Full Issue

Source: Bulletin of the British Ornithologists' Club, 143(4) : 401-616

Published By: British Ornithologists' Club

URL: https://doi.org/10.25226/bboc.v143i4.2023.a13

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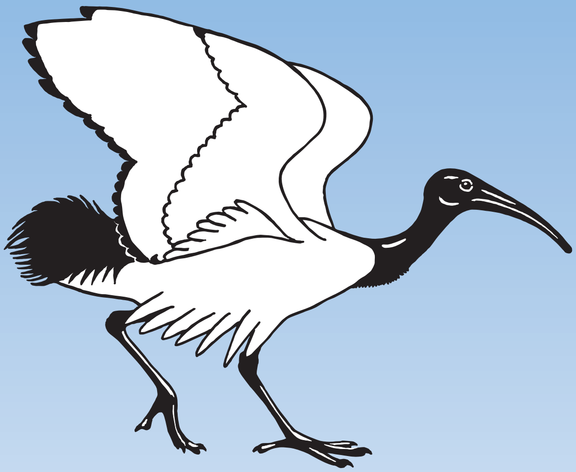
Bulletin of the British Ornithologists' Club



Volume 143 No. 4 (Online)
December 2023

ISSN 2513-9894 (Online)

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Bulletin of the British Ornithologists' Club
ISSN 2513-9894 (Online)
Edited by Guy M. Kirwan
Associate Editors: Robert Prŷs-Jones; Lincoln Fishpool; Bruce M. Beehler; Christopher J. Sharpe
Volume 143 Number 4, pages 401–616

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Registered Charity No. 1169733

www.boc-online.org

Published by the British Ornithologists' Club
Typeset by Eng-Li Green, New Mexico, USA

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Bulletin of the
BRITISH ORNITHOLOGISTS' CLUB

Vol. 143 No. 4 Published 4 December 2023

CLUB ANNOUNCEMENTS

The BOC's 2022 Annual Report and Accounts were published on 6 October 2023: the document is available to read or download at the following link: https://boc-online.org/wp-content/uploads/BOC.AnnualReportandAccounts.2022.pdf.

The 1008th meeting of the Club was held on Monday 22 May 2023 in the upstairs room at the Barley Mow, 104 Horseferry Road, London, SW1P 2EE.

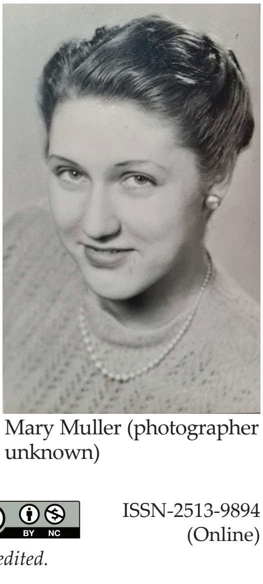
Thirteen people were present: Mr P. J. Belman, Mr K. Betton, Mr S. Chapman, Dr C. Fisher, Mr M. Howard, Mr A. Jackson, Dr R. Prŷs-Jones, Dr D. G. D. Russell, Dr R. Sales (*Speaker*), Mr S. A. H. Statham, Mr C. W. R. Storey (*Chairman*), Mr S. Watson (*Speaker*) and Mr D. Whitelegg. The meeting was recorded and a video of the event is available online at https://youtu.be/KU7MPekp41c and also via the Club website https://boc-online.org.

Dr Richard Sales, renowned for his wide-ranging research and publications on raptors, notably British falcons, and Steve Watson, who has been conducting a decades-long field study on the Peregrine Falcon *Falco peregrinus* in Gloucestershire, jointly presented a very well-illustrated talk entitled *The Peregrine Falcon*, based on their groundbreaking recent book of the same name. Richard's area of special research interest, namely the interaction between anatomy and behaviour underlying the Peregrine's flight characteristics and prey capture, synergistically complemented the broader focus by Steve on ecology and population characteristics, resulting in a particularly comprehensive overview. Broader discussion of the wide range and complex taxonomy (approaching 20 subspecies according to most authorities) of the species was not neglected, and the authors' detailed research included fascinating novel nuggets of information, including that the Peregrine's visual acuity is likely to be even greater than generally understood.

The 1009th meeting of the Club was held in conjunction with the Linnean Society of London at Burlington House, Piccadilly, London W1J 0BF, on Monday 6 November 2023 when Dr Will Smith spoke on *Rock Doves and the process of 'extinction by hybridisation'*. A detailed account of this meeting will be included in the March 2024 issue of the Bulletin.

OBITUARIES

Mary Nelson Muller (1925–2023)


Mary Muller (photographer unknown)

The bird world has lost a staunch supporter with the death in Bath, aged 98, of Mary Muller. Mary was born in Bournemouth in 1925, the daughter of Everard Nelson Exton, a WWI war hero, who was descended from a cousin of Horatio Nelson, and Clara Farnell-Watson, a teacher. Mary went to secretarial college and during WWII worked for the Special Operations Executive, the nature of her work there being still sealed by the government. In 1945 she went out to Ceylon (Sri Lanka) as a volunteer but was diverted to India.

Mary married Lloyd's underwriter Charles Muller in 1950; he was noted for taking on the insurance of 'large objects' such as airplanes, boats and dams. Charles's work took him all over the world, especially to South America, and Mary often went with him, binoculars at hand. They trekked up mountains, voyaged along the Amazon, and visited many remote places such as Robinson Crusoe Island. Birdwatching was always a big part of their travels. Mary and Charles raised four children, living firstly in London (where Charles was a councillor for Kensington and Chelsea Borough and he and Mary served as mayor and mayoress in 1968–69), then for many years in the mill house at Painswick, and from 2004 in a maisonette just off the Royal Crescent in Bath.

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ISSN-2513-9894 (Online)

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Mary spent as much time as possible doing charity work, using her secretarial skills in hospitals, schools and old peoples' homes, and with the organisation of the Poppy Appeals in Painswick, but birds were her priority.

Mary joined the British Ornithologists' Club in 1986, and became a stalwart of the organisation, attending many of the meetings (both domestic and foreign). She taught herself to use a computer when she was in her seventies so she could compile the annual index for the *Bulletin**. Her children helped her with changing fonts but were otherwise banned from disturbing her and rather dreaded the weeks each year she was incarcerated with her task. Two noisy parrots and a large collection of bird books, sculptures and pictures also testified to her passion for birds, and just before her death Mary was photographed avidly watching wildfowl and waders from the wheelchair-level window in her favourite hide at Slimbridge. She is survived by many friends, her four children, eight grandchildren and five great-grandchildren.

Clemency Fisher

* Prior to the advent of electronic 'tagging', such work was a true labour of love, and the present Hon. Editor and my predecessors, the late Dr David Snow and Prof. Chris Feare, are truly grateful for Mary's indomitable and always timely efforts.—The Hon. Editor.

Robin Restall (1937–2023)

There can be few visitors to the Neotropics unacquainted with the artwork of Robin Restall, especially through his illustrations prepared for his *magnum opus*, *Birds of northern South America* (BNSA), which spawned a series of national field guides covering Trinidad & Tobago; Aruba, Curaçao and Bonaire; Ecuador; and Venezuela.

It is less well known that Robin's 'day job' was as an advertising executive at J. Walter Thompson, where he enjoyed a highly successful professional career spanning 35 years, during which he rose to become a vice-president and member of the board. Throughout that time, and wherever he lived, Robin kept local birds in cages and aviaries, studying and writing about them. From 1960 he was a regular and well-known contributor to *Cage and Aviary Birds* and *Avicultural Magazine*. With his enthusiasm, energy and formidable autodidactic capacity, he wrote and illustrated his first book, covering four families and 350 species, *Finches and other seed-eating birds*, published by Faber & Faber in 1975. The illustrations, mostly line drawings, showcase his considerable artistic talent and his already recognisable style.

Robin was in many ways a quintessential Victorian naturalist. Birds were his vocation; he never received a professional salary, nor was he academically trained, and, although he did not collect, during his later years he dealt largely with skins, only occasionally venturing into the field, mainly on collecting expeditions. His principal contact with live birds was via his aviaries, where he kept and studied the small finch-like species beloved of aviculturists but often ignored by ornithologists, latterly *Sporophila* and munias and their allies.

Between 1989 and 1995 Robin lived in Hong Kong with his Venezuelan wife Mariela, where he ran J. Walter Thompson's Asia–Pacific office, and travelled throughout the region. He put this opportunity to study estrildids in their home range to good use, which led to the monograph *Munias and mannikins* and his first international recognition. Once the book was completed, Robin took the decision to leave his job, return to Venezuela and dedicate the rest of his life to painting and studying South American birds. Shortly after his arrival, Kathy Phelps, widow of Billy Phelps, offered him the title of Research Associate at the Phelps Ornithological Collection (COP), an honour subsequently conferred by John P. Phelps Tovar. After a day in the library and museum, Robin would retire to his house in one of the leafier parts of Caracas to document his menagerie of birds. Rigorous observations found expression in articles on Venezuelan species like: Is the Ring-necked Seedeater (*Sporophila insularis*) from Trinidad extinct, or is it a cryptic species widespread in Venezuela? (*Dept. Life Sci., Univ. West Indies, Trinidad Occ. Pap*. 11: 37–44) and (with ML) A new species of *Amaurospiza* blue seedeater from Venezuela (*Auk* 120: 600–606). But his curiosity quickly began to generate more questions than answers.

Robin quickly realised that, notwithstanding decades of published efforts by the Phelps family to document the country's avifauna (making Venezuela one of the best-studied countries in South America), there was still much to learn even about the identity of its birds, let alone their biology. One of the conundrums that Robin and ML faced in the process of identifying specimens that entered the collection was the marked inconsistency between the plumages represented in existing guides and the textual descriptions; this was exacerbated by the lack of depictions of juveniles and immatures. Robin soon began to feel the need to channel the results of his own investigations into producing a permanent catalogue and guide that others might use. Robin's friend, the publisher Christopher Helm, was immediately enthused by the idea, giving rise to his collaboration with ML and Clemencia Rodner on BNSA.

Over a period of ten years Robin invested thousands of hours in this project, which aimed to depict every distinct plumage of every bird in the region—painting more than 7,000 illustrations of in excess of 2,300 species. He was to be seen working up to 13 hours per day, six or seven days a week ensconced in his corner

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of COP, poring over a group of skins and surrounded by paints, typically to a jazz CD accompaniment. Apart from the vast amount of work undertaken at COP, the team covered their own costs travelling to collections in New York, Washington, Boston and Louisiana.

Robin Restall working in the American Museum of Natural History, New York, during preparations for the *Birds of northern South America* (Miguel Lentino)

The aim of BNSA was to produce a reference manual of the region's birds, in which Robin aimed to complete his goal to compile an illustrated catalogue of plumages. His work presented visually the immense diversity of plumages that a species can show both geographically and by age and sex, resulting in, for example, 18 figures for Bananaquit *Coereba flaveola* and 20 for Yellow Warbler *Setophaga petechia*! The plumages of some species remain poorly understood, like the diversity found in Bright-rumped—or Polymorphic—Attila *Attila spadiceus*, which Robin nonetheless faithfully painted. He was at pains to clarify that the plates were not intended to be used as a field guide, but as a supplement to the books specifically designed as field guides. In fact, Robin took great care to have his paintings show as much of the bird's plumage as possible, as one might expect to be able to appreciate in a museum—and this was typically at the expense of realistic natural poses, something for which he has sometimes been unjustly criticised. Robin worked like a draughtsman, ensuring that each species was depicted at the correct relative size within each family on a plate; and as all of his paintings were made primarily from skins, any plumage detail featured on the finished plate almost always corresponds to a character visible at close range or in the hand. Not until he was entirely happy with an illustration would he paint the sliver of highlight onto the eye, indicating that it was finished.

Apart from his more 'serious' art, Robin was always happy to put brush to paper to help a good cause, and he made countless paintings for book covers, calendars and papers, at the request of others or merely for pleasure. These sketches arguably showed him at his artistic best, allowing him much more freedom to express his flare for composition, for capturing the ineffable character ('jizz') of birds and—doubtless incorporating his advertising experience—for marrying text and illustration into an educational product. Besides birds and jazz, Robin took a keen interest in philately, publishing numerous scholarly articles on stamps in specialist journals.

Reluctantly, Robin moved with Mariela to Cambridgeshire, UK, in 2011 where they lived until his death. It is perhaps telling that he did not change his professional address, presumably (like so many Venezuelans) anticipating an eventual return to his tropical adoptive home.

Miguel Lentino & Christopher J. Sharpe

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REFEREES

I am grateful to the following, who have reviewed manuscripts submitted to the Bulletin during the last year (those who refereed more than one manuscript are denoted by an asterisk in parentheses): Jason Anderson, Norbert Bahr, Bas van Balen, Robert Bleiweiss, Peter Boesman, Alexander L. Bond, Nik Borrow, Frederik Brammer, Leandro Bugoni, Galo Buitrón-Jurado, Murray D. Bruce (*), Caio J. Carlos, Alice Cibois (*), Mario Cohn-Haft, Jacob Cooper, Robert J. Dowsett (*), Will Duckworth, James Eaton, Andy Elliott (*), Paul van Els (*), Bert Filemyr, Brian Finch, Clemency Fisher, Juan Freile, Harold F. Greeney, Steven Gregory (*), Matthew Halley, Floyd Hayes, Julian P. Hume, Santiago Imberti, Justin Jansen, Alejandro Kusch, Daniel F. Lane, Alexander C. Lees, Jônatas Lima, Michel Louette, Giselle Mangini, Manuel Marín (*), Miguel Marini, Fernando Medrano, Chris Milensky, Michael Mills, Jiří Mlíkovský, David Moyer, the late Gerhard Nikolaus, Roberta Olson, Dieter Oschadleus, Brian O'Shea, Robert Peck, Daniel Perrella, Robert Prŷs-Jones (*), Peter Pyle, Pam Rasmussen (*), Nigel Redman (*), Frank Rheindt, Robert Rockwell, Douglas Russell, Manuel Sánchez, Karl Schuchmann, Fabio Schunck (*), Manuel Schweizer, Phil Shaw, Fred Sheldon, Nicholas Sly, Frank D. Steinheimer, Martin Stervander, Simon Stuart, Paul Sweet, Joe Tobias, Till Töpfer, Angela Turner, Alan Tye, Geoff & Hilary Welch, Bret M. Whitney, and Kevin J. Zimmer.—The Hon. Editor

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Towards a more rational and stable nomenclature for Mallard *Anas platyrhynchos*, Greylag Goose *Anser anser* and their domesticates, including various priority issues, designation of lectotypes, and a First Reviser act

by Thomas M. Donegan

Received 11 May 2022; final revision 5 September 2023; published 4 December 2023

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Summary.—Three competing names were introduced by Linnaeus (1758) for Mallard, based on males (*Anas boschas*), females (*A. platyrhynchos*) and the hook-billed domestic breed (*A. adunca*). *A. domestica* (often attributed to J. F. Gmelin, 1789, but arguably better to Brünnich, 1764) was described later for domestic ducks. *A. platyrhynchos* was selected as having priority over its contemporaneous synonyms via First Reviser actions. Priority of widely used *A. p. domestica* remains threatened by the senior *A. adunca* and potentially by the mixed type series of *A. boschas* (comprising wild male Mallards and ducks of mixed or domestic origin). Lectotypes are designated here for *A. boschas* Linnaeus, 1758 (and its synonym *A. boschas fera* Brünnich, 1764, or Bechstein, 1792), using the same male Mallard specimen of wild phenotype illustrated by Albin (1734). This clarifies these names as objective synonyms of one another and as junior synonyms of *A. platyrhynchos*, as all three would then have a type series exclusively of wild Mallards from Western Europe. Garsault and Brünnich both named *Anser domesticus* in the same year, just three weeks apart—on 30 June 1764 and 23 July 1764, respectively. Garsault thus has priority. Consequently, Brünnich's *Anas anser domesticus* represents subsequent usage and his *A. boschas domestica* is not a homonym. Brünnich's *A. anser ferus* and *A. boschas fera* for wild geese and Mallards, respectively, if available, would be primary homonyms of one another. Acting as First Reviser, the latter name is here selected as having priority. Authorship of *Anser ferus* should be attributed to S. G. Gmelin (1770), whose locality of the Caspian Sea results in a potential threat to the priority heretofore afforded to *A. anser rubrirostris* Swinhoe, 1871, for the Eastern Greylag Goose. Brünnich's names *Anser boschas domestica* and *Anas boschas fera* were introduced as apparent trinominals; they were already in widespread use by 1764. In all likelihood Brünnich thought they had been described already, citing Linnaeus (1746, 1758) and Brisson (1760), but neither made these names available under the Code. Brünnich's names for domestics may not have been recognised because the same font was used in his work to denote distinct male and female plumages as for his *domesticus/a* and *ferus/a*, potentially denoting infrasubspecific variation. There is competing evidence as to whether or not he intended to name these units. Irrespective, under Art. 45.6.4 infrasubspecific names later adopted as valid are available. Regarding priority of *A. adunca*, I will separately be asking the Commission to endorse either Brünnich (1764) or J. F. Gmelin (1789) as author of *Anas boschas domestica*. Reversal of priority of *A. adunca* Linnaeus, 1758, vs. *A. boschas domestica* (Brünnich, 1764, or J. F. Gmelin, 1789), reversal of precedence of *Anser ferus* S. G. Gmelin, 1770, vs. *A. anser rubrirostris* Swinhoe, 1871, resolution of the type series for *A. anser* Linnaeus, 1758, and typification of the genus *Anser* Brisson, 1760, also all require ICZN attention.

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ISSN-2513-9894 (Online)

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Figure 1. Specimens referred to in the description of *Anas anser* Linnaeus, 1758, to the extent they were illustrated; A–E in subsection alpha ('Anser ferus'), F–G in subsection beta ('Anser domesticus') and H in subsection gamma ('Anser canadensis fuscus maculatus'). A: Gessner's (1560: 72) 'Anser ferus', probably a Bean Goose *Anser fabalis* (*sensu lato*), which was later traced by Aldrovandi (1603: 150; not reproduced here). B: Aldrovandi's (1603: 151) 'Anser ferus Ferraria missus', the specimen is poorly illustrated but accompanied by a detailed text description of a Greylag Goose. C: Aldrovandi's (1603: 152) 'Anser ferus alius ex Belgio missus à Do', probably a Bean Goose or Pink-footed Goose *Anser brachyrhynchus*. D: Aldrovandi's (1603: 153) 'Anser ferus alius quem Antonius Malchiauellus donauit', resembles no species but perhaps a Greater White-fronted Goose *Anser albifrons* or domestic goose. E: Willughby's (1678, pl. 69) 'Anser ferus' or 'Wild Goose', a juvenile Greylag Goose. F: Willughby's (1678, pl. 75) 'Anser domesticus' or 'tame Goose'. G: Gessner's (1555: 141) 'Anser domesticus'. H: Edwards' (1750, pl. 153) plate of Greater White-fronted Goose.

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Greylag Goose *Anas anser* Linnaeus, 1758, is a widespread and familiar grey goose native to Eurasia, in habitats including wetlands and urban parks. Mallard *Anas platyrhynchos* Linnaeus, 1758, is perhaps even more widespread and familiar, occurring either naturally or as an introduced species on all continents except Antarctica and often is the commonest wildfowl species around habitation.

These ducks and geese have been domesticated for centuries, related to human exploitation for meat, eggs, feathers, pâté and *foie gras*. Other wildfowl, e.g. Swan Goose *Anser cygnoides* (Linnaeus, 1758) and Muscovy Duck *Cairina moschata* (Linnaeus, 1758), have also been domesticated. Domestic wildfowl often include individuals with modified phenotypes, such as an expanded posterior body (related to egg laying), faster and more extensive development of muscle tissue for meat, reduced flight feathers or flightlessness (to minimise muscle wastage or escapism) and plumage variations such as predominant white feathering or leucism. Despite this, most domestic wildfowl can be identified by their habits, voice and morphology as being related to one of these two species. There is some introgression with other wildfowl, especially domestic geese derived from Swan Goose. However, Greylag Goose and Mallard are considered ancestral to the majority of farmyard and domestic geese and duck populations, respectively (Sun *et al*. 2014, Zhang *et al*. 2018). Molecular studies have demonstrated that all European domestic geese and one Chinese goose breed are descended from the Greylag, with a separate distinct domestic lineage descended from Swan Goose (e.g. Sun *et al*. 2014). Mallards have been domesticated for 1,800–2,600 years, with two main lineages for meat and egg-laying breeds (Zhang *et al*. 2018).

There is presently an unsustainable situation in wildfowl taxonomy, where *inter alia*: (i) the widely used subspecies name for domestic ducks, *Anas platyrhynchos domestica*, whose earliest plausible author is Brünnich (1764a), is potentially threatened by the priority of *A. boschas* Linnaeus, 1758, owing to the latter's mixed type series of both wild Mallards and mixed origin or domestic ducks; (ii) various post-1758 publications compete for authorship of *A. platyrhynchos domestica* and *Anser anser domesticus*, with interpretative difficulties as to whether certain of these publications qualify to establish an available name under the Code and two are near-contemporaneous and require further study to address the question of priority; (iii) designation of a type species for the genus *Anser* Brisson, 1760, has been attempted at least three times, as *A. anser*, *A. domesticus* and *A. ferus* but none of these is an originally included nominal species; (iv) three names were described contemporaneously for Mallard by Linnaeus (1758), with widespread usage of *Anas platyrhynchos domestica* Brünnich, 1764a, or J. F. Gmelin, 1789, for domestic ducks threatened by its senior synonym *A. adunca* Linnaeus, 1758, introduced for the unusual hook-billed domestic duck breed; (v) the type series of *Anser anser* (Linnaeus, 1758) was based upon the taxonomic concept of a single wild grey goose species, comprising at least three currently recognised species and domestic geese (Fig. 1); and (vi) a long-assumed junior synonym of *A. anser*, namely *A. ferus* S. G. Gmelin, 1770, is based on a specimen of Eastern Greylag Goose *A. a. rubrirostris* Swinhoe, 1871, creating a priority threat to the latter name.

The International Commission on Zoological Nomenclature (ICZN) will shortly be asked to resolve these priority and typification issues under forthcoming Case 3799 (see Anon. 2019) and others. Prior to that, it is advisable to resolve as many of these issues as possible, and the purpose of this paper is to address the first two of them; some background is also provided on some of the others.

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Type specimens of *Anas anser* and other names for grey geese

The widely used name *Anser anser* (Linnaeus, 1758), is based on a taxonomically mixed concept and has no extant type specimens or illustrations of this material. In the mid 1700s, it seems many ornithologists recognised just one, general grey goose concept. Specimens of most or all of the Bean Goose *Anser fabalis* (*sensu lato*), Greater White-fronted Goose *A. albifrons* and Greylag Goose had been described morphologically by this period, but they were not routinely identified as separate species. Gessner (1555) referred to four different classes of goose and Aldrovandi (1603) described some of them in different sections, but this did not gain traction. Linnaeus (1758) separately named only Lesser White-fronted Goose *Anas erythropus*, including sources depicting or describing all the other species under *A. anser* Linnaeus, 1758. Plates depicting specimens referred to in the original description of the latter name are shown in Fig. 1.

Linnaeus' (1758: 123) description of *Anas anser* starts with a vague description of unidentifiable grey geese from Sweden, then refers to the corresponding account of his earlier *Fauna Svecica* (Linnaeus 1746: 32, para. 90). Next and unusually, Linnaeus (1758) introduced a subsection labelled alpha, citing the 'Anser ferus' (or wild goose) of earlier authors, thereby cross-referencing a non-binominal name. Other names of earlier authors, many of them longer than three words, were cited by Linnaeus in the same format in his species accounts. He did not make available the names 'Anser ferus' (or 'Anser domesticus', which follows in his subsection beta), since neither name appears in the left margin and none of the words 'variety', 'form' or their abbreviations were used (Art. 45.6.4 of the *Code*). The alpha subsection cites Aldrovandi (1603), Gessner (1555), Willughby (1676) and Ray (1713). Under Art. 72.4.1, 'the type series of a nominal species-group taxon consists of all the specimens included by the author in the new nominal taxon (whether directly or by bibliographic reference)'. The most detailed account, based partly on Gessner (1555) and which the other cited authors drew upon heavily, is the 'Anser ferus' of Aldrovandi (1603: book 19, chapter 18, pp. 147–154). Aldrovandi's (1603) entire chapter 18 was cited by Linnaeus (1758), rather than specific pages or plates.

Aldrovandi (1603), following Gessner (1555, 1560), may have identified at least three and possibly four of the wild grey geese species regularly found in Europe, given four separate subsections in his 'Anser ferus'. None of these accounts was placed in his descriptions of different goose species by Linnaeus (1758). The bird in the first of Aldrovandi's (1603: 150) four plates ('Anser ferus Ornithologi') has a bicoloured relatively small bill, as detailed in the text ('rostro nigro untrinque per medium croceo'). The description is clearly a Bean Goose. The relevant plate was apparently traced by Aldrovandi (1603) from the identical plate in Gessner (1555: 158; Fig. 1A). Gessner's later *Icones* (1560: 72) includes the same plate. Gessner (1555) commented that he thought this plate to be of a Greylag Goose (using the German vernacular) but that would be inconsistent with his text and line drawing. Aldrovandi's (1603: 151) second plate ('Anser ferus Ferraria missus'; Fig. 1B) is accompanied by a text description of a specimen provided to him by Alfonso Cataneo, Duke of Ferrara, which is a perfect and detailed account of a wild Greylag, including its modified neck feathers, orange legs and bill, white vent, white markings on the wing feathers and structural similarities to domestic geese. The plate is rather odd, for example showing isolated dark secondaries, rather than the whole wing being dark. Aldrovandi's (1603: 152) third plate ('Anser ferus alius ex Belgio missus à Do'; Fig. 1C) is based on a Belgian specimen. Due to its small bill and the text description, it appears likely to be another Bean Goose or a Pink-footed Goose. Finally, Aldrovandi's (1603: 153) fourth plate entitled 'Anser ferus alius quem Antonius Malchiauellus donauit' (Fig. 1D) depicts a large-billed goose with unusually modified neck

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feathers and no white front, but belly markings broadly resembling Greater White-fronted Goose. It could be that species or an unusual domestic goose, or perhaps an interpolation based on two or more species, or an artefact. The Biblioteca Universitaria di Bologna holds coloured versions of all these plates, but in each case the colouring is interpolated, inconsistent with the corresponding text account, and therefore they are ignored here.

Also under his alpha subsection, Linnaeus (1758) cited the 'Anser ferus' or 'Wild Goose' of Willughby (1676: 274) and the 'Anser ferus' of Ray (1713: 146, no.A.4), which is an abridged version of Willughby (1676). Willughby (1676) drew extensively on Aldrovandi's (1603: 149) text. Willughby (1676, pl. 69; Fig. 1E) additionally depicted a gosling, presumably of Greylag Goose, which is the only grey goose that breeds regularly in the English Midlands, where Willughby was based (Nottinghamshire).

Next, the beta subsection references the pre-Linnean name 'Anser domesticus'. Referenced bibliographic works under subsection beta, and the specimens that they are based upon, describe or depict domestic geese descended from Greylags: (i) the 'Anser domesticus' of Gessner (1555: 141; Fig. 1G), a white domestic goose; (ii) 'Anser Domesticus' or 'The Tame Goose' of Willughby (1676: 273, pl. 75; Fig. 1F), with the plate showing an inelegant domestic goose and the text discussing domestic geese of various plumages; and (iii) the corresponding account in Ray (1713: 136) based on Willughby (1676). Finally, the gamma subsection refers to a plate and text in Edwards (1750: 153; Fig. 1H) of Greater White-fronted Goose *Anser albifrons* (Scopoli, 1769) from North America. Linnaeus' description ends with a note that *Anas anser* occurs in Europe and America, and is mostly boreal. A morphological description then follows in an unnumbered paragraph, which perfectly describes Edwards' White-fronted Goose. A separate paragraph not within any labelled subsection of a Linnean description would not usually be regarded as part of the account of a distinct variant. However, in context, as this text described only the specimen mentioned in the gamma subsection that immediately precedes it, it is better interpreted as referring only thereto.

