a red basal half and blackish tip, the two colours being separated on the mandible by a small whitish patch (Figs. 1–2 & 16), this configuration generally being *much* weaker in *senegalensis* but very occasionally approached, as in ML 640176046, while an apparently different but distinctive pattern may or may not be consistent in *mackenziei* (see Fig. 8 and below) (1).

Combining the highest three scores for plumage and the score for larger size, a total of 11 is achieved, well above the threshold of 7 set for species rank; further differences, if allowed to be scored, would add another 5 points in this case.

The differences that lead to this conclusion show well in various combinations in photographs, where it is often particularly notable how much longer the neck of *canicollis* can appear—although an impossible character to measure—than in the other taxa (see Figs. 1–2 and 14–16). The score of 1 for the much redder bill base is conservative, owing to insufficient confidence in the evidence from photographs that some individuals of the other taxa might also rarely approach the colour intensity commonly visible in *canicollis*.

The other three taxa are united by their smaller size, and the degree of plumage divergence between them is not easy to gauge. A curiously divergent and insubstantial array of characters has been used by authors attempting to distinguish *mackenziei* from *barrowii*. White (1945) invoked its larger size, rufous-buff patch on the ear-coverts and paler, pinker (less orange) tawny rufous on the upperparts and wing-coverts (but none of these is upheld in specimens—see Table 1—or photographs). Mackworth-Præd & Grant (1962) named its ‘black markings above, and... lacking the blue spot below the eye’ (but the only two males available to them—those also examined by White—show the subocular patch and have upperparts matched by some specimens of *barrowii*: see Fig. 15). As noted above, Collar *et al.* (1986) indicated that the male has a ‘mainly grey’ crown (but in the male holotype and some photographs it is mainly black; possibly birds can control their coronal colours, as do Red-crested Bustards *Lophotis ruficrista* when displaying: Collar 2023), the female is intermediate above between *senegalensis* and *barrowii* (but the NHMUK’s only two females have upperparts identical to its only two female *barrowii*), and both sexes

have 'tawny-buff' undertail-coverts (but so do both sexes of *barrowii* and, although paler, *senegalensis*, the feature being weakest in some and absent in other *canicollis*).

Photographs from the range of *mackenziei* are inconclusive. Some individuals from the Republic of the Congo and Zambia (e.g. ML 652589991, ML 216477191, ML 639207971, ML611388480) are seemingly inseparable from *barrowii*, reinforcing the notion that *mackenziei* would better be treated as a synonym of the latter. However, a few images show males with a unique bill pattern, involving a very small dark tip, a fairly large whitish section behind it on both mandibles, and a rather strong red basal half (e.g. ML 612072255 [Congo] and multiple images from Zambia [number of individuals unclear], including Fig. 8). This seems likely to reflect individual variation, but pending closer examination of the issue *mackenziei* is reluctantly and provisionally retained.

Nevertheless, it is reasonable to consider *barrowii* and *mackenziei* to be so close as to be treated as a single entity in a comparison with nominate *senegalensis*, when the characters distinguishing them jointly are the

- i. small greyish subocular line or linear patch (sometimes called blue; but anomalously blackish in NHMUK 1904.7.23.63; Fig. 16, third from right), always disconnected from the forehead and far smaller than the homologous character in *canicollis* (consistent in NHMUK material but sometimes weak in photographs, e.g. Figs. 7–8) vs. absent in *senegalensis* (Figs. 4–5; score 1);
- ii. neck-sides and hindneck richer (vs. sandier) rufous and more extensive, involving all the hindneck and neck-sides (Figs. 7–12) vs. lower half of the hindneck (Figs. 4–6), i.e. neck rufous with grey line frontally vs. neck grey with rufous line to the rear (2);
- iii. distinct whitish patch on upper forewing at carpal vs. very indistinct or none (compare, e.g., Fig. 12 with Fig. 6, and note presence on both *barrowii* in Figs. 14 & 16) (1);
- iv. clearly patterned dorsum, darker and more mottled (Figs. 7–8, 10–11, 15) vs. almost plain and sandier upperparts (Figs. 4–5, 15; score 1);
- v. slightly longer bill (effect size 1.07, score 1) but notably shorter wings (effect size –2.27, see Table 1; score 2) (3).

On this basis, a total of 7 suggests that *E. barrowii* with subspecies *mackenziei* merits species rank; but despite relatively conservative scoring this conclusion is based on characters that would seem not to be important identifiers, and is clearly far less definitive than the situation with *canicollis*.