Typification of *Anas anser* Linnaeus, 1758, is incapable of a satisfactory resolution herein because the name is universally applied to Greylag Goose and the only wild Greylag specimens in the original description (Figs. 1B, 1E) were included by Linnaeus (1758) in his *A. anser* under subsection 'alpha'. Under Art. 72.4, neither specimens included as 'distinct variants (e.g. by name, letter or number)' nor those which the author 'doubtfully attributes to the taxon' may be part of the type series. Linnaeus' (1758) citation of an alpha variant in his *A. anser* description was unusual; he more often started with an unnumbered subsection then listed other variants starting with beta. It is therefore arguable that the alpha variant is the 'main', rather than a 'distinct', variant. However, even then, the materials under alpha are likely to be 'doubtfully attributed', since the introduction of an alpha subsection was quite unusual. Some ICZN Commissioners have communicated that they would not support a lectotype designation (without recourse to plenary power) from among the alpha subsection specimens. Linnaeus' (1758) insertion of the alpha symbol in his description virtually denudes *A. anser* of any type materials, except those in his own collection, which as discussed below are no longer extant for geese. The Commission will in due course be asked to use its plenary power to set all previous designations aside and select Aldrovandi's Greylag from Ferrara as the type.

It took some decades for the other grey goose species placed by Linnaeus (1758) and subsequent authors in *Anas anser* or 'Anser ferus' to be recognised specifically. Latham (1785, 1787) first recognised the Bean Goose (his description covering both pink- and orange-legged birds) as separate from Greylag. He did so first in an English-language publication, then two years later named *Anser fabalis* Latham, 1787. He seems to have been

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the first post-1758 author to restrict *Anser anser* to Greylag, although Willughby (1676, 1678) had done so earlier for 'Anser ferus'. Latham's taxonomy largely contradicted that of earlier and contemporary authors, in which 'Anser anser' or 'Anser ferus' were usually rooted in the Bean Goose or other more migratory or northern species (e.g. Gessner 1555, 1560, Aldrovandi 1603, Linnaeus 1746, 1758, Pallas 1769, Schäffer 1774, 1789), but his restriction ultimately was accepted. Baillon (1834) later distinguished Pink-footed Goose from Bean Goose, describing *Anser brachyrhynchus* and restricting *A. fabalis* to Bean Goose.

Probably a neotype or lectotype designation will be necessary in due course for Latham's *A. fabalis*, since it has a mixed type series (see Witherby *et al*. 1943), but such a step is outside my scope here and best awaits a prior Commission ruling on the type specimens of *Anas anser*.

Authorship and dating of the name *Anser domesticus* for domestic geese

Linnaeus (1758) made available names for various domesticates of wild birds, notably *Columba oenas domestica* Linnaeus, 1758, for pigeons and two domestic breeds (*australis* Linnaeus, 1758, and *orientalis* Linnaeus, 1758) of Swan Goose *Anser cygnoides* (Linnaeus, 1758). However, he did not formally name domestic Mallards or Greylag Geese. The pre-Linnean name 'Anser domesticus' was merely referred to by Linnaeus (1758: 123) in his account of *Anas anser* under subsection 'beta' without any name in the margin, thus the name is not available. Nonetheless, Linnaeus (1758) was cited by his contemporaries and followers, and is still incorrectly cited by some today (e.g. www.GBIF.org, www.natureserve.org; Sirsat *et al*. 2006) as author of *A. anser domesticus* and *A. boschas domestica*. Linnaeus' contemporaries and followers who used names for domestic wildfowl, including Brisson, Brünnich, Pallas, S. G. Gmelin, J. F. Gmelin and Bechstein, seem to have assumed these names to have been authored by Linnaeus. It is therefore complicated to establish which of them made the names available, as in each case an assessment is required as to whether usage in works that do not purport to be descriptions meet (or do not meet) the requirements of availability under the Code. The dating and authorship of *Anser domesticus* for domestic geese are particularly problematic.

Brisson (1760: 262) first used 'Anser domesticus' (and, at p. 308, 'Anas domestica') in combination after 1758, attributing these names to Linnaeus, 1758, and establishing the genus *Anser* Brisson, 1760, for geese. Unlike his genera, Brisson's species names are not available for nomenclatural purposes pursuant to opinions, resolutions and directions of ICZN since the early 1900s (ICZN 1950, 1955, 1958, 1963). These rulings are based on the conclusion that, although Brisson (1760) used genera consistent with Linnean binominal nomenclature, his species names did not consistently use such a scheme for the purposes of Art. 11.4 (see Gentry 1987).

Four years later, Brünnich (1764a) published numerous species-group names of northern and Arctic species in *Ornitologia borealis*. Under genus 'Anas', he (at pp. 13–14) introduced 'ANSER *domesticus*' in a numbered account in the highest hierarchy of the work, following two accounts named 'ANSER *ferus*'. He then authored similarly numbered accounts (at p. 20) for 'BOSCHAS *fera*' and 'BOSCHAS *domestica*'. These would appear obvious trinomials, introduced in a way that would usually confer availability under Art. 45. They are *a priori* trinomial names, not infrasubspecific names, so Art. 10.2 does not apply to require another indication such as the word 'form' or 'variety' in order to make these names available. Brünnich (1764a) was an enthusiastic early adopter of Linnean binominal nomenclature. However, his authorship of 'Anas anser ferus', 'Anas anser domesticus', 'Anas boschas fera' and 'Anas boschas domestica' has not previously been recognised.

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For example, Sherborn (1922: 308), Phillips (1923: 3) and Richmond (1992) attributed *Anas domestica* to Gmelin (1789: 538). Richmond (1992) considered *A. anser domesticus* and *A. anser fera* to have been made available by Bechstein (1792: 382) and Schäffer (1789: 67), respectively; Sherborn (1922: 364) concurred regarding the latter. *A. domestica* of Gmelin's (1789) authorship would be based upon a mixed type series as, among others, he cited Albin's (1734) plate of the Madagascar endemic, Meller's Duck *A. melleri* (Fig. 2I). However, that is irrelevant if Brünnich (1764a) made the name available first.

Brünnich's (1764a) names for domesticates may not have been recognised as available names previously because they were introduced in the same font and hierarchy as that used for the words 'mas', 'foemina', 'pullus' and 'varietas', which indicate male, female, juvenile forms and unnamed varieties, respectively. Under Art. 1.3.5, names proposed 'as means of temporary reference and not for formal taxonomic use as scientific names in zoological nomenclature' are excluded. Under Art. 45.6.4, Brünnich's (1764a) names would be infrasubspecific if 'the content of the work unambiguously reveals that the name was proposed for an infrasubspecific entity'. His use of lower case italics to denote sex and age could be taken as an indication to denote a merely infrasubspecific feature for domestics. However, that may not be the best interpretation. In the Code's Glossary, a 'name' is defined as '(1) (general) A word, or ordered sequence of words, conventionally used to denote and identify a particular entity (e.g. a person, place, object, concept). (2) Equivalent to scientific name (q.v.). (3) An element of the name of a species-group taxon: see generic name, subgeneric name, specific name, subspecific name.' Of course, Brünnich's (1764a) usage of 'mas' and 'pullus' are not plausibly 'names', either under this definition or as a result of Art. 1.3.5, but in principle *ferus/a* and *domesticus/a* fall under the first of the Glossary's definitions. Notably, each of these was widely used as a name with taxonomic connotations or for distinct groupings of wild and domestic wildfowl in the pre-Linnean literature, as well as by Linnaeus (1746, 1758) and Brisson (1760), both of whom were cited by Brünnich (1764a) as his main sources. Adjectival names like '*fera*' and '*domestica*' are generally acceptable (Art. 11.9.1.1); the name 'domestica' was indeed already formally described for domestic populations in other avian genera, e.g. *Gallus gallus domesticus* Linnaeus, 1758, and *Columba oenas domestica* Linnaeus, 1758. Brünnich (1764a) probably assumed that his names *domesticus/a* and *ferus/a* had Linnaeus (1758) or Brisson's (1760) authorship already; whether their font is more relevant than this context can be debated; the availability of these Brünnich names will need to be considered by the Commission when it addresses the priority threat posed by *Anas adunca* to *A. domestica*. As Brünnich (1764a) is entirely in Latin, he probably had little other option than to write out 'pullus', 'mas' and 'foemina' as Latin words. He may have used the same font for two different infraspecific contexts, but it is not clear that he intended both types of usage to denote infra*sub*specific variations. Even if the evidence of font were to trump other contextual evidence, Art. 45.6.4.1 would likely still apply to save Brünnich's authorship: 'a name that is infrasubspecific under Art. 45.6.4 is nevertheless deemed to be subspecific from its original publication if, before 1985, it was either adopted as the valid name of a species or subspecies or was treated as a senior homonym'. The names *domestica/us* for geese and ducks were widely used after 1764, albeit not usually with Brünnich's (1764a) authorship, including prior to 1985. (The names *ferus/fera* are less used, being long regarded as synonyms at species and subspecies level, but still were used into the 20th century.) If his authorship is accepted, as Brünnich (1764a) placed all these names in *Anas*, his two *ferus/a* and two *domesticus/a* would *a priori* be primary homonyms. However, there is a competing claim in priority for his domestic goose name.

In the same year as Brünnich (1764a), Garsault (1764, pl. 679) used the name *Anser domesticus* alongside an original plate of a white domestic goose. Garsault included

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depictions of various taxonomic groups—plants, mammals and some birds—used in contemporary medicine. Each is given a French and Latin name on the relevant plate, and these are repeated in the index. Critically, Garsault (1764) deployed only one- or two-name epithets, and thus is a work rooted in binominal nomenclature making his names available (Welter-Schultes *et al*. 2008, Welter-Schultes & Klug 2009, 2011).

Welter-Schultes & Klug (2009) discussed possible reasons as to why Garsault's (1764) animals and birds deployed a binominal system, when neither of the same author's works on plants nor contemporary or later French authors such as Brisson (1760) or Buffon (1770–83) did so. Garsault's (1764) bird names overall seem mostly Brissonian, not Linnean, in origin as might be expected from a publication of this era by a French author, given that Brisson was at the time arguably the world's leading ornithologist (e.g. Allen 1910) and had published his career-defining *magnus opus* on birds (Brisson 1760) just a few years earlier.

Only eight of Garsault's (1764) 34 bird names are binominal (i.e., comprising genus and species names), the rest all being single, genus-like, names. Twenty-two of the 34 bird names in Garsault (1764) are the same as those in Brisson (1760) for the same species concept (disregarding a single-letter difference in the spelling of one name and a hyphen), including 'Anser domesticus'. The remaining 12 names used by Garsault (1764) show no clear pattern that might imply a single source, as noted by Welter-Schultes & Klug (2009), but none is novel, all of them having been used by pre-Linnean authors, e.g., Gessner (1555, 1560), Aldrovandi (1603 and other volumes), Belon (1555, 1557), Barrère (1745) or Charleton (1668, 1677). Several of Garsault's (1764) two-word names, e.g., 'Alcedo muta' for Common Kingfisher and 'Aquila regalis' for Golden Eagle, do not follow Linnaeus' names (these being *Alcedo ispida* Linnaeus, 1758 and *Aquila chrysaetos* Linnaeus, 1758). Arnault de Nobleville & Salerne (1756–57) may have been a source for other taxonomic groups (Welter-Schultes & Klug 2009).

There is therefore no evidence that Garsault (1764) was even aware of Linnaeus' (1758) work or bird names. His names and taxonomy are largely Brissonian; Brisson's (1760) species names were not consistently binominal and so are not available, as discussed above (ICZN 1950, 1955, 1958, 1963). Welter-Schultes *et al*. (2008) and Welter-Schultes & Klug (2009), who considered all of Garsault's (1764) animal names to be available, made reference to possible knowledge by Garsault of Linnean nomenclature via Daubenton, who went on to adopt binominal nomenclature some decades later. However, closer in time to 1764, Daubenton co-authored the *Planches enluminées* (Martinet *et al*. 1765–83), which did not include Latin names—binominals were later specified for species newly recognised therein by Statius Müller (1776), Pennant (1786), Gmelin (1789) and others. Daubenton's main collaborator, Count Buffon, adopted a French-language-only system (e.g. Buffon 1770–83), later becoming a fierce critic of binominal nomenclature (e.g. in Buffon & Daubenton 1749–67; see Sloan 1976). There is no requirement in the Code or any of the decisions or rulings on Brisson's works that an author must not be a follower of (or employ species names based upon) Brisson (1760).

Welter-Schultes *et al*. (2008), Welter-Schultes & Klug (2009, 2011) and Dubois & Bour (2010) discussed the numerous consequences for priority and authorship due to the discovery of, and assessment of the availability of names in, Garsault (1764), with a particular focus on some of his mammal and herptile names. The goose name *Anser domesticus* Garsault, 1764, was considered available by Welter-Schultes & Klug (2009), but they recommended that specialists in other taxonomic groups consider further the consequences of Garsault's proposed authorships. For birds, Welter-Schultes & Klug's (2009) suggestions were broadly accepted by Dickinson & Remsen (2013) without comment. However, they did not list subspecies names used for domesticates, so Garsault's goose name was not considered.

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For the reasons above, Garsault (1764) and Brünnich (1764a) are both regarded as likely involving a valid description of *A. anser domesticus*. These works were published in the same year and so an issue of priority arises if Brünnich's (1764a) name is available. Garsault (1767: aij) asserted that Garsault (1764) was published in June 1764. This likely constitutes sufficient evidence of the publication date for Art. 21.7. The precise date would be deemed as the last day of the month, i.e. 30 June 1764, under Art. 21.3.1.

The dating of Brünnich (1764a) is more complicated and requires other evidence to be taken into account. The work has a preface dated 20 February 1764, but this is not the publication date. Dickinson *et al*. (2011) noted that 'The dates on the preface, if any, and on the title page … generally reflect the points at which the writing and the printing of the work, respectively, were completed.' The actual publication date of Brünnich (1764a) would therefore have been later. For the reasons below, Brünnich's (1764a) work can be dated as 23 July 1764, which is three weeks after Garsault (1764).

On 23 July 1764, Brünnich wrote a three-page somewhat cryptic letter to Linnaeus which, from its context and based upon a reply of 20 August 1764, appears likely to have attached a published version of his *Ornithologia borealis*. The letter and its response have been digitised by the Uppsala University Library and are currently available online at www.alvin-portal.org. The Linnean Society in London holds Linnaeus' own copy of *Ornithologia borealis* but it contains no indications as to date of receipt (W. Beharrell *in litt*. 2022).

In understanding the context of Brünnich's July letter to Linnaeus and the latter's response, it must be mentioned that Brünnich (1764b) published another book, *Entomologia*, the same year. Its preface is dated 17 March 1764, and a similarly archived letter unambiguously attaching it, sent to Linnaeus, is dated 4 May 1764. It appears that Brünnich's *Ornithologia borealis* took longer from preface to print than *Entomologia*. Brünnich's letter of 23 July 1764 to Linnaeus mentions having already sent Linnaeus his entomological work and then cryptically states: 'En aliud, Vir Generose, in historia naturali specimen, vena frigida, quippe media hyeme in vasto avium museo elaboratum, quod si Tibi vel tantum ex parte arrideat, gaudebo; sin minus, ignoscas, Vir Generose, me stadium hoc propriis viribus et nullius consultis hactenus excoluisse. Ignotae aves, quarum icones addere ob ingentes sumtus mihi haud fuit possible, una cum aliis rarioribus a Per-illustri Possessore Dno Pennant Esqr sunt oblatae.' [Rough translation, noting that Brünnich's Latin grammar has been criticised by some scholars: 'Another thing, O Generous Man, an example in natural history, a cold vein, indeed in the middle of winter elaborated in a vast bird museum, of which if it smiles at you even in part, I shall be glad; if not, forgive me, O Generous Man, I have studied this interest with my own strength and without any counsel. Unknown birds, the plates of which it was not possible for me to add, on account of the enormous cost, together with the other rarer ones are offered by the very illustrious owner Mr. Pennant Esq.'] Notably, Brünnich's (1764a) work was based on Christian Fleischer's collection in Denmark, so the text would have been finalised on the date specified in the preface—February 1764—at the end of the winter. Linnaeus' response of 20 August 1764 acknowledged *Ornithologia borealis*, providing detailed comments on it (including on Brünnich's domestic pigeons, but not his wildfowl!), finally expressing thanks also for the copy of *Entomologia*. From this and other archived correspondence, it can be seen that Brünnich held Linnaeus in high esteem, so he might have been among the first to be sent new publications such as this. The later publication of Brünnich's *Ornithologia borealis* compared to his *Entomologia* might be explained by the author's attempts to include plates in the former work, which he ultimately decided against due to cost.

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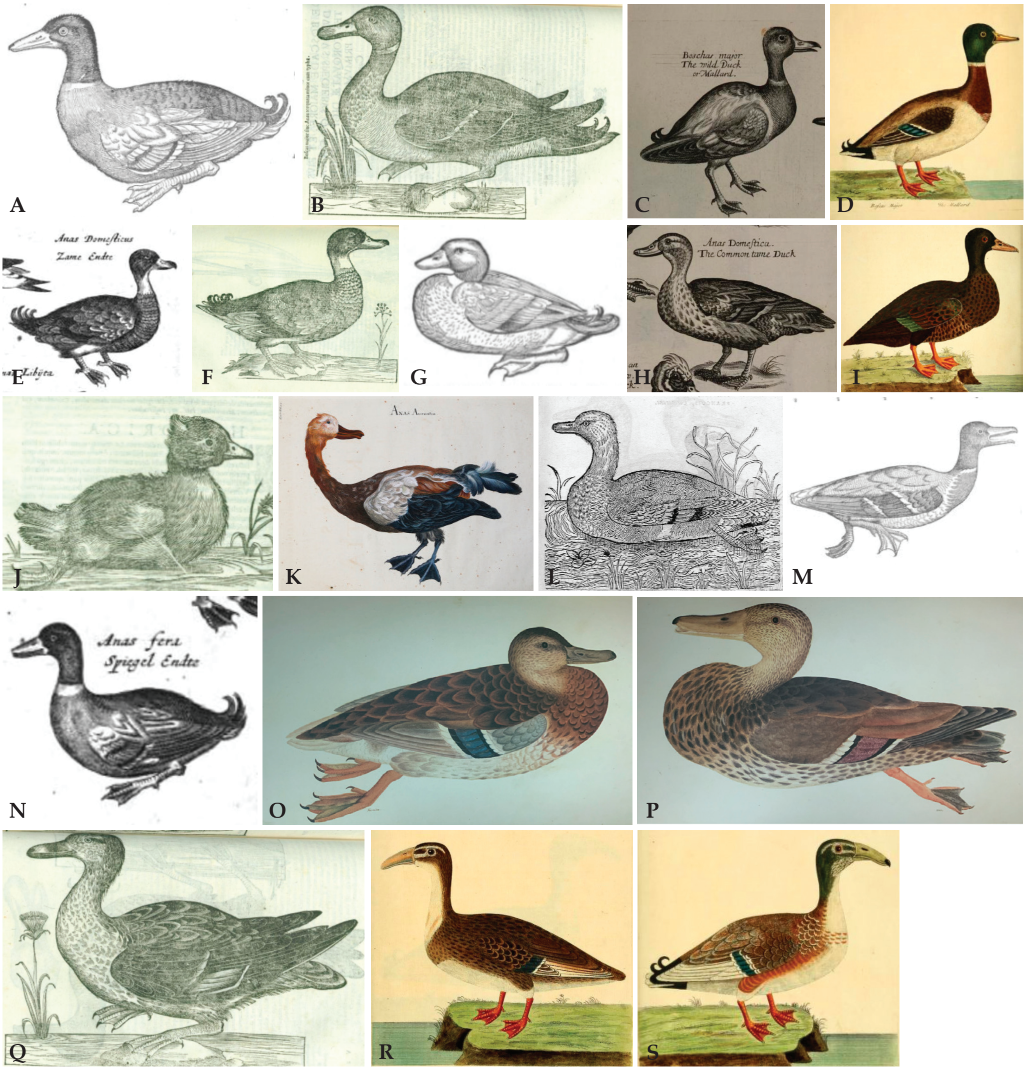

Figure 2. Specimens in the original type series of the following duck names: (i) *Anas boschas* Linnaeus, 1758 (A–D; the bird illustrated in D being designated as the lectotype); (ii) *A. boschas fera* (A–D if this name was authored by either Bechstein (1792) or Brünnich (1764a), but additionally M–N if authored by Brünnich; the bird illustrated in D being designated as the lectotype); (iii) *A. domestica* J. F. Gmelin, 1789, with direct references (E–I) and indirect references (J–L); (iv) *A. platyrhynchos* (O–Q), and (v) *A. adunca* (example only, not the full series, R). A: Gessner's (1555: 114) 'Anas fera torquata minor'. B: Aldrovandi's (1603, book 19, p. 212) 'Boscas major f. Anas torquata minor'. C: Willughby's (1678, pl. 72) 'Boschas major' or 'wild Duck or Mallard'. D: Albin's (1734, pl. 100), 'Boschas major or Mallard', the specimen illustrated here being the selected lectotype of both *A. boschas* Linnaeus, 1758, and *A. boschas fera*, whether of Brünnich, 1764, or Bechstein, 1792. E: Jonston's (1657, pl. 49) 'Anas Domesticus Zame Endre'. F: Aldrovandi's (1603: 189), 'Anas domesticus'. G: Gessner's (1555: 96), 'Anas domestica'. H: Willughby's (1676, pl. 75) 'Anas Domestica', the 'common Tame duck'. I: Albin's (1734, pl. 99) 'Madagascar Duck', i.e. Meller's Duck *A. melleri*. J: Aldrovandi's (1603: 188) duckling. K: Marsili's (1726, pl. 54) 'Anas aurantia', a Ruddy Shelduck *Tadorna ferruginea*. L: Belon's (1555: 160, 1557: 32) 'Canard", a Gadwall *Mareca strepera*. M: Gessner's (1555: 115) 'Anas fera torquata maiore'. N. Jonston's (1657, pl. 49) 'Anas fera Spiegel Endte'. O–P: Rudbeck's 'Anas flaviatilis rufa …' (both unnumbered pages in Rudbeck 1986, vol. 2). Q: Aldrovandi's (1603: 232) 'Anas platyrhynchos, pedibus luteis', with head not entirely visible due to page bend. R–S: Albin's (1734, pl. 96–97) two hook-billed ducks (a domestic Mallard breed), being the sole two illustrated syntypes of the name *Anas adunca* Linnaeus, 1758.

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Three competing names for Mallard, their history of usage and priority

Duck taxonomy was thrown into disarray at its inception with the naming of three contemporaneous subjective synonyms for Mallard by Linnaeus (1758): *Anas boschas* was the most detailed account, based mostly on wild males (Figs. 2A–D); *A. platyrhynchos* was based on wild females (Figs. 2O–Q); and *A. adunca* on the 'hook-billed' domestic breed (e.g. Fig. 2R–S).

Linnaeus (1746, 1758, 1766) and earlier authors were clearly confused by the different plumages of male and female Mallards, apparently originating with the account of 'Anas platyrhynchos, pedibus luteis' by Aldrovandi (1603, book 19, p. 232; Fig. 2Q). That work described and illustrated female Mallards separately from males. Perhaps Aldrovandi observed groups of all-female-like Mallards in Italy in early autumn, when males are in eclipse plumage and near fully grown juveniles would be in 'female' plumage. Other pre-Linnean authors (e.g. Willughby 1676) had difficulty identifying Aldrovandi's (1603) 'Anas platyrhynchos, pedibus luteis' but Linnaeus (1758) decided to name it as a separate species nonetheless. The *platyrhynchos* description is based on two plates of female Mallards by Rudbeck (published posthumously as Rudbeck 1985, 1986; Figs. 2O–P), Aldrovandi's (1603: 232) line drawing (Fig. 2Q) and texts that cited the latter work such as Willughby (1678). All of these sources refer to female, juvenile or eclipse Mallards.

Confusion was exacerbated when Linnaeus (1766) placed the name *A. platyrhynchos* Linnaeus, 1758, into subjective synonymy with the name for Northern Shoveler *A. clypeata* Linnaeus, 1758. The latter has broadly similar female plumage to Mallard, but with different wing speculum coloration and a large spatula-like bill, features not mentioned in any of the accounts or plates referred to by Linnaeus (1758) in his description of *A. platyrhynchos*.

Linnaeus' (1766) proposed synonymy of *A. platyrhynchos* with *A. clypeata* stood for over a century. Latham (1824: 293), Shaw (1824: 84), Bonaparte (1826, section 256), and Selby (1833: 305), for example, all recognised *A. boschas* for Mallard and *A. b. domestica* for domestic birds. Lönnberg (1906) first noted that *A. platyrhynchos* and *A. boschas* pertain to female and (mostly) male Mallards, respectively. Disrupting more than 150 years of usage, he chose *platyrhynchos* over *boschas*, citing 'page priority' (i.e. *platyrhynchos* appeared first in the pages of Linnaeus 1758). Today, such a designation would not accord with Recommendation 24A of the Code, since usage of *A. boschas* was well established at the time ('In acting as First Reviser … an author should select the name, spelling or nomenclatural act that will best serve stability and universality of nomenclature.'). However, this does not affect the validity of Lönnberg's (1906) First Reviser action, which predates that guidance and remains valid today, since breach of a recommendation would not invalidate it.

Lönnberg's (1906) proposal was accepted by essentially all major 20th and 21st century taxonomic works and field guides, including Hartert *et al*. (1912: 134), Peters (1931: 159), Witherby *et al*. (1943: 231), Hellmayr & Conover (1948: 325), Peterson *et al*. (1983: 58), Snow & Perrins (1998: 218), Svensson *et al*. (1999: 48, 2010: 24) and Dickinson (2003: 66). *A. platyrhynchos* Linnaeus, 1758, is the only name in use today for Mallard, including by all major bird checklists (Dickinson & Remsen 2013: 17, del Hoyo & Collar 2014: 144, Clements *et al*. 2022, Gill *et al*. 2023).

The name *A. adunca* Linnaeus, 1758, has barely been used since the 1800s. However, it has been used on a handful of occasions since 1899 (e.g. Pieters 1980: 540), precluding its treatment as a *nomen oblitum* and automatic reversal of precedence under Art. 23.9. To determine precedence among the three contemporaneously introduced names *A. platyrhynchos*, *A. adunca* and *A. boschas*, the following First Reviser actions are relevant:

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(a). *A. platyrhynchos* vs. *A. adunca*: Rookmaaker & Pieters (2000: 275) noted that a specimen labelled *A. adunca* in an historic collection refers to *A. platyrhynchos* Linnaeus, 1758. By citing both names and using *A. platyrhynchos* as valid, these authors, apparently inadvertently, acted as First Revisers under Art. 24.2.1.

(b). *A. boschas* vs. *A. adunca*: Rees (1819: no page numbers, section 'DUCK') is the earliest publication I have found that cited both names and recognised *boschas* over *aduncа*.

As it is a name for a domestic breed, *Anas adunca* Linnaeus, 1758, technically has priority over *A. boschas domestica* of Brünnich, 1764a, or *Anas domestica* J. F. Gmelin, 1789. Reversal of priority for the near-obsolete *A. adunca* Linnaeus, 1758, requires ICZN attention. The type series of *A. platyrhynchos* exclusively comprises female Mallards of apparently wild phenotype. However, that of *A. boschas* Linnaeus, 1758 involves both wild and mixed or domestic phenotypes, thereby threatening use of the name *A. domestica* Brünnich, 1764a, for domesticates.

The type series for *Anas boschas* Linnaeus, 1758

In his original description of *A. boschas*, Linnaeus (1758: 127) referred to several prior sources, whose authors' specimens constitute the type series. First, in lines 1–2, he referred to his earlier 'Anas rectricibus intermediis (maris) recurvatis, rostro recto' account in *Fauna Svecica* (Linnaeus 1746: 34–35, para. 97). This includes a text description of a male Mallard, presumably based on the author's observations or specimens, a list of vernacular names and an essentially identical list of references to earlier works as in his later account (Linnaeus 1758). Next, in lines 3–4, Linnaeus (1758) mentioned the 'Anas fera torquata minor' of Gessner (1555), Aldrovandi (1603) and Ray (1713). Taking these in turn: (i) Gessner (1555: 114; Fig. 2A) included an illustration of a male Mallard that differs from the pure wild phenotype in lacking any strong contrast between the breast and belly, so is probably of domestic or mixed origin; (ii) Aldrovandi (1603, book 19, chapter 35 [*sic* = chapter 25, p. 212]; Fig. 2B) contained a description and plate of a male Mallard, which also lacks contrast on the underparts, so is also doubtfully of wild origin; and (iii) Ray (1713: 145, para. A.1) included an abridged version of Willughby's (1676) text and referenced Aldrovandi's (1603) account. In lines 5–6, the 'Boschas major' of Willughby (1676) and Albin (1734) are cited. These are: (i) the 'wild duck or mallard' of Willughby (1676: 284, pl. 72; Fig. 2C), who illustrated a male Mallard but described both male and female in the text, while referring to Aldrovandi's (1603) account; and (ii) Albin (1734: 89, pl.100; Fig. 2D), with a colour-illustrated male Mallard consistent with a wild bird and a detailed description.

The second set of materials cited by Linnaeus (1758) are in subsection 'beta', referring to the 'Anas domestica' of earlier authors. As with the corresponding goose name, this is a subtitle for part of the *boschas* account cross-referencing a pre-Linnean name, without any new name in the margin; the name 'domestica' for ducks was not made available by Linnaeus (1758) (e.g. Sherborn 1922, Richmond 1992). None of the illustrated specimens incorporated here forms part of the type series of *A. boschas*, as they are listed under a distinct variant beta, for purposes of Art. 72.4.1, for the same reasons as discussed above in relation to subsections of the *Anas anser* Linnaeus, 1758 description. Those of the beta subsection materials based on illustrations are shown in Figs. 2E–H.

As above, Linnaeus (1746) was one of the sources cited in the same author's later original description; the relevant account referred to various of the same texts as cited in Linnaeus (1758) but his earlier work cited additional materials. The first is a wild male Mallard illustrated by Gessner (1555: 115; Fig. 2M), which was incorrectly identified by Linnaeus (1746) as a female. Although on the adjacent page of the same work as cited by

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Linnaeus (1758), this cannot properly be regarded as part of the type series as it is in a separate named section ('Anas fera torquarta maiore') and Linnaeus (1758) chose not to cite it. Additionally, Linnaeus (1746) referred to the 'Anas fera Spiegel Endte' of Jonston (1657, pl. 49; Fig. 2N), a male Mallard with a uniformly dark belly so potentially of domestic or mixed origin. Linnaeus (1758) placed this account under form beta, so it can also be ignored as not being part of the type series of *A. boschas*.

There are no Mallards (or geese) in Linnaeus' original collection in Sweden (E. Åhlander *in litt*. 2021) nor any birds in his collection in the Linnean Society in London (G. Douglas *in litt*. 2005). Thus, no extant duck specimens studied by Linnaeus are part of the type series.

Designation of a lectotype for *Anas boschas* Linnaeus, 1758

For the reasons listed above, *A. boschas* Linnaeus, 1758, has a mixed type series (as regards some widely used schemes for trinomial nomenclature), by including both wild Mallards and birds apparently of either mixed or domestic phenotype and of doubtfully wild origin. As a result, the name *A. boschas* Linnaeus, 1758, is currently at risk of competing with *A. boschas domestica* Brünnich, 1764a, or *A. domestica* J. F. Gmelin, 1789, as a name for domestic ducks. A lectotype designation is therefore necessary.

The name *A. boschas* was originally intended to encapsulate morphotypes referable to wild, male Mallards and for over a century was used for wild Mallard. Any lectotype designation should therefore promote the status of this name as a synonym at species and subspecies level for wild Mallard *A. platyrhynchos* Linnaeus, 1758, and not for domesticates. The specimen illustrated in the colour plate entitled 'Boschas major, the Mallard' by Albin (1734: 89, pl. 100; Fig. 2D) is hereby selected as lectotype. The plate unambiguously depicts a male Mallard of wild phenotype; it is accompanied by a page-long description with measurements of the specimen. Albin's plates were based on his own studies of specimens mostly in England, probably in the London area. Albin (1731, 1734) stated that he illustrated birds from life; none of the specimens from his works is extant or traceable today.

This lectotype designation restricts the type locality of *A. boschas* to England, probably the London area. This does not disrupt subspecies taxonomy of *A. platyrhynchos* and maintains the subjective synonymy of *A. boschas* with *A. platyrhynchos*. Hartert *et al*. (1912) suggested to restrict the type locality of the latter to Sweden, perhaps because the original description is based principally on specimens of female Mallards drawn by Rudbeck (1985, 1986; Figs. 2O–P) in Sweden. However, there is also an Italian Mallard type specimen in the series, described and depicted by Aldrovandi (1603; Fig. 2Q). As those authors did not designate a lectotype and because part of the type series originates outside Sweden, their restriction is incorrect. The type series of *A. platyrhynchos* is exclusively from Western Europe (Sweden and Italy). Excluding use of *domestica*, Mallard is often regarded as monotypic, although some recognise *A. p. conboschas* C. L. Brehm, 1831, for Greenland or North American populations (e.g. Clements *et al*. 2022). Both *A. platyrhynchos* and *A. boschas* now have a type series exclusively of wild-plumage Mallards from Western Europe, so they are now synonyms at both species and subspecies levels.

Names for domesticates and wild geese, and Mallards, and their authors, including a First Reviser act and a lectotype for *Anas boschas fera*

The following conclusions and nomenclatural acts follow from the above:

1. The authorship and date of the name for domestic geese is *Anser domesticus* Garsault, 1764.

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2. *Anas anser domesticus* as used by Brünnich (1764a) is a subsequent usage of Garsault's name. As Garsault (1764) used the genus *Anser* for geese, the duck *Anas boschas domestica* Brünnich, 1764, cannot be a homonym of the same author's congeneric name for geese, and so Brünnich's duck name has his authorship, unless it is regarded as infrasubspecific.
3. The names *Anas anser ferus* Brünnich, 1764, and *A. boschas fera* Brünnich, 1764, to the extent they are available, are primary homonyms because they differ from one another only by adjectival gender agreement. The first would also be a junior synonym of *Anser anser* Linnaeus, 1758, and the second also a junior synonym of *Anas boschas* Linnaeus, 1758, and *A. platyrhynchos* Linnaeus, 1758.
4. Under Recommendation 24, when acting as First Reviser 'an author should select the name, spelling or nomenclatural act that will best serve stability and universality of nomenclature'. It is therefore necessary to consider the type series for Brünnich's (1764a) names *fera* and *ferus*, and what alternative authorship and application those names would take if one or the other is afforded priority.
5. Brünnich's (1764a) goose description is problematic, as it references the 'Anser ferus' subaccount of Linnaeus (1746), which involves a mixed type series of multiple grey goose species (similar to the alpha subaccount of *Anas anser* Linnaeus, 1758, as illustrated in Fig. 1). The type series of *Anas anser* Linnaeus, 1758, will eventually be addressed in an application to ICZN. Introducing the possibility of similar actions for a putative Brünnich (1764a) description of *Anas anser ferus* of contested availability would complicate and reduce the prospects of that case. In contrast to the goose name, *Anas boschas fera* Brünnich, 1764, if selected, could be firmed up herein as a synonym of *A. platyrhynchos* Linnaeus, 1758, and *A. boschas* Linnaeus, 1758.
6. If Brünnich's (1764a) wild goose name is not selected (or is unavailable), then Gmelin (1770), a novel authorship, has priority for *Anser ferus*. His sole type specimen is no longer extant but quite clearly of Eastern Greylag Goose *A. anser rubrirostris* Swinhoe, 1871,[1] resulting in an issue of priority that will require ICZN deliberation.
7. Brünnich's (1764) description of *A. boschas domestica* is succinct: 'multis ludens coloribis; hospitatur ubique' ('playing with many colours; kept everywhere') and he gave the Danish vernacular name. His work was based principally upon Christian Fleischer's collection, although an account like this might also have rested on field observations: he mentioned no specimens in his accounts. Steinheimer (2005), who attempted to catalogue extant pre-1800 bird specimens held in Europe, did not list the Fleischer collection; similarly, van Grouw & Bloch (2015) found no trace. Brünnich's (1764a) citation of 'Fn 131' in the immediately preceding account of *boschas* refers to the relevant

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[1] The name *Anser ferus* was attributed by Richmond (1992) to Schäffer (1789: 67), whose main reference plate (Schäffer 1774) shows a Bean Goose, albeit with references to earlier authors that bring into consideration the mixed type series of *A. anser*. Pallas (1769: 26, 28) used the name 'Anser ferus' earlier in italicised form, noting its distribution and migratory status, but without citing earlier authors' accounts or any description that would count as an indication or description under Art. 12. His usage is a *nomen nudum*. Gmelin (1770: 68–69) has been overlooked to date, but seems to have been first to use the name *A. ferus* in a manner that suffices to confer availability. He travelled in south-west Russia including around the Caspian Sea and described its birds, including a goose he referred to as *A. ferus*, providing measurements and ecological remarks. Although large, his measurements are consistent with *A. anser rubrirostris* Swinhoe, 1871, which is the region's only common goose. Gmelin's (1770) specimen was reportedly 9 ft long (which must refer to wingspan—being long for Greylag and certainly bigger than any other grey goose); at >9 pounds/4.5 kg, it is at the upper end of variation in the species. In reporting the only grey goose he observed (at a locality where only one species regularly occurs), providing measurements of a specimen and ecological notes, including its hissing call when provoked, then discussing all other wildfowl he observed in the region by their different morphology and names, this suffices for a description.

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section of the second edition of *Fauna Svecica* (Linnaeus 1761: 46) and provides context, but it is included only for *A. b. fera*, not *A. b. domestica*, so neither that publication nor its sources are relevant to the latter description. There is, however, no ambiguity in Brünnich's (1764a) application of this name to domestic ducks of varied plumage, with a type series either from Fleischer's now lost collection or generally in Scandinavia (probably Denmark).

8. If *Anas boschas fera* Brünnich, 1764a, is not an available name or is not selected via First Reviser action, then authorship falls to Bechstein (1792: 389). In a perfunctory account, Bechstein (1792) did little more than cite Linnaeus (1758). It could be argued that Bechstein's (1792) name is not available pursuant to Art. 11.5.2 (citation of a previously unavailable name without taxonomic concept). However, Bechstein's (1792) attribution to Linnaeus (1758) is arguably better regarded as an incorrectly reported authorship and not subsequent use of a Linnean name. The type series of Bechstein's (1792) name would be that of the opening section of Linnaeus' (1758) *A. boschas*, including the specimens illustrated in Figs. 2A–D. Brünnich's (1764a) description would bring into account additional materials from Linnaeus (1746; see Figs. 2M–N). Thus, Brünnich's (1764a) name and Bechstein's (1792) name (if the former is unavailable) would share most of the same type series, as did *A. boschas* Linnaeus, 1758 (prior to the lectotype designation above).
9. *Anas boschas fera* Brünnich, 1764a, is hereby selected to have priority over its primary homonym *A. anser ferus* Brünnich, 1764a, pursuant to a First Reviser action under Art. 24 and 52.3.
10. The type series of *A. b. fera* is subject to the same issues of it being mixed at subspecies level, as for *A. boschas* Linnaeus, 1758, which has essentially the same type series (see above). The same lectotype chosen for *A. boschas*, i.e. 'Boschas major, the Mallard' of Albin (1734: 89, pl. 100; see Fig. 2D) is here also selected as lectotype for *A. boschas fera*. This places the names *A. boschas* and *A. b. fera* for ducks into objective synonymy and avoids any competition for priority or ambiguity with *A. b. domestica*. It also places the name *A. b. fera* into the synonymy of *A. platyrhynchos* Linnaeus, 1758, for the same reasons as for *A. boschas*.
11. If Brünnich's (1764a) trinominals for domestic and wild waterfowl are not considered available names, then the First Reviser act in para. 9 would fall away, but the lectotype for *A. boschas fera* in para. 10 remains valid, as the lectotype is part of the type series of that name and the designation is necessary, irrespective of authorship (Brünnich 1764a, or Bechstein 1792).

Conclusions

In summary, the relevant names discussed here and their authors are:

Anser anser (Linnaeus, 1758). Greylag Goose (subject to ICZN action on its type series). Potential synonym: *Anser ferus* S. G. Gmelin, 1770 (subject to Commission action on priority vs. *A. a. rubrirostris* Swinhoe, 1871; for now, prevailing usage should be maintained).
A. a. rubrirostris Swinhoe, 1871.
A. a. domesticus Garsault, 1764.

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Anas platyrhynchos Linnaeus, 1758. Mallard.
Synonym at species level: *Anas adunca* Linnaeus, 1758 (through First Reviser action of Rookmaaker & Pieters 2000). Synonyms at species and subspecies level: *A. boschas* Linnaeus, 1758 (via First Reviser action of Lönnberg 1906); *A. boschas fera* Brünnich, 1764a (author Bechstein, 1792, if former is not considered to have made the name available, i.e. if Brünnich's authorship of *A. boschas domestica* is not endorsed in the forthcoming ICZN case on *A. domestica*).
A. p. conboschas C. L. Brehm, 1831.
A. p. domestica Brünnich, 1764a (author J. F. Gmelin, 1789, if Brünnich's authorship not endorsed in the forthcoming ICZN case). Synonym at subspecies level: *A. adunca* Linnaeus, 1758 (subject to ICZN decision on priority; for now, prevailing usage should be maintained).

Other synonyms for some of these names exist and additional subspecies have been proposed. Thus, the above synonymy is not comprehensive, addressing only the senior names for the nominate wild phenotype of currently recognised subspecies in Greylag and Mallard, subspecies names for domestic wildfowl and the name *ferus*/*fera* as used for geese and ducks. Clearly, ICZN attention is necessary to deal with remaining issues affecting names of these birds.

Acknowledgements

I thank Francisco Welter-Schultes, Frank Rheindt, Laurent Raty, Edward Dickinson, three ICZN and one other reviewer for their valuable comments on the manuscripts that led to this paper. Without the Biodiversity Heritage Library, archive.org and other online repositories of historical works this paper would not have been possible. Thanks to the Linnean Society, London, and its library staff for access to some rarer publications, particularly the plates of Rudbeck, and information on its collections; and to Erik Åhlander for information on birds at the Naturhistoriska Riksmuseet, Stockholm, and Will Beharrell and Gina Douglas for information concerning holdings at the Linnean library.

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The edge of the subtropics: a preliminary list of the birds of San José de Sumaco, Ecuador

by Andrew C. Vallely, Frederick Ertl & Thierry Garcia

Received 19 January 2023; revised 24 July 2023; published 4 December 2023

http://zoobank.org/urn:lsid:zoobank.org:pub:8AF16709-BD48-4F11-BFAC-04CD85432C4D

Summary.—We present the results of an eight-year avifaunal survey and review historical collections assembled by the Olalla family at San José de Sumaco, a humid-forested locality lying at *c.*950 m elevation in the east Andean foothills of Orellana province, Ecuador. Notably high species richness is reported from a restricted area of upland *terra firme* forest, and our appendix lists 477 species considered documented, with conservation status according to IUCN, evidence and relative abundance. An additional 49 species have been reported from the site, but without documentation. Noteworthy records of 43 species are detailed, including poorly known, range-restricted taxa and those of conservation concern. Twenty-two species are regarded as either Near Threatened or Vulnerable by IUCN. Lowland (Amazonian) species dominate the avifauna, but it also includes a set of range-restricted, Andean species of which several are considered Near Threatened or Vulnerable at national or global scales (e.g., Napo Sabrewing *Campylopterus villaviscensio*, Fiery-throated Fruiteater *Pipreola chlorolepidota*, Ecuadorian Tyrannulet *Phylloscartes gualaquizae*). We report the presence of three obligate bamboo specialist species. We clarify the geographic position of the Olalla collecting locality San José de Sumaco using archival material and by reconstructing the collectors' itinerary. We list noteworthy elevational records for 89 species of which 80 are upper-elevation records of lowland (Amazonian species). While mainly Amazonian, the avifauna is discussed in relation to its biogeography indicating historical connections to both Andean and Amazonian centres of diversification. We conclude that the lower slopes of Volcan Sumaco host a distinctive, species-rich avian assemblage that is threatened immediately by deforestation and potentially by climate change, and we stress its importance for conservation and continued study.

Forests of the tropical Andes and adjacent western Amazonia harbour exceptionally high levels of biodiversity and the region also hosts concentrations of range-restricted and threatened taxa (Brooks *et al*. 2002, 2006, Orme *et al*. 2005, Rahbek *et al*. 2019). In this broad region, local species richness in birds is thought to be greatest in humid foothills at *c.*900–1,000 m (Stotz *et al*. 1996, Herzog *et al*. 2005, McCain 2009) where forested slopes of the east Andes transition between lowland and upland ('cloud') forests, an ecotone mediated by the local formation of ground-level cloud banks via adiabatic cooling. Chapman (1926) noted this transition from the Amazon to the Andes nearly a century ago in reviewing collections made by the professional firm Olalla & Hijos on the slopes of Volcán Sumaco in the east Andes of Ecuador together with temperature readings taken on his instruction. He observed that when 'they reached the old town of San José on the flanks of Sumaco, the birds sent to us indicated that they had reached the lower borders of the Subtropical Zone, and this supposition was supported by the temperature record'.

Both effective conservation planning and an improved understanding of the processes that have shaped the distribution of biodiversity require detailed inventories at all spatial

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scales, but few Andean foothill sites are well studied. Here, we describe the results of an eight-year bird survey at the historical collecting locality San José de Sumaco first described by Chapman (1926), a humid forested site at *c*.950 m elevation on the lower, eastern flank of Volcán Sumaco in Orellana province, east Ecuador, and at the intersection of the Andean and Amazonian biomes (Vivanco de la Torre *et al*. 1962). We present a preliminary list of 477 species recorded there through February 2023 (Appendix 1) and review historical collections made by the professional firm Olalla & Hijos a century ago. Together, these findings document a rich avifauna and highlight the conservation value of a threatened region.

Study area and Methods

Study area.—Field work was based at Bigal River Biological Reserve Research Station (Fig. 1). The Bigal River Biological Reserve (BRBR) is a private conservation area protecting *c*.1,000 ha of forested terrain in the east Andean foothills of Ecuador at 750–1,000 m (Fig. 1; see also Freile *et al*. 2015). The reserve lies near the western border of Orellana province on the lower, eastern slope of Volcán Sumaco (00°32′32″S, 77°25′40″W; Fig. 1) and lies south-east of, and adjacent to, the far larger Parque Nacional Sumaco-Napo-Galeras (PNSNG), a national protected area (IUCN category II) established in 1994 that covers 2,061 km² (IUCN 2023) of mostly forested terrain at 600–3,732 m.

The region receives prevailing winds from the east and the climate is extremely wet, with low seasonal variability, a relative max. rainfall in July, and the highest regional rainfall (>4 m per annum) expected at elevations of *c*.900–1,000 m (Laraque *et al*. 2007). While rainfall may be heavy, ground-level cloud cover (mist) is infrequent. A poorly defined period of less frequent precipitation lasts from January to February, corresponding to the Northern Hemisphere dry season, and dry periods may also occur in August, during the Southern Hemisphere dry season.

This hilly region is drained by the río Suno to the south and the río Bigal to the north (Fig. 1). The dominant vegetation type is tall, humid broadleaf evergreen (*terra firme*) forest (‘Western Amazon Sub-Andean Forest’ *sensu* Báez *et al*. 2010) with some canopy emergents >40 m tall. This forest is rich in tree species but dominated by *Iriartea deltoidea* and other palms (Brokaw & Ward 2023). Numerous small streams, swamps and damp ravines are features. Stands (some >5 ha) of *Guadua angustifolia* bamboo occur in some areas. Higher terrain on exposed ridges with poor soil or subject to desiccating winds hosts relatively drier forest with fewer epiphytes and more open understorey. Whereas most of the study area is clothed in tall (>30 m), closed-canopy, primary forest, some successional vegetation occurs in abandoned clearings and along a disused road. We also surveyed and include observations from nearby degraded areas, including cattle pastures, crop fields, second growth and forest fragments south of the BRBR Research Station (Fig. 1).

The area is the source of historical bird specimens collected during the early 20th century by the Olalla family (Olalla & Hijos; Fig. 2) at San José de Sumaco and synonymous or nearby localities including ‘San José Abajo’, ‘San José Nuevo’ and ‘San José Viejo’ during 1923–35, with labels bearing the names ‘Olalla Y Hijos’, ‘Olalla Y Hermanos’ and ‘Carlos Olalla’ (Chapman 1926, Paynter 1993, LeCroy & Sloss 2000, Wiley 2010; see below).

Methods.—We visited the San José de Sumaco area, usually for 11-day periods, during each August and January in the years 2015–23 for a total of 198 observer days. Birds were recorded via field observation, photography and sound-recording of vocalisations. To establish a baseline for future monitoring, formal survey methods were adopted in 2017 and followed during 18–29 August 2017, 3–14 January 2018, 13–24 August 2018, 5–16 August 2019, 6–17 January 2020 and 1–14 December 2020. FE conducted point counts along six (1.25 km) transects, all located within 2 km of the RBBR Research Station at elevations of

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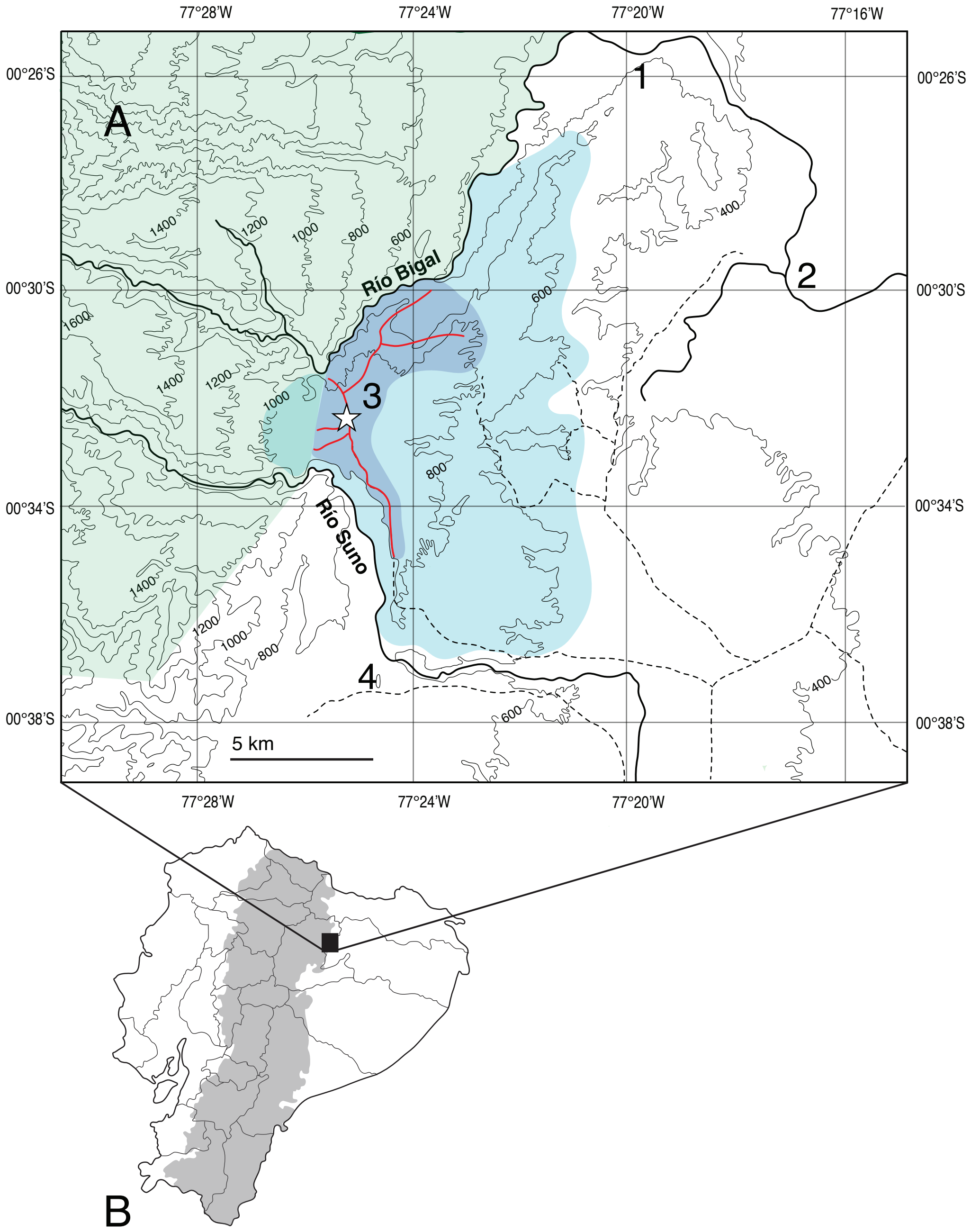

Figure 1. Map (A) showing the San José de Sumaco area and location of RBBR Research Station (star) in the Bigal-Suno interfluvial. Olive shading = eastern edge of Parque Nacional Sumaco-Galeras. Red lines = BRBR trails. Dark blue = approximate survey area. Light blue = hypothesised area collected by Olalla field parties. Dotted lines = roads. Numbered localities according to Paynter (1993) are (1) San José Nuevo (00°26'S, 77°20'W), now Pato Rumi, Comuna San José de Payamino (2) Payamino (00°30'S, 77°17'W), now Centro Poblado Parroquia, San José de Payamino (3) San José Viejo (00°32'S, 77°25'W) and (4) Avila (00°38'S, 77°25'W), now Avila Viejo. Map (B) shows position of the site in western Orellana province, Ecuador. Grey shading = areas above 800 m.

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Figure 2. An Olalla & Hijos field party in an undated photograph (archives of the Dept. of Ornithology, American Museum of Natural History, New York)

900–1,000 m (Fig. 1). Five transects followed pre-established footpaths in primary forest, and the other an unpaved road extending to the south and traversing disturbed habitats. On six mornings during each 11-day sampling period, FE conducted six counts on one of six transects at fixed points separated by 200–250 m. Point counts were conducted between sunrise (05.55–06.00 h) and two hours later. During a ten-minute period stationed at each point, FE recorded all species heard or seen. The daily order of point sampling was changed in successive visits so that each point was visited at least once closest to dawn. Not all species were equally well sampled by this method. Canopy species and species that vocalise infrequently may have been overlooked, while conspicuous or persistently vocalising species may be over-represented. To help overcome reporting bias, each point count was recorded using a Zoom 5 digital recorder equipped with omni-directional microphone and FE's written notes were later compared with the recordings, and any omissions and errors corrected. FE also compiled 280 20-species 'MacKinnon lists' (Bibby *et al*. 2000, MacLeod *et al*. 2011) and we collected additional observational data while making non-systematic visual and auditory observations along trails and roads. Relative abundance for species detected using standardised methods was determined based on encounter frequency (Appendix 1). Daily checklists including photographs and sound-recordings are available on eBird (https://ebird.org/home).