Discussion

The recognition of *E. canicollis* as a species represents a partial restoration of the status quo a century ago, when the White-bellied Bustard was judged to comprise three species (Sclater 1924, Bates 1930, Bannerman 1931, van Someren 1932–33) before Peters (1934) lumped them. In the number and strength of the characters differentiating *canicollis* from the other taxa the evidence for the split is compelling, irrespective of whether the Tobias criteria are employed. The greater quantity and arrangement of black on the head of male *canicollis* represents a powerful short-range distinction that the other taxa lack, whilst the black axillaries provide an equally powerful long-range signal of identity. The all-grey neck and breast give the bird a markedly different aspect (the English name Grey-necked Bustard seems an obvious choice for the species, reflecting its scientific name), and its overall larger dimensions, with PCA showing a complete separation from the other taxa (Fig. 13), imply an adaptation to somewhat divergent environmental conditions from those experienced by the smaller birds. These morphological distinctions carry sufficient weight to outbalance,

as taxonomic characters, the vocal similarities that appear to exist between the taxa (as also found between the species pairs Rüppell's Bustard *Heterotetrax rueppellii* and Karoo Bustard *H. vigorsii* and Northern Black Bustard *Afrotis afraoides* and Southern Black Bustard *A. afra*: Collar *et al.* 1986, Hockey *et al.* 2005), but which may in any case prove, with appropriate sampling, to possess consistent if subtle-seeming levels of divergence.

An interesting question remains over the precise distribution of *E. senegalensis* and *E. canicollis* where they approach each other in central Eritrea and northern Ethiopia. Taxon *senegalensis* occupies western Eritrea and immediately adjacent Ethiopia, whilst the latter widely inhabits the south-eastern two-thirds of Ethiopia east of a line stretching from the western border of Djibouti south-west to the western border of Omo National Park (Ash & Atkins 2009). However, this leaves a belt around 350 km wide between these two areas in northern Ethiopia in which the identity of the population has not been established, although for unstated reasons it has been referred to as 'possibly an extension of *senegalensis*' (Ash & Atkins 2009). This speculation is supported by a field sketch (ML 280361951) of a bird lacking the black subocular line of *canicollis*, from a site in Eritrea around 100 km east of the easternmost *senegalensis* square mapped in Ash & Atkins (2009). Certainly the possibility that this unattributed population would be an intergrade between the two known taxa appears too remote to be taken seriously.

Whether *E. barrowii* (with *mackenziei*) will also be restored to species rank is, however, less easy to gauge. At this stage it is perhaps premature to make the attempt. Some higher sample sizes for mensural data of birds from Cameroon and Gabon would be reassuring, along with better evidence on the size and constancy of the whitish carpal patch in *barrowii* + *mackenziei*. On the evidence of photographs on Macaulay Library there is also an interesting issue relating to iris colour. In *canicollis* all adult males invariably have dark and all females pale irides. In *barrowii* and *mackenziei* the pattern is the same. In *senegalensis*, however, adult males all appear to have pale irides (as just visible in Figs. 4–6). Intriguingly (and perhaps improbably), this circumstance may be related to differences not in iris colour but in the size of the pupil: inscriptions on the labels of two specimens of *barrowii* in NHMUK (1903.12.16.19–20) report 'pupil large and black, iris narrow & light brown'.

A second, possibly related issue concerns the coloration of the face and in particular the ear-coverts in some individuals. This study did not seek to address the differences between taxa shown by females, as their discrimination from young males is dogged by uncertainty in both museum specimens and online images. However, it is clear that females of all four taxa considered here almost invariably have (weakly to strongly marked) dull buff on the ear-coverts and sometimes on other (or all) parts of their head-sides; birds which by other characters appear to be young males also show this in varying degrees. From the Macaulay Library sample, the incidence among males of *canicollis* showing any such coloration is low, but it is relatively high in males of the other three taxa. Given the different frequencies of occurrence between the sexes, the phenomenon is unlikely to be the product of soil particle adsorption (Donald *et al.* 2017), leaving open speculation that it might be related to age or season.

It could certainly be related to sexual maturity or social dominance, as could pupil size (or at least the overall darkness of the eye). Mature males of all taxa seem always to have black eyes in white faces, suggesting that the bold visual contrast is a signal of fitness (displaying birds in Figs. 2, 5, 8, 11). An avenue into the issue might be through a photographic study of individually identifiable males over time, to determine if the overall darkness of the eye and the overall whiteness of the head-sides increase seasonally and/or with age.

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