We reviewed 10,312 photographs of birds captured by an array of 13 motion-activated passive infrared detection cameras (camera-traps) used to monitor terrestrial mammals. Camera-traps were deployed in all months during 2013–20 and sited mainly along trails and streamsides inside tall broadleaf forest. One was positioned at a 'mineral-lick' visited by both mammals and birds. We sorted the photographs into 1,169 independent events (separated by >1 hour) and calculated frequencies for each species represented (Table 1). We also sought documented observations from other observers (see Acknowledgements) and reviewed records in the citizen science database eBird (2022).

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Finally, we searched the regional literature and queried natural history collection databases for records of bird specimens collected at 'San José de Sumaco' and synonymous localities including 'San José Nuevo' and 'San José Viejo' (Chapman 1926, Paynter 1993, LeCroy & Sloss 2000, Wiley 2010; see below).

Results

***Species richness and evidence*.**—We compiled records of a combined total of 526 species representing 51 families at San José de Sumaco (Appendices 1–2). Of this total, 477 species are considered documented, including 452 with vouchers in the form of a specimen in a museum collection, photograph or sound-recording (Appendix 1). Thirty-five species were identified from camera-trap photographs (Table 1). Forty-nine species were reported from the site by other observers but lack a voucher and were not confirmed in our field work (Appendix 2). Minimum criteria for inclusion of undocumented reports from other observers in the main list (Appendix 1) include multiple reports of species considered reliably identified and biogeographically likely (i.e., there are documented records from similar elevations at sites near the study area). Of the 477 species considered documented, 456 are permanent breeding residents, 17 are seasonal residents or transients including 16 boreal migrants and one austral migrant.

We found natural history collection database registrations or published records for 1,652 bird specimens representing 306 species (Appendix 1) collected at San José de Sumaco and synonymous localities (see below) during 1923–35, and we examined 356 specimens representing 247 species in museum collections (principally the American Museum of Natural History, New York; AMNH) or via photographs (Appendix 1; see Acknowledgements). The continued presence of most species known from historical collections is confirmed by recent reports, but 22 species are known only from specimens. Appendix 1 presents a complete list of documented species with IUCN status (2023), relative abundance, and documentary evidence. Noteworthy records are detailed below.

Species accounts

GREY TINAMOU *Tinamus tao*

Rare across its circum-Amazonian distribution and considered Vulnerable at both global (IUCN 2023) and national levels (Freile *et al*. 2019). In Ecuador, known only from mid-elevations at 400–1,600 m (Ridgely & Greenfield 2001, Freile & Restall 2018). Chapman (1926) cited Salvadori & Festa (1900) who listed a specimen from 'San José' and Paynter (1993) incorrectly stated 'this probably San José Nuevo', but the itinerary for Enrico Festa in Chapman (1926) indicates that the specimen is correctly traced to Morona-Santiago province in south Ecuador. We regard the species as rare at San José de Sumaco, with presence documented by sound-recordings and camera-trap photographs.

NOCTURNAL CURASSOW *Nothocrax urumutum*

Thought to range mainly below 400 m, but recently documented at 1,481 m (Medrano-Vizcaíno & Rueda 2018). Considered rare and poorly known but recent camera-trap studies have contributed to our understanding of this enigmatic species (Solano-Ugalde & Real-Jibaja 2010, van der Hoek *et al*. 2018, Link *et al*. 2022). *N. urumutum* was among the most frequently recorded bird species in camera-trap photographs at *c*.950 m (Table 1), always during daylight hours (06.00–17.00 h). The images also document regular visits to a mineral lick, often in groups of up to four (Fig. 3), behaviour first reported recently for the species (Griffiths *et al*. 2020). We twice encountered family groups with dependent young (during

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TABLE 1

Thirty-five bird species recorded at 13 camera trap stations in 10,312 photographs (n = 1,669) events at San José de Sumaco. Independent events are defined as photo series separated by >1 hour.

English name	Scientific name	Event number
Grey Tinamou	*Tinamus tao*	2
Great Tinamou	*Tinamus major*	76
White-throated Tinamou	*Tinamus guttatus*	3
Tinamidae sp.		3
Spix's Guan	*Penelope jacquacu*	3
Wattled Guan	*Aburria aburri*	1
Nocturnal Currasow	*Nothocrax urumutum*	114
Salvin's Currasow	*Mitu salvini*	101
Cracidae sp.		2
Marbled Wood Quail	*Odontophorus gujanensis*	7
Rufous-breasted Wood Quail	*Odontophorus speciosus*	1
Sapphire Quail-Dove	*Geotrygon saphirina*	34
Ruddy Quail-Dove	*Geotrygon montana*	72
Grey-fronted Dove	*Leptotila rufaxilla*	5
White-throated Quail-Dove	*Zentrygon frenata*	1
Grey-winged Trumpeter	*Psophia crepitans*	1,085
Red-winged Wood Rail	*Aramides calopterus*	6
Fasciated Tiger Heron	*Tigrisoma fasciatum*	34
Greater Yellow-headed Vulture	*Cathartes melambrotus*	1
White Hawk	*Pseudastur albicollis*	6
Black-faced Hawk	*Pseudastur albicollis*	1
Band-bellied Owl	*Pulsatrix melanota*	1
Strigidae sp.		1
Rufous Motmot	*Baryphthengus martii*	47
Barred Forest Falcon	*Micrastur ruficollis*	8
Lined Forest Falcon	*Micrastur gilvicollis*	3
Dusky-throated Antshrike	*Thamnomanes ardesiacus*	1
Sooty Antbird	*Hafferia fortis*	1
Spot-backed Antbird	*Hylophylax naevius*	2
Scaled Antpitta	*Grallaria guatimalensis*	1
Short-tailed Antthrush	*Chamaeza campanisona*	2
Black-banded Woodcreeper	*Dendrocolaptes picumnus*	1
Grey-tailed Piha	*Snowornis subalaris*	2
Half-collared Gnatwren	*Microbates cinereiventris*	1
Speckled Nightingale-Thrush	*Catharus maculatus*	38
Swainson's Thrush	*Catharus ustulatus*	29
Black-billed Thrush	*Turdus ignobilis*	1
White-necked Thrush	*Turdus albicollis*	28

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daylight hours) and detected *N. urumutum* regularly by voice at night as birds called from midstorey perches.

SALVIN'S CURASSOW *Mitu salvini*
Considered Near Threatened (Freile *et al*. 2019) in Ecuador, where found mainly below 400 m (Freile & Restall 2018) although Ridgely & Greenfield (2001) noted historical records from 700–900 m and there are recent reports at 800 and 900 m in southern Ecuador (Ordóñez-Delgado *et al*. 2017, Pozo-Zamora *et al*. 2022). We encountered *M. salvini* regularly in the vicinity of the RBBR at *c*.950 m, and the species was among the most frequently recorded by camera-traps (Table 1).

RUFOUS-VENTED GROUND CUCKOO *Neomorphus geoffroyi*
Forest-dependent and rare across its vast range. Considered Vulnerable by IUCN (2023) and Near Threatened in Ecuador (Freile *et al*. 2019). Chapman (1926) listed three males in AMNH. These are AMNH 179093–094 taken at 'San José de Sumarco' [*sic*] on 20 and 21 March 1923, and AMNH 179095 taken 'below San José de Sumarco' [*sic*]' on 31 March 1923. One was heard calling at the RBBR Research Station at *c*.950 m on 8–10 December 2020. Another was reportedly seen nearby on 21 July 2022 (R. McKay *in litt*. 2022).

OILBIRD *Steatornis caripensis*
Locally distributed in the Ecuadorian Andes and adjacent eastern lowlands (Freile & Restall 2018). Undertakes local or seasonal movements away from nesting areas (Cárdenas *et al*. 2020) with a colony recently reported from lowlands on the río Pusuno in southern Napo province (Cisneros-Heredia *et al*. 2012). We have reports from December–April and the species is documented by a sound-recording made on 9 April 2022 at the RBBR Research Station at *c*.950 m.

LONG-TAILED POTOO *Nyctibius aethereus*
Rare and local in east Ecuador, where reported mainly in *terra firme* forest below 700 m (Ridgely & Greenfield 2001, Freile & Restall 2018). A female at AMNH (178975) was taken on 31 March 1923 'below San José' (Chapman 1926). We did not encounter the species during our survey.

SPOT-FRONTED SWIFT *Cypseloides cherriei*
Rare in Ecuador (Marín 1993, Ridgely & Greenfield 2001) and considered Data Deficient at both global (IUCN 2023) and national levels (Freile *et al*. 2019). We observed the species regularly in small numbers and obtained photographs, typically late in the day, as swifts made regular movements from the south-east to north-west, perhaps returning from the lowlands to nesting or roosting sites at higher elevations on Volcán Sumaco. *C. cherriei* was typically seen with other swifts including the more numerous White-collared *Streptoprocne zonaris* and Chestnut-collared Swifts *S. rutilus*.

WHITE-CHINNED SWIFT *Cypseloides cryptus*
Rare and poorly known in Ecuador (Marín 1993, Ridgely & Greenfield 2001). Review of several thousand photographs suggests that *C. cryptus* is the commonest of the three *Cypseloides* at San José de Sumaco. As with the previous species, *C. cryptus* was typically seen in mixed groups of swifts that included larger numbers of White-collared *Streptoprocne zonaris* and Chestnut-collared Swifts *S. rutilus*. *Cypseloides* were sometimes present overhead throughout the day but were most often seen in early evening while feeding or transiting over the RBBR Research Station clearing (Fig. 4).

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Figure 3. Camera-trap photograph of four Nocturnal Curassows *Nothocrax urumutum* emerging from a subterranean mineral lick (A), Red-winged Wood Rail *Aramides calopterus* (B; Frederick Ertl), Solitary Eagle *Buteogallus solitarius* (C; Frederick Ertl) and Orange-breasted Falcon *Falco deiroleucus* (D; Andrew C. Vallely)

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WHITE-CHESTED SWIFT *Cypseloides lemosi*

Rare and long known only from south-west Colombia but recently reported from east Ecuador, Peru and Bolivia (Ridgely & Greenfield 2001, Howell 2002, Roesler *et al*. 2009). *C. lemosi* was the least common *Cypseloides* at San José de Sumaco (Fig. 4) and was typically seen with larger numbers of White-collared Swift *Streptoprocne zonaris*.

ECUADORIAN PIEDTAIL *Phlogophilus hemileucurus*

Restricted to east Andean foothills. Formerly considered Vulnerable by IUCN (2016) and treated as Near Threatened in Ecuador (Freile *et al*. 2019). Specimens (presumably AMNH 179053, 185059, 185062–063) from 'below San José' were mentioned by Chapman (1926). Among the most frequently encountered hummingbirds of interior forest understorey at San José de Sumaco. We found *P. hemileucurus* at ten (32%) of 31 forest interior-transect points and regard it as fairly common.

LONG-TAILED SYLPH *Aglaiocercus kingii*

A mid-montane species (*sensu* Stotz *et al*. 1996) considered to range above 1,600 m in Ecuador (Ridgely & Greenfield 2001, Freile & Restall 2018). Chapman (1926) listed two females from 'below San José', presumably AMNH 179059–060 taken on 12–13 March 1923. These specimens might document a low-elevation occurrence but, because the precise elevation where they were taken is uncertain, we do not regard the record as documenting an elevational range extension. We did not encounter the species during our field work.

RUFOUS-VENTED WHITETIP *Urosticte ruficrissa*

A mid-montane species (*sensu* Stotz *et al*. 1996) thought to range above 900 m in Ecuador (Ridgely & Greenfield 2001, Freile & Restall 2018) where considered Near Threatened (Freile *et al*. 2019). Chapman (1926) listed five males and two females from 'below San José'. We located five of these in AMNH (179050–179052, 185064, 185066). We have several recent sight reports from *c*.950 m at RBBR.

PINK-THROATED BRILLIANT *Heliodoxa gularis*

Endemic to east Andean foothills. Considered Vulnerable in Ecuador and formerly globally by IUCN (2016). Rare, local, and poorly known in Ecuador with records from Sucumbíos, Orellana, Napo and Zamora-Chinchipe provinces (Ridgely & Greenfield 2001, Pitman *et al*. 2002, Freile *et al*. 2013). Described by Gould (1860) from 'Río Napo'. Zimmer (1951) suggested the type locality be restricted to 'San José, Ecuador' but his basis is unclear, and there is no indication that the holotype is from the locality San José de Sumaco worked by Olalla & Hijos. Specimens (one male, and five females) from 'below San José' are mentioned in Chapman (1926). We located four of these in AMNH (179040–041, 185112–113). We found *H. gularis* to be fairly common and among the most frequently encountered hummingbirds in the forest interior (see also Freile *et al*. 2015). *H. gularis* was detected at 13 (42%) of 31 forest transect points. An adult was photographed on a nest on 8 January 2020 (Fig. 4) and a nest with young was found on 8 November 2017 (G. M. Kirwan *et al*. pers. obs.).

LITTLE WOODSTAR *Chaetocercus bombus*

Rare and poorly known. Considered Near Threatened by IUCN (2023) and Vulnerable in Ecuador (Freile *et al*. 2019). Most Ecuadorian records are from the Pacific slope, but it is known also from the east slope foothills of Morona-Santiago and Zamora-Chinchipe provinces in southern Ecuador (Chapman 1926, Collar *et al*. 1992, Janni 2004). Chapman (1926) mentioned two female specimens in AMNH from 'below San José', documenting

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Figure 4. White-chested Swift *Cypseloides lemosi* (A; Andrew C. Vallely), White-chinned Swift *C. cryptus* (B; Andrew C. Vallely), Napo Sabrewing *Campylopterus villaviscensio* (C; Andrew C. Vallely), specimen of Little Woodstar *Chaetocercus bombus* (AMNH 179065) right, with specimen of Gorgeted Woodstar *C. heliodor cleavsi* (AMNH 180154), left, for comparison, at the American Museum of Natural History, New York (D), Pink-throated Brilliant *Heliodoxa gularis* on nest (E; Chris Fischer)

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occurrence on the east slope north to the Volcán Sumaco region (see Zimmer 1953, Ridgely & Greenfield 2001) but there have been no reports from the area since. We located just one female at AMNH (179065). The label reads 'below San José de Sumarco [*sic*]. E. Ecuador. Tropical Zone' Date: Mch. 16, 1923. On the reverse is 'Olalla & Sons'. The original collectors tag reads '16 Marzo 1923 H.P. [= hembra pequeño indicating a female with small ovaries] S. José abajo. Olalla y Hijos Ecuador'. Although this specimen shows a few rufous feathers on the rump, it agrees with other female specimens of *C. bombus* at AMNH (*n* = 11) and differs from those of Gorgeted Woodstar *C. heliodor cleavsi* (*n* = 6) in its narrower-based bill, straighter (less decurved) culmen, and more extensive black on the rectrices (Fig. 4).

NAPO SABREWING *Campylopterus villaviscensio*
Confined to east Andean foothills and considered Near Threatened (IUCN 2023, Freile *et al*. 2019). Five specimens from 'below San José' (AMNH 179015–016, 185132–133, 185135) were mentioned by Chapman (1926). We encountered the species regularly and obtained photographs (Fig. 4). *C. villaviscensio* was detected at three (10 %) of 31 forest-interior transect points and we consider it uncommon.

GREY-WINGED TRUMPETER *Psophia crepitans*
Considered Near Threatened in Ecuador (Freile *et al*. 2019) where known mainly from below 700 m (Freile & Restall 2018) but *P. crepitans* was the most frequently recorded species in camera-trap photographs (*c*.950 m), accounting for 1,085 (65%) of 1,669 independent events and typically was recorded in large groups. Together, a set of large-bodied terrestrial species comprising Great Tinamou *Tinamus major*, *P. crepitans*, Salvin's Curassow *Mitu salvini* and Nocturnal Curassow *Nothocrax urumutum*, accounted for 1,376 (82%) of the total 1,669 events (Table 1).

RED-WINGED WOOD RAIL *Aramides calopterus*
Rare, poorly known and considered Near Threatened in Ecuador (Freile *et al*. 2019), but with a concentration of historical specimens (Chapman 1926, Norton 1965) and recent records in the Volcán Sumaco region of Napo and Orellana provinces (Ridgely & Greenfield 2001, Vaca *et al*. 2006). Four specimens in AMNH 178884–885, 185353, 185255) are labelled 'San José Abajo' and 'San José de Sumarco' [*sic*]. We encountered the species sporadically at *c*.950 m and obtained sound-recordings, camera-trap photographs (Fig. 3) and video.

GREY-COWLED WOOD RAIL *Aramides cajaneus*
Widespread in South America's lowlands. In Ecuador, known mainly from below 400 m (Ridgely & Greenfield 2001, Freile & Restall 2018). FE observed one at close range on 12 January 2016 at *c*.950 m in tall forest near the BRBR Research Station. The all-grey neck and rufous breast were clearly visible. Another was reportedly heard in the same area on 28 November 2021 (H. Jacob).

CRESTED EAGLE *Morphnus gujanensis*
Rare. Considered Near Threatened by IUCN (2023) and Vulnerable in Ecuador (Freile *et al*. 2019). In eastern Ecuador, generally confined to lowlands below 300 m (Freile & Restall 2018). A female at AMNH (178949) was taken on 23 March 1923 by Olalla & Hijos and was listed by Chapman (1926) with locality 'below San José' (hence, the precise elevation is uncertain).

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HARPY EAGLE *Harpia harpyja*
Rare, considered Vulnerable (IUCN 2023), and generally confined to elevations below 400 m. An adult was videotaped at *c*.950 m near the BRBR on 25 August 2019 (L. Navarrete *in litt*. 2022).

SEMICOLLARED HAWK *Microspizias collaris*
Rare and poorly known (Bierregaard *et al*. 2022). Considered Near Threatened in Ecuador (Freile *et al*. 2019) where reported at 1,500–2,200 m (Ridgely & Greenfield 2001) but has been recorded as low as 600 m in Colombia (Hilty & Brown 1986). Included here based on a sight record: ACV studied a single bird through a telescope as it perched motionless in the open crown of an emergent tree at the BRBR Research Station on 12 January 2019 at *c*.950 m. Coarse barring on the underparts, dark ear-coverts, and a pale collar were clearly visible.

SOLITARY EAGLE *Buteogallus solitarius*
Rare and local throughout its vast range and considered Near Threatened (IUCN 2023). Reported from several sites in the east Andean foothills of adjacent Napo province (Ridgely & Greenfield 2001) but regarded as Critically Endangered in Ecuador (Freile *et al*. 2019). We photographed and obtained sound-recordings of an adult on 20 August 2018 on a steep ridge above the río Bigal *c*.5 km north of the BRBR Research Station (Fig. 3). One was heard calling at the same site on 9 January 2020.

RUFESCENT SCREECH OWL *Megascops ingens*
Widespread in the subtropical Andes, but poorly known (Freile & Castro 2013). In Ecuador thought to range from 1,200 to 2,400 m (Freile & Restall 2018). One was documented by a sound-recording near the BRBR at *c*.950 m on 18 September 2021 (P. Baruah; XC676460).

SUBTROPICAL PYGMY OWL *Glaucidium parkeri*
Endemic to the East Andes. Relatively recently described (Robbins & Howell 1995) and poorly known (Freile & Castro 2013, Acevedo-Charry *et al*. 2015). Most Ecuadorian records are from above 1,100 m (Ridgely & Greenfield 2001, Freile & Restall 2018). One was sound-recorded near the BRBR Research Station at *c*.950 m on 28 July 2021 (C. Fischer).

ORANGE-BREASTED FALCON *Falco deiroleucus*
Rare and local. Considered Near Threatened by IUCN (2023) and Endangered in Ecuador (Freile *et al*. 2019). There have been occasional reports from San José de Sumaco. One was photographed on 21 January 2023 (Fig. 3).

RED-AND-GREEN MACAW *Ara chloropterus*
Rare and local in east Ecuador (Ridgely & Greenfield 2001) where known mainly from the lowlands below 500 m (Freile & Restall 2018) and considered Vulnerable (Freile *et al*. 2019). A female specimen was mentioned by Chapman (1926), presumably AMNH 178951 taken on 31 March 1923 'below San José', but we could not locate the specimen. We photographed and obtained sound-recordings from a pair at *c*.950 m on 11 August 2019.

FIERY-THROATED FRUITEATER *Pipreola chlorolepidota*
Endemic to east Andean foothills where rare (Kirwan & Green 2011). Considered Vulnerable in Ecuador (Freile *et al*. 2019) and formerly considered Near Threatened by IUCN (2016). Five specimens from 'below San José' were mentioned by Chapman (1926). We located just one, a male (183718) at AMNH. In our field work, we encountered the species regularly in

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small numbers, often with mixed-species flocks that included various canopy-inhabiting tanagers. We consider it uncommon.

GREY-TAILED PIHA *Snowornis subalaris*
Endemic to east Andean foothills and outlying ridges (Kirwan & Greene 2011). Considered Near Threatened in Ecuador (Freile *et al*. 2019) and formerly globally by IUCN (2016). Chapman (1926) mentioned five specimens (AMNH 179616–617, 183735–736, 183835) from 'below San José'. Common and readily detected by its loud vocalisations. We found *S. subalaris* at 21 (68%) of 31 forest-interior transect points.

SHRIKE-LIKE COTINGA *Laniisoma elegans*
Rare and local in the east Andean foothills of Ecuador (Ridgely & Greenfield 2001, Kirwan & Green 2011). Considered Near Threatened by IUCN (2023) and Vulnerable in Ecuador (Freile *et al*. 2019). A female specimen in the Moore Laboratory of Zoology, Los Angeles (MLZ 33855) was taken 'below San José' by Carlos Olalla on 13 April 1927 (Fig. 5). We did not encounter the species and there seem to be no reports from San José de Sumaco.

RÍO SUNO ANTWREN *Myrmotherula sunensis*
Described by Chapman (1925) from nearby 'Río Suno below Avila' (LeCroy & Sloss 2000); considered rare in Ecuador (Ridgely & Greenfield 2001). The holotype is a female (AMNH 184582). A second female in AMNH (184583) taken 'below San José' was also mentioned by Chapman (1926). The widespread Slaty Antwren *M. schisticolor* has been considered an elevational replacement of this species (Whitney 1994) but the two are apparently syntopic at San José de Sumaco.

STRIATED ANTBIRD *Drymophila devillei*
Widespread and common in south-west Amazonia (Ridgely & Tudor 2009) but rare and local in Colombia, and in Ecuador (Ridgely & Greenfield 2001, Freile & Restall 2018), where considered Endangered (Freile *et al*. 2019). *D. devillei* is documented in Ecuador by a small number of specimens including five taken by Olalla & Hijos in present-day western Orellana province. Two of these are from 'Río Suno, above Avila' (AMNH 179319–320; Chapman 1926) with three from 'San José Abajo' (AMNH 184460–462) taken on 30–31 March and 1 April 1924. There are also recent reports from Avila (Fig. 1) and near Archidona in neighbouring Napo province (Ridgely & Greenfield 2001; eBird). An obligate bamboo specialist (Kratter 1997, Parker *et al*. 1997), we found small numbers of *D. devillei* in a large stand of *Guadua angustifolia* bamboo at *c*.950 m and obtained sound-recordings and photographs (Fig. 5). In Ecuador, previously known at 300–750 m (Freile & Restall 2018). Our records confirm the presence of the species at the site of the earliest Ecuadorian records (Chapman 1926) and extend the local elevational range to 950 m.

BLACKISH ANTBIRD *Cercomacroides nigrescens*
Chapman (1926) treated foothill populations of *C. nigrescens* as *C. n. approximans* and did not list San José de Sumaco (or any of its variant) for the species although he mentioned two males and two females taken by Olalla & Hijos at 'Lower Sumaco'. Shortly after, Zimmer (1931) described *C. n. aequatorialis*, designating a female from that series taken on 9 January 1926 as the holotype (AMNH 184517). The allied lowland form *C. fuscicauda* described by Zimmer (1931), now treated as a separate species, Riparian Antbird, following Mayer *et al*. (2014), is not known from San José de Sumaco. Identification difficulties and a paucity of comparative material in museums has impeded understanding of the distributions of

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Figure 5. Specimen (MLZ 33855) of Shrike-like Cotinga *Laniisoma elegans* at the Moore Laboratory of Ornithology, Los Angeles (A), Striated Antbird *Drymophila devillei* (B; Chris Fischer), Spectacled Redstart *Myioborus melanocephalus* (C; Michel Mifsud), Red-crested Finch *Coryphospingus cucullatus* (D; Chris Fischer), Slate-coloured Seedeater *Sporophila schistacea* (E; Chris Fischer)

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these forms. Two female specimens in MLZ (7639, 7688) were registered as Dusky Antbird *C. tyrannina*, later identified as *C. fuscicauda* (R. Terrill *in litt*. 2022), but from photographs they appear to be Black Antbird *C. serva*. A male (USNM 323078) taken by Olalla & Hijos on 20 April 1924, at 'Abajo, San José', was received by USNM in exchange from AMNH in 1930 and catalogued as '*Cercomacra serva*'. The USNM label bears the notation '*Cercomacra nigricans* A.W.' (= Alexander Wetmore) but this determination is puzzling in view of the bird's uniform dark tail and is perhaps best explained as a *lapsus* for *Cercomacra* (now *Cercomacroides*) *nigrescens*. We found *C. nigrescens* infrequently and regard it as rare at San José de Sumaco where it is presumably represented by Zimmer's *aequatorialis*.

SLENDER-BILLED XENOPS *Xenops tenuirostris*

Rare and poorly known in eastern Ecuador, where reported mainly below 600 m (Ridgely & Greenfield 2001, Freile & Restall 2018) but ranges at least locally to *c*.1,000 m (Freile *et al*. 2022). One was photographed at *c*.950 m as it foraged with a mixed-species flock on 28 July 2021 at RBBR. The similar Streaked Xenops *X. rutilans* is expected at this elevation, and has been reported from the area but without voucher.

RUFOUS-TAILED FOLIAGE-GLEANER *Anabacerthia ruficaudata*

Considered rare and local in Ecuador (Ridgely & Greenfield 2001, Freile & Restall 2018). Chapman (1926) mentioned five specimens from 'below San José', of which we located three in New York (AMNH 184267, 184269, 184270). We encountered the species regularly in small numbers at *c*.950 m and obtained photographs and sound-recordings. *A. ruficaudata* was typically found with canopy mixed-species flocks including various tanagers. We consider it an uncommon resident.

BROWN-RUMPED FOLIAGE-GLEANER *Automolus melanopezus*

Rare in east Ecuador, mainly in Napo and Sucumbíos provinces at elevations below 600 m (Ridgely & Greenfield 2001). Considered a bamboo specialist in Peru (Parker 1982). A specimen in the Carnegie Museum, Pittsburgh (CM 142784) was taken by Carlos Olalla on 10 April 1927 at 'San José Nuevo'. Chapman (1926) mentioned four males and a female from 'below San José'. We found three specimens in AMNH (184287–288, 184290). There are occasional sight reports and one was photographed on 11 February 2023 at *c*.950 m at San José de Sumaco.

ECUADORIAN TYRANNULET *Phylloscartes gualaquizae*

Endemic to the east Andean foothills and considered Near Threatened (Freile *et al*. 2019, IUCN 2023). Not listed for the site by Chapman (1926), but there is a specimen in AMNH (184000) annotated '*Pogonotriccus orbitalis*', taken on 19 April 1924 by Olalla & Hijos at 'San José abajo'. We encountered the species regularly with mixed-species flocks and consider it fairly common at San José de Sumaco.

CINNAMON MANAKIN-TYRANT *Neopipo cinnamomea*

Rare in western Amazonia (Ridgely & Tudor 2009). In Ecuador, known mainly from below 400 m, but recently reported at *c*.1,000 m in Morona-Santiago province (Pozo-Zamora *et al*. 2022). We encountered solitary individuals in forest understorey at *c*.950 m and regard the species as rare at San José de Sumaco. One was photographed by FE on 25 August 2017.

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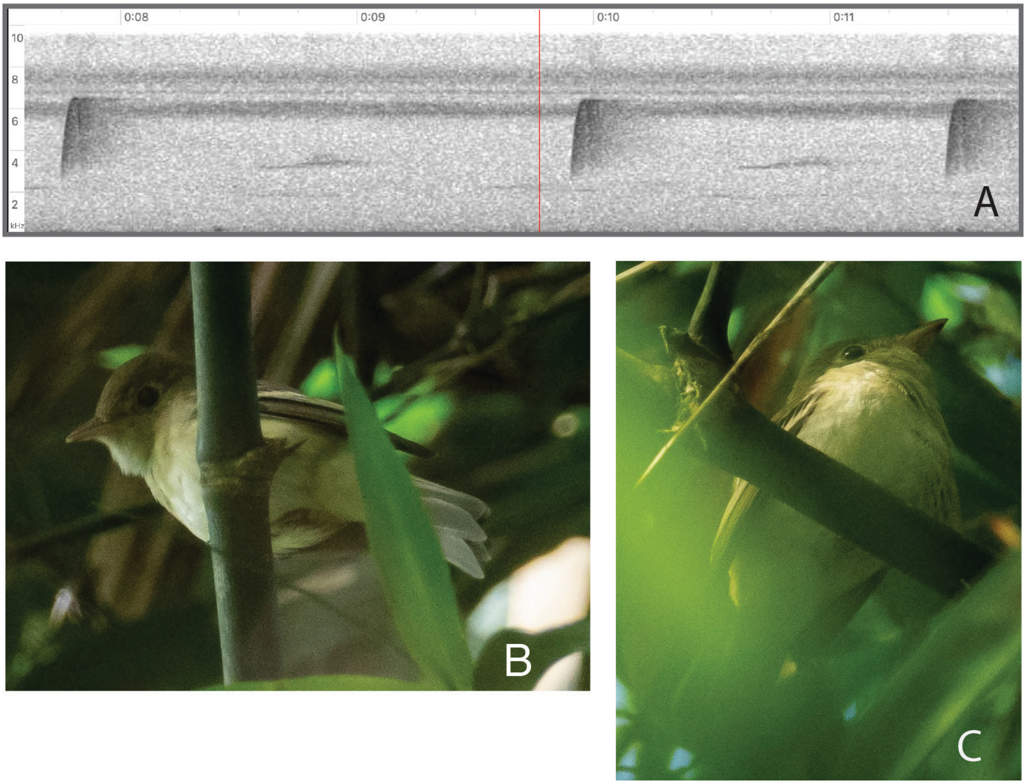

Figure 6. Sonogram of Acadian Flycatcher *Empidonax virescens* call notes (A), and photographs of the same bird (B–C; Chris Fischer)

ACADIAN FLYCATCHER *Empidonax virescens*
A boreal migrant (Ridgely & Tudor 2009). In Ecuador, known mainly from the Pacific slope (Ridgely & Greenfield 2001, Freile & Restall 2018). We found one in a large stand of *Guadua* bamboo on 13 January 2020 and obtained a sound-recording and photographs (Fig. 6).

RUFOUS-NAPED GREENLET *Pachysylvia semibrunnea*
Endemic to the north Andean foothills. In Ecuador, known mainly from the Volcán Sumaco region (Ridgely & Greenfield 2001) and considered Near Threatened (Freile *et al*. 2019). Now considered monotypic, but the type locality of *P. s. leucogastra* is 'below San José de Sumaco' (Chapman 1924). *P. semibrunnea* was detected at ten (32%) of 31 forest-interior transect points and we encountered the species regularly with mixed-species canopy flocks. We consider it fairly common.

RED-CRESTED FINCH *Coryphospingus cucullatus*
Formerly known in Ecuador only from Zamora-Chinchipe and Morona-Santiago provinces (Ridgely & Greenfield 2001, Freile *et al*. 2013, Freile & Restall 2018) and generally associated with arid scrub. Rapidly expanding north with deforestation, and recently reported in adjacent southern Colombia for the first time (Delgado & Rodríguez 2018). A male was photographed on 17 January 2020 in a cattle pasture at *c*.800 m (Fig. 5) and another was photographed there on 6 February 2023. We regard it as very rare.

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SLATE-COLOURED SEEDEATER *Sporophila schistacea*

A bamboo specialist that is perhaps nomadic (Willis & Eisenmann 1979). Rare in east Ecuador (Ridgely & Greenfield 2001). We obtained photographs and sound-recordings of several singing birds in the canopy of an extensive stand of *Guadua angustifolia* at *c*.950 m on 8, 11 and 15 January 2020, and on 8 December 2020, including yellow-billed, grey-plumaged, adult males (Fig. 5).

CERULEAN WARBLER *Setophaga cerulea*

A scarce boreal migrant. Considered Near Threatened by IUCN (2023) and Vulnerable in Ecuador (Freile *et al*. 2019). Chapman (1926) mentioned specimens from 'below San José' (AMNH 183542, 183544). We know of only a small number of sight records, all in December–January, and we suspect that our survey area at *c*.950 m is slightly below the main wintering elevational range (Colorado *et al*. 2012). We regard the species as a rare winter resident at San José de Sumaco.

CASQUED CACIQUE *Cacicus oseryi*

Endemic to western Amazonia (Ridgely & Tudor 2009). Rare in Ecuador, where known mainly from below 300 m (Ridgely & Greenfield 2001). A male (CM 102665) was taken on 30 March 1923 by Olalla & Hijos at 'San José abajo'. While this is from the period when these collectors were working for Chapman, and the specimen bears an AMNH label, Chapman (1926) did not list San José (or variants) in his monograph, but he listed five males taken in adjacent lowlands at 'Río Suno'. A second skin (MLZ 3802) was taken 2 April 1927 at 'San José Nuevo abajo' by Carlos Olalla. We did not encounter the species.

Discussion

Historical collections and the locality San José de Sumaco.—In 1923–24, the firm Olalla & Hijos (Fig. 2), professional collectors then under contract to Frank M. Chapman at AMNH, worked at a series of collecting stations along an elevational transect on the east slope of Volcán Sumaco. Their foothill station, San José de Sumaco, was worked principally during 2–31 March 1923 and 12 March–29 April 1924 (Chapman 1926, Paynter 1993, LeCroy & Sloss 2000, Wiley 2010). The resulting collections include at least 213 specimens taken in 1923 and 746 specimens in 1924. Much of this material is referenced, albeit without collection registration numbers, in Chapman (1926), and most is at AMNH. This material includes the holotypes of at least six taxa including *Leucopternis princeps zimmeri* Friedmann, 1935, *Megascops guatemalae napensis* (Chapman, 1928), *Dysithamnus mentalis napensis* Chapman 1925, *Myrmothera campanisona signata* J. T. Zimmer, 1934, *Pachysylvia semibrunnea leucogastra* Chapman, 1924, and *Microbates cinereiventris hormotus* Olson, 1980.

In the following years (1927–35), while Alfonso & Ramón Olalla worked in Peru and Brazil, Carlos Olalla remained in Ecuador (Wiley 2010) and returned to collect on the lower slopes of Volcán Sumaco during 1–18 April 1927, 1–27 January 1929, 13–25 August 1929, 9 July–28 August 1932, 18–25 September 1932, 10–20 March 1933 and 11–12 August 1935. This later material (1927–35), numbering >400 specimens, is held mainly at MLZ and appears never to have been published. Unlike the 1923–24 material, museum database registrations for specimens taken during 1927–35 appear to be incomplete and additional specimens taken in the area by Carlos Olalla are likely to be held elsewhere.

Chapman (1926) did not have coordinates or an elevation for San José de Sumaco and admitted some ambiguity by noting 'the site of the town is shifted in response to the need for fresh ground for crops, the present San José being apparently lower than the preceding one (San José Viejo)' but added that 'it should be understood that all American

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Museum specimens recorded from 'San José' or 'below San José' are from or near San José de Sumaco'. Because Chapman did not explicitly address the locality name 'San José Nuevo' vs. 'San José de Sumaco', the precise geographic origin of specimens bearing that locality is somewhat less certain. Some with the locality 'San José Nuevo' may have been taken at elevations below those areas that we surveyed most intensively. Paynter's (1993) coordinates locate San José Nuevo in the lowlands *c.*10 km north-east of San José Viejo (Fig. 1), whereas a hand-drawn map, prepared by W. T. Atyeo in the archives of the Dept. of Ornithology at AMNH, locates San José Nuevo in the foothills west of that position. See Fig. 1 for the present-day names of these communities and their geographic positions according to Paynter (1993). The collector's translated itinerary in the archives of the Dept. of Ornithology at AMNH (LeCroy & Sloss 2000) records the field parties, in both 1923 and 1924, collecting at Avila (Fig. 1) then moving north, paralleling the río Suno, following the east (left) bank to reach San José de Sumaco (= San José Viejo in Paynter 1993), before turning west to ascend the volcano. Review of the itinerary followed by Carlos Olalla using collection database records suggests he followed a similar route in later years, approaching the area from either Avila or Concepción in the south. We conclude that the Olalla & Hijos collecting station 'San José' (and variants) is best understood as the interfluvial of the ríos Suno and Bigal, from elevations of *c.*1,000 m (where the two rivers approach most closely) extending several km north-east and south across a fan-shaped area of *c.*200 km^2 on the eastern flank of Volcán Sumaco to at least 500 m, but possibly as low as 400 m (Fig. 1). The upper elevation portion of this area includes the present-day RBBR Research Station and our survey transects (Fig. 1).

The common place name 'San José' has invited some confusion in the literature and in museum database registrations involving Olalla collecting stations on Volcán Sumaco, certain localities on the upper Pacific slope in Pichincha province (e.g., 'Cerro San José'), and on the east slope in Morona-Santiago province ('San José' and 'Río San José'). Paynter (1993), for example, listed the locality 'San José, Ecuador' worked by Enrico Festa in 1896 (Salvadori & Festa 1899, 1900) as 'unlocated', and considered it to be 'presumably in the vicinity of Río Suno', and 'probably San José Nuevo', but the itinerary for Festa given by Chapman (1926) makes clear that it is correctly traced to Morona-Santiago province in southern Ecuador.

Noteworthy elevational records.—We report high-elevation records for 80 species, and low-elevation records for nine species (Appendix 1). We define noteworthy elevational records as recent observations at *c.*950 m at RBBR that are outside the elevational ranges given in standard references for Ecuadorian birds (Ridgely & Greenfield 2001, Freile & Restall 2018) although, in several cases, comparable records have recently been reported from foothill sites on outlying Andean ridges in southern Ecuador (e.g., Solano-Ugalde & Real-Jibaja 2010, Freile *et al.* 2014, 2022, Pozo-Zamora *et al.* 2022). We do not include 19 species documented only by specimens because the precise elevation at which they were taken is uncertain and some may have been taken as low as 500 m (e.g., Brown Nunlet *Nonnula brunnea*, Chestnut-belted Gnateater *Conopophaga aurita*, Banded Antbird *Dichrozona cincta*). In a few cases, we found temperate zone species (e.g., Blue-and-back Tanager *Tangara vassorii*, Black-capped Tanager *Stilpnia heinei*) at *c.*950 m during periods of cold, wet weather. Other cases of presumed elevational movement in species that are generally distributed at higher elevations include a Spectacled Whitestart *Myioborus melanocephalus* photographed near *c.*950 m (Fig. 5), sight records of White-tailed Hillstar *Urochroa bougueri*, and specimens of Long-tailed Sylph *Aglaiocercus kingii* and White-booted Racket-tail *Ocreatus underwoodii* (Appendix 1). These low-elevation records all refer to canopy or edge-inhabiting, frugivores or nectivores that may undertake facultative elevational movements in response to weather

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conditions (Levey & Stiles 1992, Boyle *et al*. 2010). Thirty-four records concern lowland species found 400 m or more above their published elevational ranges for Ecuador in standard references (Ridgely & Greenfield 2001, Freile & Restall 2018). In contrast to the low-elevation records (involving relatively vagile species) many of these high-elevation records (n = 80) involve sedentary, forest-interior species (e.g., Striated Antthrush *Chamaeza nobilis*, Black-tailed Leaftosser *Sclerurus caudacutus*, Cinereous Mourner *Laniocera hypopyrra*) that we detected regularly and that we assume are breeding residents. Of these 80 high-elevation records, all pertain to species not represented in the Olalla collections from a century ago and are consistent with a pattern of upward elevational range shifts in montane forest birds also reported at other re-surveyed sites in the East Andes and attributed to climate change (Freeman *et al*. 2018, Neate-Clegg *et al*. 2021).

Bamboo specialists.—Bamboo specialisation in Amazonian birds was first described and is best known from south-west Amazonia, especially southern Peru (Kratter 1997, Parker *et al*. 1997), but is also a feature of bird communities in north-west Amazonia, where stands of *Guadua* bamboo are less common and tend to be smaller. We regularly detected three obligate or near-obligate bamboo specialists (*sensu* Kratter 1997; Large-headed Flatbill *Ramphotrigon megacephalum*, Black-and-white Tody-Flycatcher *Poecilotriccus capitalis* and Striated Antbird *Drymophila devillei*). The first two species were present in most stands of bamboo, including smaller areas and those near or adjacent to forest edge, whilst *Drymophila devillei* was found only in the largest stand covering >20 ha. Most bamboo specialists recorded are insectivores, but two granivores, Slate-coloured Seedeater *Sporophila schistacea* and Slaty Finch *Haplospiza rustica*, were also documented. The occurrence of the former appeared to be unrelated to the availability of a *Guadua angustifolia* seed crop, and we did not witness seeding ('masting') bamboo, nor did we see evidence of mass die-off during our survey. A single specimen of Slaty Finch from San José de Sumaco (AMNH 179715) may represent an unusually low occurrence but the precise elevation where the specimen was taken is uncertain. In addition to these specialists, some globally widespread species such as Scale-crested Pygmy Tyrant *Lophotriccus pileatus* and Ornate Antwren *Epinecrophylla ornata* are locally associated with, or perhaps confined to, *Guadua angustifolia* bamboo stands at San José de Sumaco.

Historical change.—We describe a forest avifauna generally similar to that documented by the Olallas a century ago (Appendix 1) although we note that large-bodied species (e.g., *Mitu salvini*, *Nothocrax urumutum*), now recorded frequently by camera traps, are not represented in the Olalla collections. Non-forest bird communities have undergone more profound changes with the recent creation of large clearings planted with non-native grasses (pasture). In some cases, noteworthy elevational records (Appendix 1) involve non-forest species that are probably expanding upslope with deforestation (e.g., Ruddy Ground Dove *Columbina talpacoti*, Yellow-headed Caracara *Milvago chimachima*). Whilst the Olalla collections include some species typical of forest edge, small clearings and successional habitats (e.g., Great Antshrike *Taraba major*, Bluish-grey Saltator *Saltator coerulescens*, Orange-backed Troupial *Icterus croconotus*, Yellow-rumped Cacique *Cacicus cela*), none of the grassland species now common in non-forest areas at San José de Sumaco are represented (e.g., Yellow-browed Sparrow *Ammodramus aurifrons*, Blue-black Grassquit *Volatinia jacarina* and various *Sporophila*). Scant information is available to characterise ecological conditions during the time of the Olallas field work at San José de Sumaco, but a contemporaneous account by the adventurer G. M. Dyott (1929) suggests the area was then at least thinly populated. We assume that the area then consisted of a matrix of tall humid forest, secondary forest and some shifting cultivation as Chapman's remarks suggest (1926; see above). Twenty-two species represented in the Olalla collections were not confirmed

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during our field work, and we are not aware of any documented records from the area (Appendix 1). These species may no longer occur, may be locally rare, or may have been taken at (and are perhaps locally confined to) elevations below the areas we surveyed most intensively at *c.*950 m.

Species richness.—Freile *et al*. (2015) reported 460 species from BRBR but did not include a full list. White & Patiño (2018) reported 340 species at San José de Payamino in the nearby lowlands (Fig. 1). This study increases the number of species documented from San José de Sumaco by 202 over the total of 275 listed by Chapman (1926). The resulting total of 477 species includes 425 'core' tall-forest species (Appendix 1). Whilst variation in methods, spatial extent and period of study preclude rigorous comparison (Remsen 1994, Lees *et al*. 2014, Robinson *et al*. 2018) the apparent richness of the San José de Sumaco avifauna remains notable because the site is relatively restricted in area, is dominated by a single major natural vegetation type (upland *terra firme* forest) and lacks the major aquatic habitats and riparian forest types (e.g., *várzea*) that have 'inflated' estimates of diversity at Amazonian lowland sites (Stotz *et al*. 1996, Lees *et al*. 2013).

Local and global rarity.—Rarity presents a methodological impediment to survey effort but is also a general feature of tropical forest avian communities (Wallace 1878, Thiollay 1994, Jankowski & Rabenold 2007). A sample of 280 twenty-species 'MacKinnon lists' (Fig. 8; see Methods) captured just 73% ($n = 347$ species) of the total known species richness ($n = 477$ species, Appendix 1) and we consider more than half of the 477 documented species to be locally rare or very rare, with 110 species (22%) known from three or fewer reports. A generally positive relationship between abundance and geographic area suggests rare species are especially vulnerable to extirpation (Kattan 1992, Gaston & Blackburn 2000). Against this general pattern we note that several species recognised by Stattersfield *et al*. (1998) as East Andes of Ecuador endemics, and at least formerly considered Vulnerable or Near Threatened based on their restricted ranges (IUCN 2016, 2023), are among the more commonly detected species of forest interior at San José de Sumaco (e.g., Ecuadorian Piedtail *Phlogophilus hemileucurus*, Pink-throated Brilliant *Heliodoxa gularis* and *Phylloscartes gualaquizae*).

Endemism and biogeography.—Patterns of endemism are of interest to both conservationists and biogeographers and several general features of the San José de Sumaco assemblage are noteworthy in this respect. First, analyses of the distribution of restricted-range species reveal a global concentration at the Andean / Amazonian interface (Orme *et al*. 2005, Herzog & Kattan 2011, Fjeldså 2012), a pattern that invites explanation as the outcome of historical processes and identifies the region as a logical priority for conservation or a 'hotspot'.

Second, the site lies near the western margin of the North Amazon (Napo) area (Haffer 1974, Cracraft 1985), and among the range-restricted taxa present are both Napo endemic forms with sister species confined to the adjacent lowland Inambari area (e.g., Fulvous Antshrike *Frederickena fulva*, Dusky Spinetail *Synallaxis moesta*, Golden-winged Tody-Flycatcher *Poecilotriccus calopterus*), and East Andean endemic taxa with sister lineages in foothill and highland areas outside Amazonia including the Pacific slope (e.g., *Heliodoxa gularis*, Orange-eared Tanager *Chlorochrysa calliparaea*, *Pipreola chlorolepidota*; Stattersfield *et al*. 1998, Hazzi *et al*. 2018). Sympatry in taxa representative of distantly related Andean and Amazonian centres of endemism indicates a compound history (Haffer 1974, Cracraft 1985, Stattersfield *et al*. 1998, Hazzi *et al*. 2018) and this is consistent with studies elsewhere in the East Andean foothills that have reported low phylogenetic similarity between assemblages at 900 and 1,200 m (Dehling *et al*. 2014), a pattern marking the interface between older Amazonian and younger Andean biota (Weir 2006, Fjeldså & Irestedt 2009).

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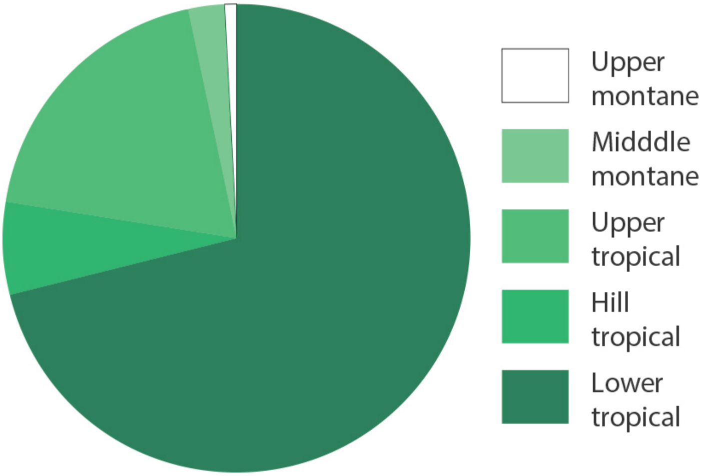

Figure 7. Proportional representation in the resident San José de Sumaco avifauna (n = 461 species; Appendix 1, excluding 16 long-distance migrant species) by 'centre of abundance' categories (median, continent-wide elevational range as given by Stotz *et al*. 1996). Lower tropical (n = 327, 71.1%), Hill tropical (n = 30, 6.6%), Upper tropical (n = 86, 18.9%), Middle montane (n = 12, 2.6%), Upper montane (n = 3, 0.7%).

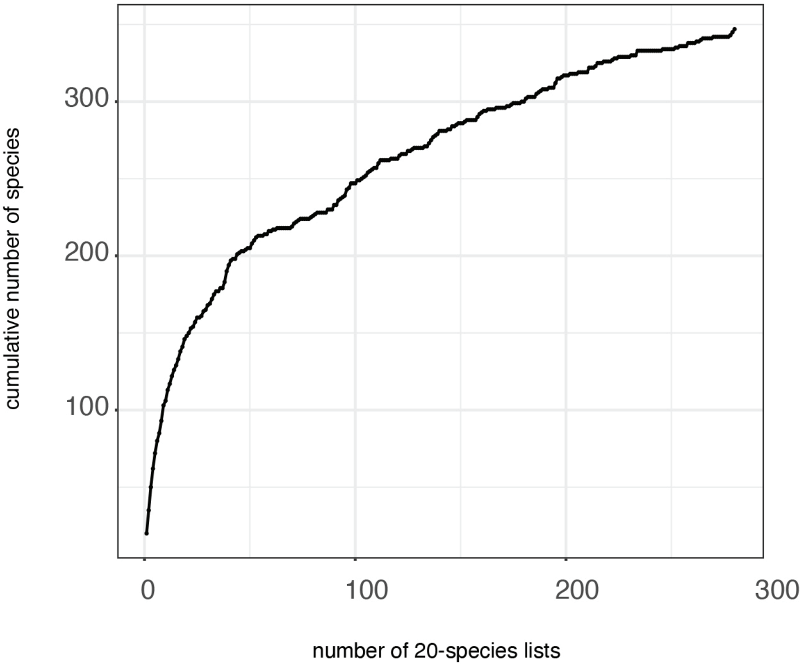

Figure 8. Species accumulation curve for the San José de Sumaco avifauna drawn from twenty-species MacKinnon lists (n = 280 lists, see Methods).

Third, whilst the San José de Sumaco avifauna is dominated by widespread Lower tropical species, it also includes a set of range-restricted Hill tropical or Upper tropical species (*sensu* Stotz *et al*. 1996; Fig. 7) that are confined to a narrow elevational band below the distribution of subtropical ('cloud') forests (e.g., *Heliodoxa gularis*, *Pipreola chlorolepidota*, *Phyllomyias gualaquizae*) and at least formerly considered Vulnerable or Near Threatened (IUCN 2016, 2023). The congruent foothill distributions of these taxa, each

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arisen from a widespread Andean clade, form a nested area within the greater East Andes area of endemism and suggest that while relationship patterns among the broad, disjunct Amazonian areas are relatively well studied, both discovery and relationships among areas in the tropical Andes remain poorly resolved and additional subcentres (nested areas) are likely to be recognised as more distributional data, taxonomic revisions and fine-scale regionalisation become available.

Finally, the San José de Sumaco avifauna includes taxa thought to have relatively extensive distributions in foothills, but considered rare (e.g., *Cypseloides lemosi*, *Snowornis subalaris* and Plain-backed Antpitta *Grallaria haplonota*), with some exhibiting circum-Amazonian distributions (e.g., *Tinamus tao*, *Laniisoma elegans* and *Synallaxis moesta*), as well as forest-dependent lowland species, in some cases with distributions reaching trans-Andean regions, but always at low densities (e.g., *Buteogallus solitarius*, *Neomorphus geoffroyi*, *Nyctibius aethereus*). While considered widespread, such taxa deserve attention from biogeographers and conservationists alike.

Conservation.—Long-term studies of tropical forest bird communities have demonstrated losses of functional and taxonomic diversity in both disturbed (Palacio *et al*. 2019, Gómez *et al*. 2021, Luther *et al*. 2022) and undisturbed landscapes (Blake & Loiselle 2015), but the forest avifauna we describe appears largely intact, suggesting the area still presents a valuable opportunity for conservation. For example, large-bodied, terrestrial species sensitive to local extirpation from hunting pressure (Peres 2001) including *Psophia crepitans*, *Mitu salvini* and *Nothocrax urumutum* are regularly recorded by camera-traps (Table 1). Neotropical forest understorey species often decline following disturbance (Laurance *et al*. 2011, Palacio *et al*. 2019), including ground insectivores and obligate ant-following species, but are regularly observed at San José de Sumaco. Large raptors typically confined to extensive undisturbed areas including *Buteogallus solitarius*, Ornate Hawk-Eagle *Spizaetus ornatus*, *Morphnus gujanensis* and *Harpia harpyja* are present, and the regular occurrence of 16 species of boreal migrants, notably including the Near Threatened *Contopus cooperi* and *Setophaga cerulea* (IUCN 2023) further underscore the area's value for conservation. Twenty-two species known only from historical specimens (Appendix 1) have diverse ecologies and do not appear likely to have declined locally because of anthropogenic change. Under current IUCN treatments (2023), the San José de Sumaco avifauna includes 15 species classified as Near Threatened and seven as Vulnerable (2023; Appendix 1). We regard five of the combined 22 Near Threatened and Vulnerable species as common, fairly common or uncommon at San José de Sumaco. At the national level, the Ecuadorian Red List (Freile *et al*. 2019) treats one species as Critical (*Buteogallus solitarius*), three as Endangered (*Falco deiroleucus*, Military Macaw *Ara militaris*, *Drymophila devillei*), 26 as Near Threatened and 11 as Vulnerable.

Following the construction of the Archidona to Loreto road the larger Sumaco region has undergone intensive deforestation and agricultural expansion (Sierra 2000). Pastures and other degraded anthropogenic landscapes now extend along a network of new roads stretching north from the paved highway connecting the cities of Loreto and Coca (Fig. 1). Whilst subtropical forests at higher elevations on Volcán Sumaco are protected in PNSNG and are thought to remain largely pristine, the lower eastern slopes have been approached from the south by an expanding agricultural frontier, and deforestation now threatens to sever the corridor that currently connects the subtropical forests of PNSNG and the lowland forests of San José de Payamino. Ecotonal areas (i.e., gradients of temperature or moisture) may be especially sensitive to synergistic effects of climate change and deforestation (Linck *et al*. 2021), but also offer valuable opportunities for conservation as even small additions to protected areas in regions with high beta diversity (i.e., mountain slopes) can

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be expected to incorporate many new species including range-restricted taxa and narrowly adapted local populations (Bush 2002, Jankowski *et al*. 2009). Irrespective of this, efforts to protect the remaining forests of San José de Sumaco from human disturbance and secure a biological corridor are already warranted because local extinctions and biodiversity erosion driven by the cascading effects of fragmentation are now well documented in Neotropical forests (Lees & Peres 2006, Laurance *et al*. 2011). While the East Andes and Amazonia have been found to rank below critically threatened regions of the Pacific slope in national-scale prioritisation schemes (Sierra *et al*. 2002, Cuesta *et al*. 2017), the Sumaco region still emerges as a priority for biodiversity conservation when feasibility is included as a criterion (Lessmann *et al*. 2014).

Conclusions

The collections assembled by the Olallas on the slopes of Volcán Sumaco a century ago helped to shape Chapman's (1926) understanding of elevational zonation and avian distributions (Kattan *et al*. 2016). Today, the lower East Andean slopes are known to harbour some of the world's richest local bird communities, an avifauna also characterised by high irreplaceability owing to the uniqueness of its evolutionary history (Haffer 1990, Herzog & Kattan 2011). Whilst these patterns are still under investigation, few undisturbed forested transects remain available for conservation or study (Stotz 1998, Kattan *et al*. 2016). San José de Sumaco hosts a rich avifauna including rare, threatened and poorly known taxa. The site's geographic position in an undisturbed foothill gradient, together with its history as the source of important collections underscore its value for conservation and continued study.

We hope that the results presented here will serve as a baseline for future monitoring efforts in the face of potential anthropogenic change including elevational range shifts and biodiversity degradation. Continued field work, ideally including a sustained programme of mist-netting, could add significantly to the list presented here by documenting species hitherto known only from sight records and uncovering the presence of additional rare resident species, invasive or expanding species, and migrants. We encourage visitors to document and publish their observations from San José de Sumaco.

Acknowledgements

We are grateful to the staff of Fundación Sumac Muyu for their assistance throughout this project. We thank Neil Bostock, Gilles Delforge, Mark Dorriesfield, Tom Feild, Juan Freile, Hervé & Noëlle Jacob, Geraldine King, Guy Kirwan, Robert McKay, Michel Mifsud, Lelis Navarrete, Andrew Hart Reeve, John Schenck and especially Chris Fischer for sharing their observations, photographs and sound-recordings. John S. Ascher, Nicholas Brokaw, Juan Freile, Stuart Pimm and Sheila Ward made helpful comments on an earlier draft. Jonas Nilsson shared his expert knowledge of the Sumaco avifauna. We thank Paul Sweet and Tom Trombone for help with database queries and locating archival materials in the AMNH Dept. of Ornithology. Christopher Milensky and Jacob Saucier permitted us to examine specimens at the National Museum of Natural History, Smithsonian Institution, Washington DC. We are very grateful to the museum workers that answered our queries and provided photographs and information including John McCormack, Ryan S. Terrill and Russell Campbell at MLZ, Serina S. Brady at CM, and Ulf Johansson at the Naturhistoriska Riksmuseet, Stockholm. Tom Stephenson offered advice on recording equipment. Henry Albert Ertl helped prepare the figures. Comments and corrections from the editors, Guy Kirwan and Chris Sharpe, and three reviewers, improved the manuscript.

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Appendix 1

List of 477 species recorded from San José de Sumaco, Orellana province, Ecuador. Systematic order and scientific nomenclature follow Remsen *et al.* (2023). Twenty-two species known only from historical (specimen) records are marked *. Fifty-two species found only in open areas (non-'core' species) are marked †. IUCN (2023) status categories: LC = Least Concern; NT = Near Threatened; VU = Vulnerable; DD = Data Deficient. Evidence categories: Sp = specimen published or registered in museum database; **Sp** = specimen examined in a museum collection or photograph; P = photograph or video image; R = sound-recording. Abundance categories: A = abundant (recorded daily in the field in appropriate habitat, often in large numbers); VC = very common (recorded almost daily, but usually not in such large numbers as the previous category); C = common (recorded on substantially more than 50% of all days in the field); FC = fairly common (recorded on *c.*50% of all days in the field); UC = uncommon (recorded on substantially fewer than 50% of all days in the field, but more common than species in the following category); R = rare (recorded on fewer than 10% of all days in the field); VR = very rare (very few records and never in large numbers). Under Elevation extension we give deviation from the elevational range found in standard references (Ridgely & Greenfield 2001, Freile & Restall 2018) for 89 species found at *c.*950 m.

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Family/English name	Scientific name	IUCN	Evidence	Abundance	Elevation extension
TINAMIDAE					
Grey Tinamou	*Tinamus tao*	VU	P,R	VR	
Great Tinamou	*Tinamus major*	LC	**Sp**,P,R	FC	
White-throated Tinamou	*Tinamus guttatus*	NT	**Sp**,P	VR	
Cinereous Tinamou	*Crypturellus cinereus*†	LC	R	VR	
Little Tinamou	*Crypturellus soui*	LC	**Sp**,R	U	
Undulated Tinamou	*Crypturellus undulatus*†	LC	R	R	+350
CRACIDAE					
Sickle-winged Guan	*Chamaepetes goudotii*	LC		VR	
Spix's Guan	*Penelope jacquacu*	LC	Sp,P,R	U	
Blue-throated Piping Guan	*Pipile cumanensis*	LC	**Sp**,P,R	U	+550
Wattled Guan	*Aburria aburri*	NT	P	R	–250
Speckled Chachalaca	*Ortalis guttata*†	LC	Sp,R	U	
Nocturnal Curassow	*Nothocrax urumutum*	LC	P,R	FC	
Salvin's Curassow	*Mitu salvini*	LC	P,R	U	+550
ODONTOPHORIDAE					
Marbled Wood Quail	*Odontophorus gujanensis*	LC	**Sp**,P,R	U	
Rufous-breasted Wood Quail	*Odontophorus speciosus*	LC	**Sp**,P	VR	
COLUMBIDAE					
Scaled Pigeon	*Patagioenas speciosa*	LC	Sp,P,R	U	
Pale-vented Pigeon	*Patagioenas cayennensis*†	LC	P	VR	
Plumbeous Pigeon	*Patagioenas plumbea*	LC	**Sp**,P,R	VC	
Ruddy Pigeon	*Patagioenas subvinacea*	LC	R	U	
Sapphire Quail-Dove	*Geotrygon saphirina*	LC	**Sp**,P,R	U	
Ruddy Quail-Dove	*Geotrygon montana*	LC	**Sp**,P,R	FC	
Grey-fronted Dove	*Leptotila rufaxilla*	LC	**Sp**,P,R	R	
Ruddy Ground Dove	*Columbina talpacoti*†	LC	P,R	U	+450
White-throated Quail-Dove	*Zentrygon frenata*	LC	P	VR	
CUCULIDAE					
Smooth-billed Ani	*Crotophaga ani*†	LC	**Sp**,P,R	FC	
Rufous-vented Ground Cuckoo	*Neomorphus geoffroyi*	VU	**Sp**	VR	+550
Squirrel Cuckoo	*Piaya cayana*	LC	Sp,P,R	U	
Black-bellied Cuckoo	*Piaya melanogaster*	LC	P,R	U	
STEATORNITHIDAE					
Oilbird	*Steatornis caripensis*	LC	R	VR	
NYCTIBIIDAE					
Great Potoo	*Nyctibius grandis*	LC	P	VR	
Long-tailed Potoo	*Nyctibius aethereus**	LC	**Sp**		
Common Potoo	*Nyctibius griseus*	LC	**Sp**,R	VR	

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Family/English name	Scientific name	IUCN	Evidence	Abundance	Elevation extension
CAPRIMULGIDAE					
Blackish Nightjar	*Nyctipolus nigrescens*	LC	P,R	U	
Common Pauraque	*Nyctidromus albicollis*	LC	R	R	
Ocellated Poorwill	*Nyctiphrynus ocellatus*	LC		VR	+450
APODIDAE					
Spot-fronted Swift	*Cypseloides cherriei*	DD	P	R	
White-chinned Swift	*Cypseloides cryptus*	LC	P	R	
White-chested Swift	*Cypseloides lemosi*	LC	P	R	
Chestnut-collared Swift	*Streptoprocne rutila*	LC	P	U	
White-collared Swift	*Streptoprocne zonaris*	LC	Sp,P	A	
Grey-rumped Swift	*Chaetura cinereiventris*	LC	P	FC	
Chimney Swift	*Chaetura pelagica*	VU	P	VR	
Short-tailed Swift	*Chaetura brachyura*	LC	P	FC	
Lesser Swallow-tailed Swift	*Panyptila cayennensis*	LC	P	VR	
TROCHILIDAE					
White-necked Jacobin	*Florisuga mellivora*	LC	**Sp**,P	R	
White-tipped Sicklebill	*Eutoxeres aquila*	LC	**Sp**,R	U	
Buff-tailed Sicklebill	*Eutoxeres condamini*	LC	P	R	
Rufous-breasted Hermit	*Glaucis hirsutus*	LC	**Sp**	VR	
Pale-tailed Barbthroat	*Threnetes leucurus*	LC	**Sp**,P	R	
Black-throated Hermit	*Phaethornis atrimentalis**	LC	**Sp**		
Grey-chinned Hermit	*Phaethornis griseogularis*	LC	**Sp**,P,R	U	
White-bearded Hermit	*Phaethornis hispidus*	LC	**Sp**,R	R	
Green Hermit	*Phaethornis guy*	LC	**Sp**,P	U	
Straight-billed Hermit	*Phaethornis bourcieri*	LC	**Sp**,P	VR	
Great-billed Hermit	*Phaethornis malaris*	LC	**Sp**,P,R	U	
Green-fronted Lancebill	*Doryfera ludovicae*	LC	**Sp**,P	VR	
Blue-fronted Lancebill	*Doryfera johannae*	LC	**Sp**,P,R	FC	
Brown Violetear	*Colibri delphinae*	LC	Sp	VR	
Lesser Violetear	*Colibri cyanotus*	LC	**Sp**,P	VR	
Sparkling Violetear	*Colibri coruscans*	LC	P	R	
Black-eared Fairy	*Heliothryx auritus*	LC	**Sp**,P	R	
Black-throated Mango	*Anthracothorax nigricollis*†	LC		VR	
Black-bellied Thorntail	*Discosura langsdorffi*	LC	Sp,P	R	
Ecuadorian Piedtail	*Phlogophilus hemileucurus*	LC	**Sp**,P,R	FC	
Long-tailed Sylph	*Aglaiocercus kingii**	LC	**Sp**		
Booted Racket-tail	*Ocreatus underwoodii**	LC	**Sp**		
Rufous-vented Whitetip	*Urosticte ruficrissa*	LC	**Sp**	VR	–200
Pink-throated Brilliant	*Heliodoxa gularis*	LC	**Sp**,P,R	C	
Black-throated Brilliant	*Heliodoxa schreibersii*	LC	**Sp**,P,R	U	
Gould's Jewelfront	*Heliodoxa aurescens*	LC	**Sp**,P	R	
White-bellied Woodstar	*Chaetocercus mulsant*	LC	P	VR	
Little Woodstar	*Chaetocercus bombus**	NT	**Sp**		
Gorgeted Woodstar	*Chaetocercus heliodor*	LC	**Sp**,P	VR	–200

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Family/English name	**Scientific name**	**IUCN**	**Evidence**	**Abundance**	**Elevation extension**
Amethyst Woodstar	*Calliphlox amethystina*	LC	P	R	
Blue-tailed Emerald	*Chlorostilbon mellisugus**	LC	**Sp**		
Violet-headed Hummingbird	*Klais guimeti*	LC	**Sp**	VR	
Grey-breasted Sabrewing	*Campylopterus largipennis*	LC	**Sp**,P	R	
Napo Sabrewing	*Campylopterus villaviscensio*	NT	**Sp**,P	U	
Fork-tailed Woodnymph	*Thalurania furcata*	LC	**Sp**,P	FC	
Many-spotted Hummingbird	*Taphrospilus hypostictus*	LC	**Sp**,P	VR	
Golden-tailed Sapphire	*Chrysuronia oenone*	LC	**Sp**,P,R	U	
Glittering-throated Emerald	*Chionomesa fimbriata*†	LC	P	R	
Rufous-throated Sapphire	*Hylocharis sapphirina*	LC	P	VR	+550
PSOPHIIDAE					
Grey-winged Trumpeter	*Psophia crepitans*	LC	**Sp**,P,R	R	+250
RALLIDAE					
Chestnut-headed Crake	*Anurolimnas castaneiceps*	LC	**Sp**,R	R	
Grey-breasted Crake	*Laterallus exilis*†	LC	R	R	+100
Grey-cowled Wood Rail	*Aramides cajaneus*	LC		VR	+550
Red-winged Wood Rail	*Aramides calopterus*	LC	**Sp**,P,R	R	
EURYPYGIDAE					
Sunbittern	*Eurypyga helias*	LC	Sp	VR	
ARDEIDAE					
Fasciated Tiger Heron	*Tigrisoma fasciatum*	LC	Sp,P	VR	
Cattle Egret	*Bubulcus ibis*†	LC	P	R	
CATHARTIDAE					
King Vulture	*Sarcoramphus papa*	LC	P	R	+450
Black Vulture	*Coragyps atratus*	LC	P	U	
Turkey Vulture	*Cathartes aura*	LC	P	U	
Greater Yellow-headed Vulture	*Cathartes melambrotus*	LC	P	R	
ACCIPITRIDAE					
Hook-billed Kite	*Chondrohierax uncinatus*†	LC		VR	
Swallow-tailed Kite	*Elanoides forficatus*	LC	**Sp**,P	FC	
Crested Eagle	*Morphnus gujanensis**	NT	**Sp**		
Harpy Eagle	*Harpia harpyja*	NT	P	VR	+650
Black Hawk-Eagle	*Spizaetus tyrannus*	LC	P,R	U	
Black-and-white Hawk-Eagle	*Spizaetus melanoleucus*	LC	P	VR	
Ornate Hawk-Eagle	*Spizaetus ornatus*	NT	P,R	U	+450
Double-toothed Kite	*Harpagus bidentatus*	LC	**Sp**,P	R	
Plumbeous Kite	*Ictinia plumbea*	LC	P	U	
Bicolored Hawk	*Accipiter bicolor*	LC	**Sp**,P	R	
Semicollared Hawk	*Microspizias collaris*	LC		VR	–550
Solitary Eagle	*Buteogallus solitarius*	NT	P,R	R	

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Barred Hawk	*Morphnarchus princeps*	LC	**Sp**	VR	
Roadside Hawk	*Rupornis magnirostris*†	LC	**Sp**,P,R	FC	
White Hawk	*Pseudastur albicollis*	LC	**Sp**,P,R	FC	
Black-faced Hawk	*Leucopternis melanops*	LC	P	VR	
Broad-winged Hawk	*Buteo platypterus*	LC	P	VR	
Short-tailed Hawk	*Buteo brachyurus*	LC	P	VR	
STRIGIDAE					
Tropical Screech Owl	*Megascops choliba*	LC	R	VR	+250
Rufescent Screech Owl	*Megascops ingens*	LC	R	VR	–300
Foothill Screech Owl	*Megascops roraimae*	LC	**Sp**,P,R	U	
Tawny-bellied Screech Owl	*Megascops watsonii*	LC	Sp	VR	
Crested Owl	*Lophostrix cristata*	LC	R	VR	
Spectacled Owl	*Pulsatrix perspicillata*	LC	P	VR	
Band-bellied Owl	*Pulsatrix melanota*	LC	**Sp**,P,R	FC	
Black-banded Owl	*Strix huhula*	LC	Sp,R	VR	
Subtropical Pygmy Owl	*Glaucidium parkeri*	LC	R	VR	–150
Ferruginous Pygmy Owl	*Glaucidium brasilianum*†	LC	R	R	
TROGONIDAE					
Pavonine Quetzal	*Pharomachrus pavoninus*	LC	Sp,P,R	U	+350
Golden-headed Quetzal	*Pharomachrus auriceps*	LC	**Sp**,R	VR	
Black-tailed Trogon	*Trogon melanurus*	LC	**Sp**,R	VR	+550
Green-backed Trogon	*Trogon viridis*	LC	**Sp**,P,R	VC	
Amazonian Trogon	*Trogon ramonianus*	LC	P,R	R	+450
Blue-crowned Trogon	*Trogon curucui*	LC	P,R	FC	
Black-throated Trogon	*Trogon rufus*	LC	R	R	+150
Collared Trogon	*Trogon collaris*	LC	**Sp**,P,R	C	
MOMOTIDAE					
Broad-billed Motmot	*Electron platyrhynchum*	LC	**Sp**,R	VR	
Rufous Motmot	*Baryphthengus martii*	LC	**Sp**,P,R	C	
ALCEDINIDAE					
Ringed Kingfisher	*Megaceryle torquata*	LC	Sp	VR	
GALBULIDAE					
Purplish Jacamar	*Galbula chalcothorax*	LC		VR	
Great Jacamar	*Jacamerops aureus*	LC	P,R	U	
BUCCONIDAE					
Collared Puffbird	*Bucco capensis*	LC	P,R	R	+450
Western Striolated Puffbird	*Nystalus obamai*	LC	P,R	R	
White-chested Puffbird	*Malacoptila fusca*	LC	**Sp**,P	R	
Brown Nunlet	*Nonnula brunnea**	LC	**Sp**		
Black-fronted Nunbird	*Monasa nigrifrons*	LC	P	VR	+400

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ISSN-2513-9894
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Family/English name	**Scientific name**	**IUCN**	**Evidence**	**Abundance**	**Elevation extension**
White-fronted Nunbird	*Monasa morphoeus*	LC	P,R	U	
Yellow-billed Nunbird	*Monasa flavirostris*	LC	R	R	+150
CAPITONIDAE					
Gilded Barbet	*Capito auratus*	LC	**Sp**,P,R	VC	
Lemon-throated Barbet	*Eubucco richardsoni*	LC	**Sp**,R	R	
Red-headed Barbet	*Eubucco bourcierii*	LC	**Sp**	U	
RAMPHASTIDAE					
Yellow-throated Toucan	*Ramphastos ambiguus*	NT	**Sp**,P,R	U	
White-throated Toucan	*Ramphastos tucanus*	LC	**Sp**,P,R	VC	
Channel-billed Toucan	*Ramphastos vitellinus*	LC	**Sp**,R	U	
Chestnut-tipped Toucanet	*Aulacorhynchus derbianus*	LC	**Sp**	VR	
Golden-collared Toucanet	*Selenidera reinwardtii*	LC	**Sp**,P,R	FC	
Lettered Aracari	*Pteroglossus inscriptus*	LC	P	VR	+450
Chestnut-eared Aracari	*Pteroglossus castanotis*	LC	P,R	U	
Many-banded Aracari	*Pteroglossus pluricinctus*	LC	**Sp**,P,R	U	+150
Ivory-billed Aracari	*Pteroglossus azara*	LC	**Sp**	R	
PICIDAE					
Lafresnaye's Piculet	*Picumnus lafresnayi*	LC	**Sp**,P	U	
Rufous-breasted Piculet	*Picumnus rufiventris*	LC	**Sp**,R	R	
Yellow-tufted Woodpecker	*Melanerpes cruentatus*	LC	**Sp**,P,R	C	
Little Woodpecker	*Dryobates passerinus*	LC		R	
Red-stained Woodpecker	*Dryobates affinis*	LC	P,R	R	+150
Red-necked Woodpecker	*Campephilus rubricollis*	LC	Sp,P,R	FC	+450
Crimson-crested Woodpecker	*Campephilus melanoleucos*	LC	Sp,P,R	FC	
Lineated Woodpecker	*Dryocopus lineatus*	LC	**Sp**,P	R	
Scale-breasted Woodpecker	*Celeus grammicus*	LC	R	VR	+450
Cream-coloured Woodpecker	*Celeus flavus*	LC	R	VR	+250
Chestnut Woodpecker	*Celeus elegans*	LC	P,R	VR	+250
White-throated Woodpecker	*Piculus leucolaemus*	LC	**Sp**,P,R	FC	
Spot-breasted Woodpecker	*Colaptes punctigula*†	LC	P	R	
FALCONIDAE					
Laughing Falcon	*Herpetotheres cachinnans*†	LC	P	R	
Barred Forest Falcon	*Micrastur ruficollis*	LC	**Sp**,P,R	U	
Lined Forest Falcon	*Micrastur gilvicollis*	LC	P,R	R	
Collared Forest Falcon	*Micrastur semitorquatus*	LC	**Sp**,R	R	
Buckley's Forest Falcon	*Micrastur buckleyi*	LC	**Sp**	VR	
Red-throated Caracara	*Ibycter americanus*	LC	**Sp**,P,R	FC	
Black Caracara	*Daptrius ater*	LC	P,R	R	
Yellow-headed Caracara	*Milvago chimachima*†	LC	P	R	+650
Bat Falcon	*Falco rufigularis*	LC	P	R	
Orange-breasted Falcon	*Falco deiroleucus*	NT	P	VR	

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PSITTACIDAE					
Scarlet-shouldered Parrotlet	*Touit huetii*	LC		VR	
Cobalt-winged Parakeet	*Brotogeris cyanoptera*	LC	P,R	C	
Red-billed Parrot	*Pionus sordidus*	LC		VR	
Blue-headed Parrot	*Pionus menstruus*	LC	P,R	VC	
Yellow-crowned Parrot	*Amazona ochrocephala*	LC	R	VR	
Mealy Parrot	*Amazona farinosa*	LC	**Sp**,P,R	FC	
Orange-winged Parrot	*Amazona amazonica*	LC	P,R	VR	+450
Dusky-billed Parrotlet	*Forpus modestus*	LC	Sp,P	VR	
Maroon-tailed Parakeet	*Pyrrhura melanura*	LC	Sp,R	FC	
Chestnut-fronted Macaw	*Ara severus*	LC	P,R	FC	
Military Macaw	*Ara militaris*	VU	P,R	FC	
Scarlet Macaw	*Ara macao*	LC		VR	+500
Red-and-green Macaw	*Ara chloropterus*	LC	Sp,P,R	VR	+450
White-eyed Parakeet	*Psittacara leucophthalmus*†	LC	Sp,P,R	U	
THAMNOPHILIDAE					
Fasciated Antshrike	*Cymbilaimus lineatus*	LC	**Sp**,P,R	FC	
Fulvous Antshrike	*Frederickena fulva*	LC	P,R	U	+250
Great Antshrike	*Taraba major*†	LC	**Sp**,R	R	
Lined Antshrike	*Thamnophilus tenuepunctatus*†	VU	**Sp**	VR	
Plain-winged Antshrike	*Thamnophilus schistaceus*	LC	**Sp**,P,R	FC	
White-shouldered Antshrike	*Thamnophilus aethiops*	LC	**Sp**,P,R	C	
Russet Antshrike	*Thamnistes anabatinus*	LC	**Sp**,P,R	U	
Plain Antvireo	*Dysithamnus mentalis*	LC	**Sp**,R	VC	
Yellow-breasted Antwren	*Herpsilochmus axillaris*	VU		R	
Rusty-winged Antwren	*Herpsilochmus frater*	LC	**Sp**,P,R	VC	
Dusky-throated Antshrike	*Thamnomanes ardesiacus*	LC	Sp,P,R	FC	+450
Cinerous Antshrike	*Thamnomanes caesius**	LC	**Sp**		
Plain-throated Antwren	*Isleria hauxwelli*	LC		R	+550
Spot-winged Antshrike	*Pygiptila stellaris**	LC	**Sp**		
Ornate Stipplethroat	*Epinecrophylla ornata*	LC	**Sp**	VR	
Rufous-tailed Stipplethroat	*Epinecrophylla erythrura*	LC	**Sp**	VR	
Foothill Stipplethroat	*Epinecrophylla spodionota*	LC	**Sp**,P,R	C	
Pygmy Antwren	*Myrmotherula brachyura*	LC	**Sp**,P	VR	+300
Moustached Antwren	*Myrmotherula ignota*	LC	**Sp**,P,R	FC	+350
White-flanked Antwren	*Myrmotherula axillaris*	LC	**Sp**,P,R	C	
Slaty Antwren	*Myrmotherula schisticolor*	LC	P	R	
Rio Suno Antwren	*Myrmotherula sunensis*	LC	**Sp**	VR	
Long-winged Antwren	*Myrmotherula longipennis*	LC	P,R	U	+450
Plain-winged Antwren	*Myrmotherula behni*	LC	R	R	
Grey Antwren	*Myrmotherula menetriesii*	LC	**Sp**,P,R	U	
Banded Antbird	*Dichrozona cincta**	LC	**Sp**		
Dot-winged Antwren	*Microrhopias quixensis**	LC	**Sp**		
Striated Antbird	*Drymophila devillei*	LC	**Sp**,P,R	R	+200
Peruvian Warbling Antbird	*Hypocnemis peruviana*†	LC	**Sp**,P,R	U	

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Black Antbird	*Cercomacroides serva*	LC	**Sp**,R	C	
Blackish Antbird	*Cercomacroides nigrescens*	LC	**Sp**	R	
Grey Antbird	*Cercomacra cinerascens*	LC	**Sp**,R	FC	
Western Fire-eye	*Pyriglena maura*	LC	R	R	
Black-faced Antbird	*Myrmoborus myotherinus*	LC	**Sp**,P,R	C	
Spot-winged Antbird	*Myrmelastes leucostigma*	LC	**Sp**,P,R	R	
Sooty Antbird	*Hafferia fortis*	LC	Sp,P,R	FC	+350
White-plumed Antbird	*Pithys albifrons*	LC	P,R	U	
White-cheeked Antbird	*Gymnopithys leucaspis*	LC	P,R	FC	+200
Hairy-crested Antbird	*Rhegmatorhina melanosticta*	LC	Sp,P,R	R	
Spot-backed Antbird	*Hylophylax naevius*	LC	**Sp**,P,R	C	
Common Scale-backed Antbird	*Willisornis poecilinotus*	LC	**Sp**,P,R	FC	
Reddish-winged Bare-eye	*Phlegopsis erythroptera*	LC		VR	+200
CONOPOPHAGIDAE					
Chestnut-belted Gnateater	*Conopophaga aurita**	LC	**Sp**		
GRALLARIIDAE					
Scaled Antpitta	*Grallaria guatimalensis*	LC	**Sp**,P,R	FC	
Plain-backed Antpitta	*Grallaria haplonota*	LC	P,R	U	–200
White-lored Antpitta	*Myrmothera fulviventris*†	LC	**Sp**,R	R	+200
Thrush-like Antpitta	*Myrmothera campanisona*	LC	**Sp**,R	C	
RHINOCRYPTIDAE					
White-crowned Tapaculo	*Scytalopus atratus*	LC	**Sp**	VR	
FORMICARIIDAE					
Rufous-capped Antthrush	*Formicarius colma*	LC	**Sp**	VR	+450
Black-faced Antthrush	*Formicarius analis*	LC	**Sp**	VR	
Short-tailed Antthrush	*Chamaeza campanisona*	LC	**Sp**,R	U	
Striated Antthrush	*Chamaeza nobilis*	LC	P,R	U	+450
FURNARIIDAE					
South American Leaftosser	*Sclerurus obscurior*	LC	**Sp**,R	FC	
Short-billed Leaftosser	*Sclerurus rufigularis*	LC	P	R	+650
Black-tailed Leaftosser	*Sclerurus caudacutus*	LC	**Sp**,P,R	R	+450
Olivaceous Woodcreeper	*Sittasomus griseicapillus*	LC	P,R	R	
Long-tailed Woodcreeper	*Deconychura longicauda*	NT	P,R	R	
Plain-brown Woodcreeper	*Dendrocincla fuliginosa*	LC	**Sp**,P,R	C	
Wedge-billed Woodcreeper	*Glyphorynchus spirurus*	LC	**Sp**,P,R	FC	
Cinnamon-throated Woodcreeper	*Dendrexetastes rufigula*	LC	R	VR	
Amazonian Barred Woodcreeper	*Dendrocolaptes certhia*	LC	**Sp**,P,R	VR	
Black-banded Woodcreeper	*Dendrocolaptes picumnus*	LC	P,R	VU	
Strong-billed Woodcreeper	*Xiphocolaptes promeropirhynchus*	LC	**Sp**,P,R	C	
Ocellated Woodcreeper	*Xiphorhynchus ocellatus*	LC	**Sp**,P,R	C	
Buff-throated Woodcreeper	*Xiphorhynchus guttatus*	LC	**Sp**,P,R	FC	

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Olive-backed Woodcreeper	*Xiphorhynchus triangularis*	LC	**Sp**,P,R	R	
Straight-billed Woodcreeper	*Dendroplex picus*	LC	R	VR	+550
Red-billed Scythebill	*Campylorhamphus trochilirostris*	LC	**Sp**,R	FC	
Duida Woodcreeper	*Lepidocolaptes duidae*	LC	P,R	FC	
Slender-billed Xenops	*Xenops tenuirostris*	LC	P	VR	+350
Plain Xenops	*Xenops minutus*	LC	**Sp**,P	U	
Rufous-tailed Xenops	*Microxenops milleri*	LC	P,R	VR	
Sharp-tailed Streamcreeper	*Lochmias nematura*	LC	**Sp**	R	
Dusky-cheeked Foliage-gleaner	*Anabazenops dorsalis*	LC	**Sp**,P	VR	
Rufous-rumped Foliage-gleaner	*Philydor erythrocercum*	LC	Sp,P,R	FC	
Cinnamon-rumped Foliage-gleaner	*Philydor pyrrhodes*	LC	P,R	FC	+150
Rufous-tailed Foliage-gleaner	*Anabacerthia ruficaudata*	LC	**Sp**,P,R	U	
Chestnut-winged Hookbill	*Ancistrops strigilatus*	LC		VR	+350
Buff-fronted Foliage-gleaner	*Dendroma rufa*	LC	P	VR	
Ruddy Foliage-gleaner	*Clibanornis rubiginosus*	LC	**Sp**,R	C	
Black-billed Treehunter	*Thripadectes melanorhynchus*	LC	**Sp**,R	U	
Brown-rumped Foliage-gleaner	*Automolus melanopezus*	LC	**Sp**,P	VR	+350
Buff-throated Foliage-gleaner	*Automolus ochrolaemus*	LC	**Sp**,R	R	+150
Striped Woodhaunter	*Automolus subulatus*	LC	**Sp**,P,R	C	
Olive-backed Foliage-gleaner	*Automolus infuscatus*	LC	Sp,R	R	+250
Spotted Barbtail	*Premnoplex brunnescens*	LC	**Sp**	R	
Plain Softtail	*Thripophaga fusciceps**	LC	**Sp**		
Ash-browed Spinetail	*Cranioleuca curtata*	LC	**Sp**,P,R	R	
Speckled Spinetail	*Cranioleuca gutturata*	LC	**Sp**,P,R	R	+350
Dusky Spinetail	*Synallaxis moesta*†	LC	**Sp**,R	R	
Dark-breasted Spinetail	*Synallaxis albigularis*†	LC	Sp	VR	
PIPRIDAE					
Dwarf Tyrant-Manakin	*Tyranneutes stolzmanni*	LC	**Sp**,P,R	C	
Blue-backed Manakin	*Chiroxiphia pareola**	LC	**Sp**		
Golden-winged Manakin	*Masius chrysopterus*	LC	**Sp**	VR	
Green Manakin	*Cryptopipo holochlora*	LC	**Sp**,P,R	FC	
Blue-capped Manakin	*Lepidothrix coronata*	LC	Sp,R	VR	
Blue-rumped Manakin	*Lepidothrix isidorei*	LC	**Sp**,P	R	
White-bearded Manakin	*Manacus manacus*	LC	**Sp**	VR	
Wire-tailed Manakin	*Pipra filicauda**	LC	**Sp**		
Striolated Manakin	*Machaeropterus striolatus*	LC	**Sp**,P,R	FC	
White-crowned Manakin	*Pseudopipra pipra*	LC	**Sp**,P,R	FC	
Golden-headed Manakin	*Ceratopipra erythrocephala*	LC	**Sp**,P,R	U	
COTINGIDAE					
Fiery-throated Fruiteater	*Pipreola chlorolepidota*	LC	**Sp**,R,P	R	
Andean Cock-of-the-rock	*Rupicola peruvianus*	LC	**Sp**	VR	
Grey-tailed Piha	*Snowornis subalaris*	LC	**Sp**,P,R	VC	
Amazonian Umbrellabird	*Cephalopterus ornatus*	LC	Sp,P,R	U	
Plum-throated Cotinga	*Cotinga maynana*	LC	**Sp**,P	R	+250

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Spangled Cotinga	*Cotinga cayana*	LC	P	R	+550
Screaming Piha	*Lipaugus vociferans*	LC	P,R	FC	
TITYRIDAE					
Black-crowned Tityra	*Tityra inquisitor*	LC	P	R	
Black-tailed Tityra	*Tityra cayana*	LC	P	R	
Masked Tityra	*Tityra semifasciata*	LC	P	U	
Foothill Schiffornis	*Schiffornis aenea*	LC	**Sp**	R	
Cinereous Mourner	*Laniocera hypopyrra*	LC	P,R	U	+550
White-browed Purpletuft	*Iodopleura isabellae*	LC	P	VR	
Shrike-like Cotinga	*Laniisoma elegans**	LC	**Sp**		
Green-backed Becard	*Pachyramphus viridis*†	LC	**Sp**	R	
White-winged Becard	*Pachyramphus polychopterus*	LC	P,R	R	
Black-and-white Becard	*Pachyramphus albogriseus*	LC	Sp	VR	
Pink-throated Becard	*Pachyramphus minor*	LC		R	+350
ONYCHORHYNCHIDAE					
Ruddy-tailed Flycatcher	*Terenotriccus erythrurus*	LC	**Sp**,P	VR	
Tawny-breasted Flycatcher	*Myiobius villosus*	LC	**Sp**,P	U	
TYRANNIDAE					
Wing-barred Piprites	*Piprites chloris*	LC	**Sp**,R	FC	
Cinnamon Manakin-Tyrant	*Neopipo cinnamomea*	LC	Sp,P,R	R	
White-throated Spadebill	*Platyrinchus mystaceus*	LC	Sp	VR	
Golden-crowned Spadebill	*Platyrinchus coronatus*	LC	Sp	VR	
Marble-faced Bristle Tyrant	*Phylloscartes ophthalmicus*	LC	P	VR	
Spectacled Bristle Tyrant	*Phylloscartes orbitalis*	LC	**Sp**,P	R	
Ecuadorian Tyrannulet	*Phyllomyias gualaquizae*	NT	**Sp**,P,R	FC	
Olive-striped Flycatcher	*Mionectes olivaceus*	LC	**Sp**,P,R	U	
Ochre-bellied Flycatcher	*Mionectes oleagineus*	LC	**Sp**,P,R	R	
Slaty-capped Flycatcher	*Leptopogon superciliaris*	LC	Sp,P,R	FC	
Olivaceous Flatbill	*Rhynchocyclus olivaceus*	LC	Sp,R	FC	+250
Grey-crowned Flycatcher	*Tolmomyias poliocephalus*	LC	R	U	+350
Yellow-margined Flycatcher	*Tolmomyias assimilis*	LC	**Sp**,P,R	FC	+250
Yellow-breasted Flycatcher	*Tolmomyias flaviventris*†	LC	**Sp**,P,R	U	+150
Scale-crested Pygmy Tyrant	*Lophotriccus pileatus*	LC	**Sp**,R	R	
Double-banded Pygmy Tyrant	*Lophotriccus vitiosus*	LC	**Sp**,P,R	C	+350
White-eyed Tody-Tyrant	*Hemitriccus zosterops*	LC	P,R	R	
Black-and-white Tody-Flycatcher	*Poecilotriccus capitalis*	LC	**Sp**,P,R	FC	
Golden-winged Tody-Flycatcher	*Poecilotriccus calopterus*†	LC	**Sp**,P,R	R	
Common Tody-Flycatcher	*Todirostrum cinereum*†	LC	**Sp**	VR	
Ornate Flycatcher	*Myiotriccus ornatus*	LC	**Sp**,P,R	VC	
Golden-faced Tyrannulet	*Zimmerius chrysops*	LC	P,R	C	
White-lored Tyrannulet	*Ornithion inerme*	LC	**Sp**,R	R	+350
Mottle-backed Elaenia	*Elaenia gigas*†	LC		VR	
Grey Elaenia	*Myiopagis caniceps*	LC	P,R	R	

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Yellow Tyrannulet	*Capsiempis flaveola*†	LC	**Sp**	VR	
Rough-legged Tyrannulet	*Phyllomyias burmeisteri*	LC	P,R	R	
Yellow-crowned Tyrannulet	*Tyrannulus elatus*	LC	P,R	R	+350
Bright-rumped Attila	*Attila spadiceus*	LC	R	U	
Piratic Flycatcher	*Legatus leucophaius*	LC	R	U	+150
Large-headed Flatbill	*Ramphotrigon megacephalum*	LC	P,R	U	
Great Kiskadee	*Pitangus sulphuratus*†	LC		R	
Boat-billed Flycatcher	*Megarynchus pitangua*†	LC	P,R	U	
Golden-crowned Flycatcher	*Myiodynastes chrysocephalus*	LC	P	VR	
Social Flycatcher	*Myiozetetes similis*†	LC	P	R	
Grey-capped Flycatcher	*Myiozetetes granadensis*†	LC	**Sp**,P,R	R	
Dusky-chested Flycatcher	*Myiozetetes luteiventris*	LC	R	R	+350
Lemon-browed Flycatcher	*Conopias cinchoneti*	VU	P	VR	
Tropical Kingbird	*Tyrannus melancholicus*†	LC	P	FC	
Fork-tailed Flycatcher	*Tyrannus savana*†	LC		VR	
Greyish Mourner	*Rhytipterna simplex*	LC	P,R	FC	
White-rumped Sirystes	*Sirystes albocinereus*	LC	P,R	VR	+450
Dusky-capped Flycatcher	*Myiarchus tuberculifer*	LC	Sp,P,R	C	
Short-crested Flycatcher	*Myiarchus ferox*	LC	P,R	U	
Long-tailed Tyrant	*Colonia colonus*	LC	**Sp**,P,R	U	
Olive-chested Flycatcher	*Myiophobus cryptoxanthus*†	LC	**Sp**,P,R	R	
Bran-coloured Flycatcher	*Myiophobus fasciatus**†	LC	**Sp**		
Euler's Flycatcher	*Lathrotriccus euleri*	LC	**Sp**,P,R	FC	
Acadian Flycatcher	*Empidonax virescens*	LC	P,R	VR	
Olive-sided Flycatcher	*Contopus cooperi*	NT	P,R	U	
Western Wood Pewee	*Contopus sordidulus*	LC	**Sp**,P,R	FC	
Eastern Wood Pewee	*Contopus virens*	LC	Sp,P,R	R	
Blackish Pewee	*Contopus nigrescens*	LC	P,R	FC	
VIREONIDAE					
Olivaceous Greenlet	*Hylophilus olivaceus*	LC	**Sp**,R	R	
Lemon-chested Greenlet	*Hylophilus thoracicus*	LC	R	VR	+550
Slaty-capped Shrike-Vireo	*Vireolanius leucotis*	LC	**Sp**,P,R	FC	
Tawny-crowned Greenlet	*Tunchiornis ochraceiceps*	LC	**Sp**,P,R	FC	+250
Rufous-naped Greenlet	*Pachysylvia semibrunnea*	LC	**Sp**,P,R	FC	
Red-eyed Vireo	*Vireo olivaceus*	LC	Sp,R	R	
Yellow-green Vireo	*Vireo flavoviridis*	LC	**Sp**,P	VR	
CORVIDAE					
Violaceous Jay	*Cyanocorax violaceus*	LC	**Sp**,P,R	FC	
Green Jay	*Cyanocorax yncas*	LC	**Sp**	VR	
HIRUNDINIDAE					
Blue-and-white Swallow	*Pygochelidon cyanoleuca*†	LC		R	
White-thighed Swallow	*Atticora tibialis*†	LC	P	U	
Southern Rough-winged Swallow	*Stelgidopteryx ruficollis*†	LC	P	U	

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Family/English name	Scientific name	IUCN	Evidence	Abundance	Elevation extension
Grey-breasted Martin	*Progne chalybea*†	LC		VR	
TROGLODYTIDAE					
Scaly-breasted Wren	*Microcerculus marginatus*	LC	Sp,R	FC	
Wing-banded Wren	*Microcerculus bambla*	LC	**Sp**,P,R	FC	
House Wren	*Troglodytes aedon*†	LC	P,R	FC	
Thrush-like Wren	*Campylorhynchus turdinus*	LC	Sp,P,R	FC	
Coraya Wren	*Pheugopedius coraya*	LC	**Sp**,R	R	
White-breasted Wood Wren	*Henicorhina leucosticta*	LC	**Sp**,P,R	VC	
Musician Wren	*Cyphorhinus arada*	LC	Sp,P,R	FC	
POLIOPTILIDAE					
Half-collared Gnatwren	*Microbates cinereiventris*	LC	**Sp**,P,R	U	
DONACOBIIDAE					
Black-capped Donacobius	*Donacobius atricapilla*†	LC	P,R	R	
TURDIDAE					
Andean Solitaire	*Myadestes ralloides*	LC	R	R	
Speckled Nightingale-Thrush	*Catharus maculatus*	LC	**Sp**,R	C	
Swainson's Thrush	*Catharus ustulatus*	LC	**Sp**,P,R	FC	
Pale-eyed Thrush	*Turdus leucops*	LC	**Sp**,R	U	
Lawrence's Thrush	*Turdus lawrencii*	LC	R	VR	+350
Black-billed Thrush	*Turdus ignobilis*	LC	P,R	R	
White-necked Thrush	*Turdus albicollis*	LC	**Sp**,P,R	VC	
FRINGILLIDAE					
Blue-naped Chlorophonia	*Chlorophonia cyanea*	LC	P	R	
Golden-bellied Euphonia	*Euphonia chrysopasta*	LC	P,R	R	
White-vented Euphonia	*Euphonia minuta*	LC	P,R	U	+200
Thick-billed Euphonia	*Euphonia laniirostris*	LC	P,R	R	
Orange-bellied Euphonia	*Euphonia xanthogaster*	LC	**Sp**,P,R	VC	
Bronze-green Euphonia	*Euphonia mesochrysa*	LC	P,R	U	
Rufous-bellied Euphonia	*Euphonia rufiventris*	LC	Sp,P	U	
PASSERELLIDAE					
Yellow-throated Chlorospingus	*Chlorospingus flavigularis*	LC	**Sp**,P,R	FC	
Yellow-browed Sparrow	*Ammodramus aurifrons*†	LC	P,R	U	
Orange-billed Sparrow	*Arremon aurantiirostris*	LC	**Sp**,P,R	FC	
Chestnut-capped Brushfinch	*Arremon brunneinucha*	LC	**Sp**	VR	
ICTERIDAE					
Russet-backed Oropendola	*Psarocolius angustifrons*	LC	P,R	VC	
Green Oropendola	*Psarocolius viridis*	LC	**Sp**,P,R	R	
Crested Oropendola	*Psarocolius decumanus*	LC	**Sp**,P	FC	
Olive Oropendola	*Psarocolius bifasciatus*	LC	**Sp**,P	R	+350

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Family/English name	**Scientific name**	**IUCN**	**Evidence**	**Abundance**	**Elevation extension**
Solitary Black Cacique	*Cacicus solitarius**	LC	**Sp**		
Ecuadorian Cacique	*Cacicus sclateri**	LC	**Sp**		
Yellow-rumped Cacique	*Cacicus cela*†	LC	**Sp**,P,R	FC	
Casqued Cacique	*Cacicus oseryi**	LC	**Sp**		
Orange-backed Troupial	*Icterus croconotus*†	LC	**Sp**,P,R	R	+200
Epaulet Oriole	*Icterus cayanensis*	LC	**Sp**,P,R	U	
Giant Cowbird	*Molothrus oryzivorus*	LC	**Sp**,P	R	
PARULIDAE					
Northern Waterthrush	*Parkesia noveboracensis*	LC		VR	
American Redstart	*Setophaga ruticilla*	LC	**Sp**,P	R	
Cerulean Warbler	*Setophaga cerulea*	NT	**Sp**,P	R	
Blackburnian Warbler	*Setophaga fusca*	LC	Sp	R	
Blackpoll Warbler	*Setophaga striata*	NT	**Sp**,P	R	
Buff-rumped Warbler	*Myiothlypis fulvicauda*	LC	**Sp**	VR	
Three-striped Warbler	*Basileuterus tristriatus*	LC	**Sp**	VR	
Canada Warbler	*Cardellina canadensis*	LC	**Sp**,P,R	FC	
Slate-throated Redstart	*Myioborus miniatus*	LC	**Sp**,P	FC	
Spectacled Redstart	*Myioborus melanocephalus*	LC	P	VR	–1,050
CARDINALIDAE					
Summer Tanager	*Piranga rubra*	LC	**Sp**,P,R	FC	
Scarlet Tanager	*Piranga olivacea*	LC	**Sp**,P	U	
Carmiol's Tanager	*Chlorothraupis carmioli*	LC	P,R	U	
Amazonian Grosbeak	*Cyanoloxia rothschildii*	LC	**Sp**,R	R	
THRAUPIDAE					
Yellow-shouldered Grosbeak	*Parkerthraustes humeralis*	LC	Sp,P	R	
Green Honeycreeper	*Chlorophanes spiza*	LC	**Sp**,P	FC	
Guira Tanager	*Hemithraupis guira*	LC	Sp,P	VR	
Yellow-backed Tanager	*Hemithraupis flavicollis*	LC	**Sp**,P	U	
Slaty Finch	*Haplospiza rustica**	LC	**Sp**		
Blue-black Grassquit	*Volatinia jacarina*†	LC	P,R	FC	
Flame-crested Tanager	*Loriotus cristatus*	LC	**Sp**,P	U	
White-shouldered Tanager	*Loriotus luctuosus*	LC	**Sp**	VR	
Fulvous-crested Tanager	*Tachyphonus surinamus*	LC	**Sp**,P	R	
White-lined Tanager	*Tachyphonus rufus*	LC		R	
Red-crested Finch	*Coryphospingus cucullatus*†	LC	P	R	
Silver-beaked Tanager	*Ramphocelus carbo*†	LC	**Sp**,P,R	FC	
Fulvous Shrike-Tanager	*Lanio fulvus*	LC	**Sp**,P,R	C	
Short-billed Honeycreeper	*Cyanerpes nitidus*	LC	P	VR	+550
Purple Honeycreeper	*Cyanerpes caeruleus*	LC	P	FC	
Swallow Tanager	*Tersina viridis*	LC	**Sp**,P	FC	
Black-faced Dacnis	*Dacnis lineata*	LC	**Sp**,P	FC	
Yellow-bellied Dacnis	*Dacnis flaviventer*	LC	Sp,P	R	
Blue Dacnis	*Dacnis cayana*	LC	Sp,P	FC	

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Family/English name	Scientific name	IUCN	Evidence	Abundance	Elevation extension
Chestnut-bellied Seedeater	*Sporophila castaneiventris*†	LC	P,R	U	
Chestnut-bellied Seed Finch	*Sporophila angolensis*†	LC	P,R	FC	
Black-billed Seed Finch	*Sporophila atrirostris*†	LC		VR	
Black-and-white Seedeater	*Sporophila luctuosa*†	LC	P	R	
Slate-coloured Seedeater	*Sporophila schistacea*	LC	P,R	R	+550
Buff-throated Saltator	*Saltator maximus*	LC	**Sp**,P,R	C	
Blue-grey Saltator	*Saltator coerulescens*†	LC	**Sp**,R	U	
Slate-coloured Grosbeak	*Saltator grossus*	LC	**Sp**,R	U	
Bananaquit	*Coereba flaveola*	LC	**Sp**	R	
Orange-eared Tanager	*Chlorochrysa calliparaea*	LC	**Sp**	R	
Magpie Tanager	*Cissopis leverianus*†	LC	**Sp**,P	FC	
Black-capped Tanager	*Stilpnia heinei*	LC		VR	–150
Masked Tanager	*Stilpnia nigrocincta*	LC	P	U	
Blue-necked Tanager	*Stilpnia cyanicollis*	LC	**Sp**,P	FC	
Blue-and-black Tanager	*Tangara vassorii*	LC		VR	–1,100
Turquoise Tanager	*Tangara mexicana*	LC	P	R	
Paradise Tanager	*Tangara chilensis*	LC	**Sp**,P	FC	
Opal-rumped Tanager	*Tangara velia*	LC	P	U	+350
Opal-crowned Tanager	*Tangara callophrys*	LC	P	U	+350
Bay-headed Tanager	*Tangara gyrola*	LC	**Sp**,P	FC	
Green-and-gold Tanager	*Tangara schrankii*	LC	**Sp**,P,R	C	
Golden Tanager	*Tangara arthus*	LC	**Sp**,P	FC	
Blue-grey Tanager	*Thraupis episcopus*	LC	P	FC	
Palm Tanager	*Thraupis palmarum*	LC	P	FC	
Yellow-bellied Tanager	*Ixothraupis xanthogastra*	LC	**Sp**,P	U	
Spotted Tanager	*Ixothraupis punctata*	LC	**Sp**,P	U	

Appendix 2

List of 49 species reported from San José de Sumaco, Orellana province, Ecuador, without voucher: Band-tailed Pigeon *Patagioenas fasciata*, Dark-billed Cuckoo *Coccyzus melacoryphus*, Pale-rumped Swift *Chaetura egregia*, Tawny-bellied Hermit *Phaethornis syrmatophorus*, Wire-crested Thorntail *Discosura popelairii*, White-tailed Hillstar *Urochroa bougueri*, Violet-fronted Brilliant *Heliodoxa leadbeateri*, Long-billed Starthroat *Heliomaster longirostris*, Black-banded Crake *Anurolimnas fasciatus*, Rufous-sided Crake *Laterallus melanophaius*, Grey-headed Kite *Leptodon cayanensis*, Tiny Hawk *Microspizias superciliosus*, Great Black Hawk *Buteogallus urubitinga*, Coppery-chested Jacamar *Galbula pastazae*, Black-streaked Puffbird *Malacoptila fulvogularis*, Smoky-brown Woodpecker *Dryobates fumigatus*, Crimson-bellied Woodpecker *Campephilus haematogaster*, Golden-olive Woodpecker *Colaptes rubiginosus*, Spot-winged Parrotlet *Touit stictopterus*, Blue-and-yellow Macaw *Ara ararauna*, Riparian Parrotlet *Forpus crassirostris*, White-streaked Antvireo *Dysithamnus leucostictus*, Mouse-coloured Antshrike *Thamnophilus murinus*, White-browed Antbird *Myrmoborus leucophrys*, White-chinned Woodcreeper *Dendrocincla merula*, Streaked Xenops *Xenops rutilans*, Rusty-winged Barbtail *Premnornis guttuliger*, Spectacled Prickletail *Siptornis striaticollis*, Montane Foliage-gleaner *Anabacerthia striaticollis*, Purple-throated Cotinga *Porphyrolaema porphyrolaema*, Black-tailed Flycatcher *Myiobius atricaudus*, Fulvous-breasted Flatbill *Rhynchocyclus fulvipectus*, Red-billed Tyrannulet *Zimmerius cinereicapilla*, Foothill Elaenia *Myiopagis olallai*, Variegated Bristle Tyrant *Phylloscartes poecilotis*, Yellow-olive Flycatcher *Tolmomyias sulphurescens*, Yellow-browed Tody-Flycatcher *Todirostrum chrysocrotaphum*, Yellow-throated Flycatcher *Conopias parvus*, Eastern Kingbird *Tyrannus tyrannus*, Chestnut-crowned Becard *Pachyramphus castaneus*, Chestnut-breasted Wren *Cyphorhinus thoracicus*, Grey-cheeked Thrush *Catharus minimus*, Olivaceous Siskin *Spinus olivaceus*, Ashy-throated Chlorospingus *Chlorospingus canigularis*, Tropical Parula *Setophaga pitiayumi*, White-winged Tanager *Piranga leucoptera*, Golden-collared Honeycreeper *Iridophanes pulcherrimus*, Golden-naped Tanager *Chalcothraupis ruficervix*, Beryl-spangled Tanager *Tangara nigroviridis*

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A consolidated checklist and new avifaunal records for southern Tigray, Ethiopia

by Abadi Mehari Abrha, Kai Gedeon, Shimelis Aynalem Zelelew, Guesh Negash Haile, Habtu Kiros Nigus, Assefa Hidgot, Mengesha Hayelom Siyoum, Ziada Abdelhadi Abdelwahab, Mebrahtom Nguse, Berhe Gebremichael Weldetnsae, Hailemariam Gebrewahed & Till Töpfer

Received 20 February 2023; revised 22 May 2023; published 4 December 2023

http://zoobank.org/urn:lsid:zoobank.org:pub:FBB9F29C-0D17-4D1C-9672-109D6FAA8141

Summary.—We recorded 17 bird taxa new for southern Tigray across a mosaic of habitats. Some of these records document substantial geographical extensions of previously known ranges. Many are *Acacia* woodland and bushland species but were documented in habitats subject to considerable human disturbance. New records for Tigray include White-breasted Cormorant *Phalacrocorax lucidus*, Pygmy Falcon *Polihierax semitorquatus*, Three-banded Courser *Rhinoptilus cinctus mayaudi*, Orange-breasted Bushshrike *Chlorophoneus sulfureopectus*, House Sparrow *Passer domesticus indicus* and White-headed Buffalo Weaver *Dinemellia dinemelli*. In addition, the endemic subspecies *erlangeri* of Blanford's Lark *Calandrella blanfordi*, previously known only from the central highlands of Ethiopia, was recorded for the first time in southern Tigray. Focusing on Hugumbirda and Gra-Kahsu State Forest and human-dominated landscapes in southern Tigray, we found key drivers of habitat modification in the area to be the expansion of settlements, farmland and bare land.

Birds are key indicators of biological diversity (Gregory *et al*. 2003, Fraixedas *et al*. 2020) and habitat conditions (Smetzer *et al*. 2014, Whelan *et al*. 2015, BirdLife International 2018, Morelli *et al*. 2021). In mainland Africa, >2,000 bird species occur (Burgess *et al*. 2004), of which *c*.1,600 are endemic to sub-Saharan Africa (Jetz & Rahbek 2001). The largest number of these endemics is in the Albertine Rift, followed by the East African and Ethiopian Highlands (de Klerk *et al*. 2002). In Ethiopia, the region of Tigray has four Important Bird and Biodiversity Areas (IBAs), Lake Hashenge (sometimes incorrectly spelled Ashenge), Dessa'a forest, Hugumbirda and Gra-Kahsu (Hugumburda and Grat-Kahsu) forests, and Shire lowlands in the Tekeze Valley (Tilahun *et al*. 1996, Fishpool & Evans 2001, Ash & Atkins 2009, BirdLife International 2023a). Both Lake Hashenge and Hugumbirda and Gra-Kahsu forests are in southern Tigray, which region is characterised by a complex of mountains, a highland lake and plains, interspersed with a heterogeneous farmland mosaic that varies from relatively intact to substantially human-dominated. These characteristics also provide considerable potential to develop ecotourism in the region (Deribew *et al*. 2022).

Recently, both Hugumbirda and, especially, Gra-Kahsu forest have become increasingly fragmented and transformed into human-dominated landscapes. Raya Valley, though human dominated, remains a unique lowland habitat in Tigray, including agricultural fields, mixed plantations (coffee *Coffea arabica*, khat *Catha edulis* and fruits), Cactus pear *Opuntia ficus-indica* dominated habitat, *Acacia* woodland and wetlands. Lake Hashenge is also affected by farming, grazing, sedimentation and other human impacts (Yazew *et al*. 2013), yet is a unique aquatic habitat for resident and migratory bird species in the region (Alemayehu *et al*. 2017).

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The avifauna of Tigray is sparsely known, although data from this region were included in the two benchmark publications on Ethiopian and Eritrean birds (Urban & Brown 1971, Ash & Atkins 2009). Taking data from Ash & Atkins (2009), we found the avifauna of Tigray and southern Tigray (i.e. the study area) to comprise 473 and 283 bird species, respectively.

Recent publications (Hering *et al*. 2015, Rannestad 2016, Dove *et al*. 2017, Gedeon *et al*. 2017, Buechley *et al*. 2019, 2022) have detailed new species and other notable records, as well as providing annotated checklists for poorly known parts of the Horn of Africa. Nevertheless, these studies were all the product of relatively short visits by a small number of researchers. Ongoing habitat change and human population growth have prompted us to document the avian diversity of Tigray. Here, we document new bird records for southern Tigray made during 2018–20. We also include information on habitat preferences and spatiotemporal patterns. Furthermore, we assessed land use and land cover (LULC) change using GIS and remote-sensing tools between 1985, 2000 and 2020, to examine trends in habitat modification due to anthropogenic activity.

Study area and Methods

Study area.—Located *c*.600 km north of Addis Ababa and 160 km south of Mekelle, capital of Tigray National Regional State, between 12°14′50″–12°52′11″N and 39°20′59″–39°52′30″E, at 949–3,699 m, the total area of southern Tigray is 10,139.3 km^2 and that of the study area is 2,328.24 km^2. With reference to Ash & Atkins (2009: 63) map squares, the study area lies mostly in half-degree squares 31b and 31d, with very small extensions into 31a and 31c (Figs. 1–2).

Hugumbirda and Gra-Kahsu State Forest is spread across Raya Azebo, Endamekoni, Ofla and Raya Alamata districts. The state forest is at 1,500–3,000 m and is part of the dry evergreen Afromontane forest and grassland complex (hereafter DAF). Dominant trees are African juniper *Juniperus procera* and African olive *Olea europaea cuspidata* (Woldemichael

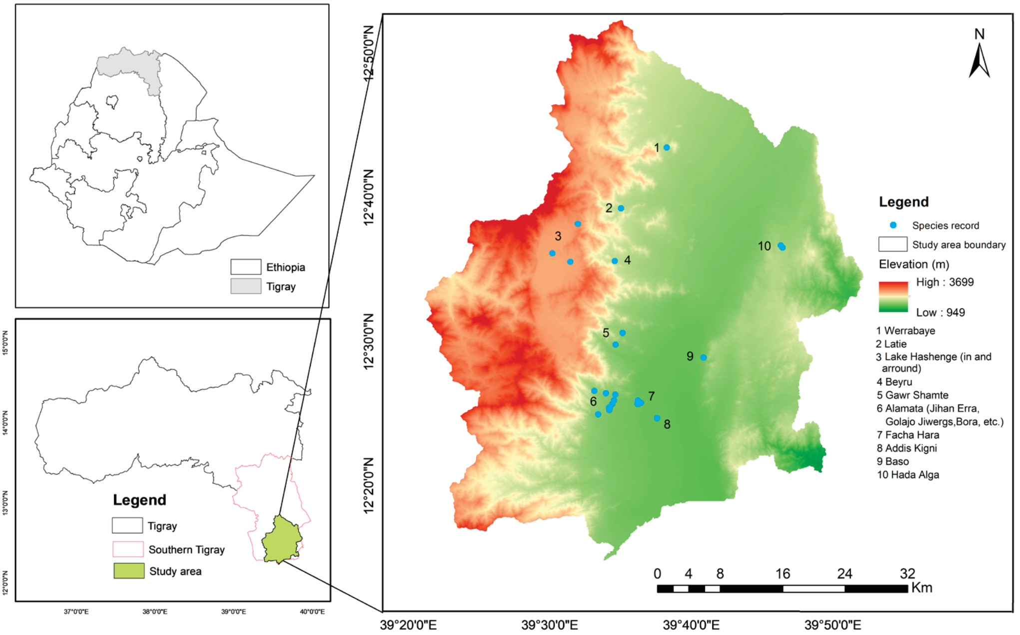

Figure 1. Location of the study area in Ethiopia and of bird records in southern Tigray.

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et al. 2010). The lowland area (Raya Valley) is at 949–1,600 m. The valley's vegetation comprises *Acacia-Commiphora* woodland and bushland (hereafter ACB) (Friis *et al*. 2010).

Due to human disturbance (including infrastructure development), the Raya Valley is currently characterised by fragmented *Acacia* woodland, settlements, farmland with scattered trees and mixed plantations (Table 1, Fig. 2), and is also affected by overgrazing and invasive plant species (e.g. *Parthenium hysterophorus*, *Prosopis juliflora*, *Coleus* sp.). The major land use land cover (LULC) categories in the study area are bare land, farmland, forest, grassland, settlements and water (Fig. 2). As the area covers both lowlands and highlands, mean annual min. temperature varies from 14–30°C in the lowlands (Raya Alamata and Raya Azebo districts) to 8–25°C in the highlands (Ofla district), respectively (Yemane *et al*. 2020).

Methods.—The study was conducted between 2018 and 2020. We used point counts ($n = 134$) to census birds along elevational gradients in Hugumbirda and Gra-Kahsu State Forest (relatively intact natural habitat). Other sites were surveyed using line transects ($n = 22$) in the human-dominated landscape at Raya Valley, and at Lake Hashenge and the

TABLE 1

Description of habitat types at various localities, mostly human-dominated ecosystems, in southern Tigray, Ethiopia. Abbreviations: DAF = Dry evergreen Afromontane forest and grassland complex, and ACB = *Acacia-Commiphora* woodland and bushland proper (Friis *et al*. 2010).

Locality	**Elevation (m)**	**Habitat type**	**Habitat features**
Facha Hara, Addis Kigni, Golajo Jiwergs, Kabri Silam and Werrabbaye	1,400–1,550	ACB	Dominated by *Acacia*. Threatened by human pressure except at churchyards and Muslim tombs.
Hada Alga and Baso	1,500–1,700	ACB	Dense *Acacia-Commiphora* stands, and succulent vegetation mixed with small- to medium-sized perennial woody plants.
Addibbo Mosa and Menkere	2,200–2,450	Aquatic	Lake Hashenge (sometimes incorrectly spelled Ashenge) is one of Ethiopia's highland lakes; it harbours resident and migratory birds, and breeding and non-breeding visitors.
Chekon, Facha Gama and Kukufto	1,400–1,650	Cactus pear	Dominated by cactus pear *Opuntia ficus-indica* with sparse *Acacia* and shrub tree species. In southern Tigray the recently introduced invasive cochineal bug *Dactylopius coccus* infests cactus pear.
Jihan Erra, Harksa, Bora, Kukufto, Hayyalo and Hashenge	1,500–1,650 and 2,200–2,500	Farmland	Suitable land for cultivation in southern Tigray is located in the Raya Valley (lowlands), where sampling sites included Jihan Erra, Harksa, Bora and Kukufto, and highland areas of Lake Hashenge and Hayyalo. Main three cereals are teff *Eragrostis tef*, sorghum and maize varieties.
Hugumbirda and Gra-Kahsu (Hugumburda and Grat-Kahsu) State Forest	1,500–3,000	DAF	Dominant African juniper *Juniperus procera* and African olive *Olea europaea cuspidata*.
Silakunie and Ela Bu'eye	1,400–1,500	Wetland and farmland	Grazing land; typical grass species are *Pennisetum* sp. and *Hyparrhenia* sp.
Latie, Beyru, Gra Asmerom Tikuye, Gawr Shamte, Raya Grand Resort Hotel	1,500–1,700	Plantation	Mixed plantation, including coffee *Coffea arabica*, khat *Catha edulis*, and fruits mainly in Latie and Beyru, whereas Gra Asmerom Tikuye, Gawr Shamte, and Raya Grand Resort Hotel grow mainly fruits.
Hayyalo and Hashenge grazing land	2,200–2,500	Wetland and farmland	Previously dominated by Cattail *Typha latifolia* but now replaced by papyrus, weed, grass and other plant species.

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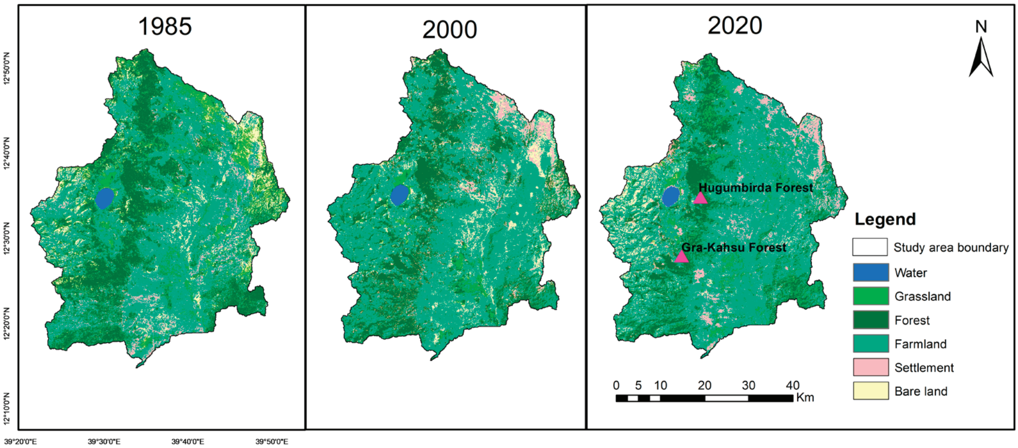

Figure 2. Land use land cover (LULC) change maps of the study area in southern Tigray from 1985 to 2020.

Figure 3. Habitat types in southern Tigray from left to right: (top) farmland at Facha Hara and *Acacia* woodland at Sera Addi Ebo; (middle) *Acacia-Commiphora* woodland and bushland at Hada Alga and cactus pear *Opuntia ficus-indica* between Chekon and Facha Gama; and (bottom) Lake Hashenge and dry evergreen Afromontane forest and grassland complex at Hugumbirda, all December 2018 (Mulugeta Kiros)

surrounding grazing land and farmland (Fig. 3). Field visits were generally conducted 2–4 times a month in the morning (06.00–09.00 h) and evening (16.00–18.00 h) in the dry season (October–June). Birds were identified using the field guide by Redman *et al*. (2011).

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We compared our new records with previously documented occurrence based on tetrad coverage by Ash & Atkins (2009). For inclusion herein, the criteria for new bird records were: (1) major range extension; (2) minor range extension, first report in Tigray; (3) discrepancy between distributions in different sources (Ash & Atkins 2009, Redman *et al*. 2011, BirdLife International 2023a, Gill *et al*. 2023); and (4) taxonomic questions. Some species met more than one criterion. A major extension is defined as previous occurrence only in remote tetrads, whereas a minor extension involves species previously recorded in directly adjoining tetrad/s but not those we surveyed. For taxonomy, we follow Gill *et al*. (2023).

Remote sensing data.—Land use and land cover (LULC) change maps were produced using Landsat Thematic mapper (TM 1985), Landsat Enhanced Thematic Mapper plus (ETM+ 2000) and Landsat Operational Land Imager (OLI 2020) captured in January and February during the dry season. Landsat images (https://earthexplorer.usgs.gov), including TM, ETM+ and OLI were acquired for 2 January 1985, 5 February 2000 and 19 January 2020, respectively. We used bands 1–5 and 7 of TM and ETM+ and bands 1–7 of OLI for image analysis and classification. These Landsat images cover path 168 and rows 51–52 of TM and ETM+ and 51 of OLI. All bands used had 30 m resolution. Standard supervised classification was performed using ERDAS IMAGINE software and max. likelihood algorithm was applied. Overall accuracy and kappa coefficient were checked to assess the accuracy of the classified images.

Results

Species accounts.—We recorded 287 bird species in the study area during the period (2018–20) of which 55 were new for southern Tigray (Supplementary Information). Thirteen of the records were new for Tigray, of which eight involved major range extensions. Based on the criteria above, 13 new taxa for Tigray and four taxa new for southern Tigray are described below.

WHITE-BREASTED CORMORANT *Phalacrocorax lucidus*

First records for Tigray. Commonly encountered at Lake Hashenge (12°36′09″N, 39°30′14″E; 2,442 m) in association with other waterbirds in December 2018 and April 2019, including a non-breeding adult and a juvenile there on 17 April 2019 (Fig. 4).

Figure 4. Non-breeding adult (left) and juvenile White-breasted Cormorants *Phalacrocorax lucidus* with Egyptian Geese *Alopochen aegyptiaca*, a Great White Pelican *Pelecanus onocrotalus*, African Sacred Ibis *Threskiornis aethiopicus* and Northern Shoveler *Spatula clypeata*, Lake Hashenge, Ofla, Ethiopia, April 2019 (Abadi Mehari Abrha)

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PYGMY FALCON *Polihierax semitorquatus*
First records for Tigray. Three on 16 January 2019 and two on 22 January 2020 at Hada Alga (12°36′30″N, 39°46′31″E; 1,672 m) in *Acacia-Commiphora* woodland.

AFRICAN HOBBY *Falco cuvierii*
First record for southern Tigray. On 2 March 2018, an adult perched on Christ's thorn jujube *Ziziphus spina-christi* and umbrella thorn *Vachellia tortilis* trees at Facha Hara (12°25′40″N, 39°36′14″E; 1,461 m).

THREE-BANDED COURSER *Rhinoptilus cinctus mayaudi*
First record for Tigray. On 26 January 2019, two were in St George churchyard (Golajo Jiwergs; 12°25′56″N, 39°34′34″E; 1,523 m) in an area of wooded grassland with planted and natural *Acacia* trees.

GREATER HONEYGUIDE *Indicator indicator*
First records for southern Tigray. During our three-year study, we repeatedly recorded the species at Facha Hara (12°25′54″N, 39°36′15″E; 1,457 m) *Acacia* woodland, singing sporadically between 10.00 and 14.00 h. Local people also know the value of this species to locate natural bee hives in hollow trees including *Acacia* and *Ficus*.

EASTERN GREY WOODPECKER *Dendropicos spodocephalus*
First records for Tigray. A pair was constructing a nest cavity on 17 March 2018 at Facha Hara (12°25′44″N, 39°36′17″E; 1,457 m). A total of eight was recorded in *Acacia* woodland at St Rufael churchyard (Werrabbaye; 12°43′29″N, 39°38′20″E; 1,752 m) and Facha Hara on 26 May 2019 (Fig. 5). We also recorded a male and female at Alamata (12°24′57″N, 39°33′26″E; 1,563 m) on 28 May 2019, and a pair was found nesting in wooded grassland at Dessa'a Forest Reserve on 29 December 2019 (13°40′02″N, 39°46′25″E; 2,363 m). Another individual was seen feeding on the bark of the bamboo *Yushania alpina* in the Choke Mountains in Amhara National Regional State in 2019 (10°37′23″N, 37°46′42″E; 3,100 m). Ash & Atkins (2009) stated that the species is recorded only to 1,820 m in Ethiopia.

Figure 5. Female (left) and male Eastern Grey Woodpecker *Dendropicos spodocephalus* with a nest cavity in a snag of umbrella thorn *Vachellia tortilis*, Facha Hara, Raya Alamata, Ethiopia, March 2018 (Abadi Mehari Abrha)

BLANFORD'S LARK *Calandrella blanfordi erlangeri*
First records for Tigray. *C. b. erlangeri* is endemic to the central highlands of Ethiopia (Ash & Atkins 2009). It was found over large areas of Tigray, but especially in highland habitats of southern Tigray (Hashenge; 12°35′33″N, 39°31′30″E; 2,453 m; Fig. 6). The first record

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was on 28 February 2018. The species was also identified at Alula Abba Nega International Airport (13°28′30″N, 39°31′56″E; 2,231 m, tetrad 23d) and at Mekelle University Endayesus campus (13°28′37″N, 39°29′06″E; 2,197 m, tetrad 23d). We also encountered *C. b. blanfordi* in the Atsbi highlands (13°38′37″N, 39°46′30″E; 2,727 m, tetrad 23d) and in Dessa'a Forest Reserve (13°56′51″N, 39°43′46″E; 2,430 m, tetrad 23d). In our study area, *C. b. erlangeri* is a farmland and grassland specialist. Breeding males in December 2018 climbed *c.*40–60 m above ground, singing for 2–5 minutes while circling.

Figure 6. Blanford's Lark *Calandrella blanfordi erlangeri*, around Lake Hashenge, Ofla, Ethiopia, February 2018 (Abadi Mehari Abrha)

HORSFIELD'S BUSH LARK *Mirafra javanica marginata*

First record for Tigray. One was recorded on 7 January 2019 on unploughed farmland at Jihan Erra (12°25′39″N, 39°34′26″E; 1,523 m), feeding in carrot grass *Parthenium hysterophorus*, an invasive weed species (Fig. 7). The subspecies *marginata*, previously

Figure 7. Horsfield's Bush Lark *Mirafra javanica marginata* in harvested *Eragrostis tef*; the green weed is the invasive carrot grass *Parthenium hysterophorus*, Jihan Erra, Raya Alamata, Ethiopia, January 2019 (Abadi Mehari Abrha)

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treated in Singing Bush Lark *M. cantillans*, is now considered part of Horsfield's Bush Lark *M. javanica* (Gill *et al*. 2023).

AFRICAN STONECHAT *Saxicola torquatus albofasciatus*

First records for Tigray. *S. t. albofasciatus* is nearly endemic to Ethiopia, reaching marginally into South Sudan and Uganda (Gill *et al*. 2023). An adult male and female were recorded on the highland plateau of Endodo (12°38′11″N, 39°32′02″E; 2,556 m), near Lake Hashenge on 18 November 2018 and 10 March 2019 (Fig. 8). Two were also recorded on 24 May 2017 in the Atsbi highlands in eastern Tigray (13°53′19″N, 39°43′38″E; 2,705 m). Only Siberian Stonechat *S. maurus variegatus*, a Palearctic winter visitor, has previously been recorded in much of northern and eastern Tigray (Ash & Atkins 2009).

Figure 8. Male (above) and female African Stonechat *Saxicola torquatus albofasciatus*, Addibbo Mosa (Tabiya Hashenge), Ofla, Ethiopia, November 2018 (Abadi Mehari Abrha)

ORANGE-BREASTED BUSHSHRIKE *Chlorophoneus sulfureopectus*

First record for Tigray. On 16 April 2018, four were observed in *Acacia* at Latie (12°35′36″N, 39°34′38″E; 1,796 m) and Addis Kigni (12°24′34″N, 39°37′39″E; 1,429 m). On 19 March 2019, we recorded it again at the same location.

RÜPPELL'S STARLING *Lamprotornis p. purpuroptera*

First records for Tigray. Throughout the study period, *L. p. purpuroptera* was very common in *Acacia* woodland at Facha Hara (12°25′40″N, 39°36′17″E; 1,462 m) and Addis Kigni (12°24′46″N, 39°37′8″E; 1,441 m). Moreover, we encountered several adults with juveniles around the villages of Bora (12°26′30″N, 39°33′52″E; 1,606 m) and Harksa (12°26′04″N, 39°33′32″E; 1,584 m) at the foot of Mt. Gra-Kahsu in December 2018 and January 2019 (Fig. 9). The longer-tailed *L. p. aeneocephalus* has previously been recorded in north and

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Figure 9. Rüppell's Starling *Lamprotornis p. purpuroptera*, Addis Kigni, Raya Alamata, Ethiopia, December 2018 and January 2019 (Abadi Mehari Abrha)

west Tigray and in a small part of western Ethiopia bordering Sudan (Ash & Atkins 2009). Recently, *L. p. aeneocephalus* was also confirmed to occur in Kafta Shirao National Park (Buechley *et al*. 2022; AMA, KG & TT pers. obs.).

HOUSE SPARROW *Passer domesticus indicus*

First records for Tigray. Recorded from arid and semi-arid areas of Afar and southern Ethiopia (*P. d. indicus*) (Gedeon *et al*. 2015) and western Tigray (*P. d. rufidorsalis*) (Gedeon *et al*. 2015, Buechley *et al*. 2022). An adult *indicus* was recorded on 25 January 2019 together with Swainson's Sparrows *P. swainsonii* at Jihan Erra (12°25′25″N, 39°34′13″E; 1,532 m). Several *rufidorsalis* were breeding at Setit Humara (14°17′22″N, 36°36′34″E; 580 m) in northern Ethiopia on 29 November 2018 (AMA, KG & TT pers. obs.).

CHESTNUT SPARROW *Passer eminibey*

First records for Tigray. Fairly common in *Acacia* woodland at Facha Hara (12°25′45″N, 39°36′28″E; 1,451 m), Jihan Erra (12°25′14″N, 39°34′7″E; 1,537 m), Gawr Shamite (12°30′43″N, 39°34′50″E; 1,622 m) and Serra Addi Ebo (adjacent to Silakunie wetland; 12°26′18″N, 39°37′7″E; 1,430 m) and in farmland. It was encountered continuously in both the wet and dry seasons in 2018–19 and observed in urban and peri-urban habitats.

CHESTNUT-CROWNED SPARROW-WEAVER *Plocepasser superciliosus*

First records for southern Tigray. Common in lowland *Acacia* woodland from Harksa (12°26′35″N, 39°33′10″E; 1,627 m), near Alamata, to Kukufto (12°37′13″N, 39°38′29″E;

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Figure 10. Chestnut-crowned Sparrow-Weaver *Plocepasser superciliosus* collecting carrot grass *Parthenium hysterophorus* (a), a grass stalk (b), bird inside the nest chamber (c) and perched on *Vachellia xanthophloea* (d), Bora, Raya Alamata, Ethiopia, January 2019 (Abadi Mehari Abrha)

1,646 m), at the foot of Hugumbirda and Gra-Kahsu forests. A male and female were recorded nestbuilding in the lower branches of a *Vachellia xanthophloea* on 25 January 2019 (Fig. 10). The most important nest materials were *Eragrostis tef*, *Parthenium hysterophorus* and other dry herbaceous species. The nest typically differs from other weavers because the dried plant material is interleaved into a complex structure without intertwining. Unlike the next species, individual nests are not in contact and the upper part of the structure includes non-thorny twigs and sticks (Fig. 10c).

WHITE-HEADED BUFFALO WEAVER *Dinemellia dinemelli*

First records for Tigray. The hilly dryland areas of Hada Alga (12°36′39″N, 39°46′23″E; 1,665 m) and Baso (12°28′53″N, 39°40′55″E; 1,460 m) are preferred by the species including areas dominated by bush, shrub woodland, scattered *Acacia* trees and succulent vegetation. A total of 12 was found nesting on *Vachellia tortilis* and *V. etbaica* on 12 December 2018, sited between 2 and 6 m above ground, along the road and amid *Acacia-Commiphora* woodland and bushland, with the lowest nests away from settlements (Fig. 11).

RED-BILLED BUFFALO WEAVER *Bubalornis niger*

First record for Tigray. Fifteen observed nestbuilding on the lower branches of umbrella thorn trees on 2 March 2019 in *Acacia* woodland at Facha Hara (12°25′25″N, 39°34′16″E; 1,458 m). Nests were sited between 12 and 17 m (mean 14.3 m) above ground.

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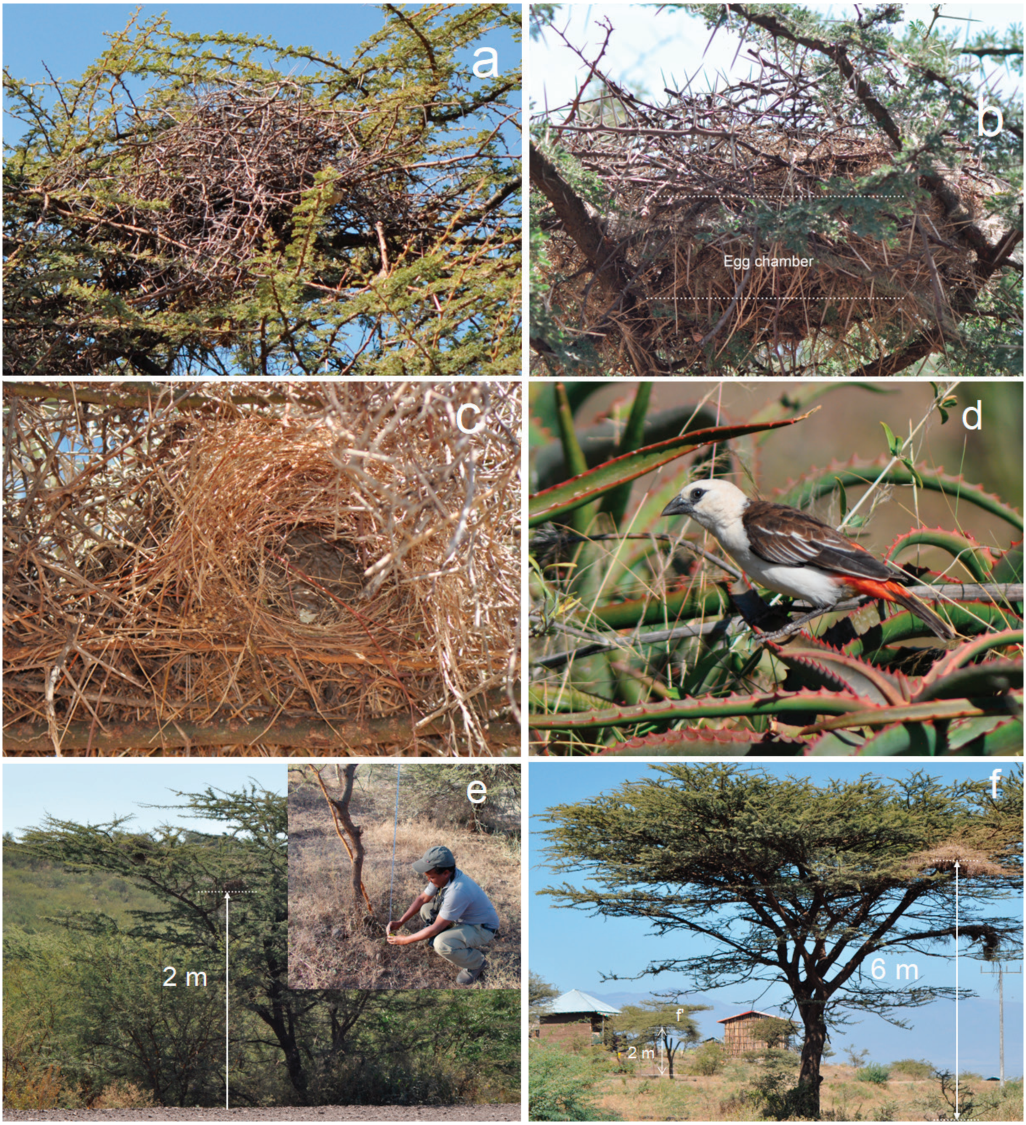

Figure 11. Nests of White-headed Buffalo Weaver *Dinemellia dinemelli* showing (a) nest exterior largely constructed of thorny sticks, (b) egg chamber, (c) entrance, (d) a breeding bird, (e) nest in comparatively undisturbed *Acacia-Commiphora* woodland and bushland, and (f) nest close to a settlement, although note that there are no nests in the low *Acacia* trees nearest to the building (f′), Hada Alga, Raya Azebo, Ethiopia, January 2019 (Abadi Mehari Abrha)

BRONZE MANNIKIN *Spermestes cucullata*

First records for southern Tigray. On 24 November 2018 and 3 January 2019 several were found in coffee and khat plantations and farmland at Latie and Beyru (12°39′15″N, 39°35′5″E; 1,772 m). At Latie, the birds were using abandoned nests of Baglafecht Weaver *Ploceus baglafecht* to breed. We also observed a Bronze Mannikin nest being raided by a Baglafecht Weaver with the nestling being thrown out (Fig. 12). Elsewhere at Latie, an adult was observed feeding a fledged juvenile (Fig. 12).

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Figure 12. Bronze Mannikins *Spermestes cucullata* used deserted nests of Baglafecht Weaver *Ploceus baglafecht*, but the latter did not always accept the new occupants: (a) a female weaver enters a nest, (b), throws out a nestling mannikin, which (c) survived the *c*.4 m fall to the ground, and (d), an adult mannikin returned to the nest to feed the newly evicted young; (e) adult Bronze Mannikin feeding a fledged juvenile, Latie, Raya Azebo, Ethiopia, November 2018 and January 2019 (Abadi Mehari Abrha)

Land use and land cover (LULC) change.—Farmland cover in the study area increased from 51.0% (1,188.2 km^2) in 1985 to 57.5% (1,339.1 km^2) and 62.6% (1,458.5 km^2) in 2000 and 2020, respectively. During 1985–2000, there was a decrease in forest cover from 26.5% (616.7 km^2) to 22.4% (521.1 km^2) and then to 16.9% (392.7 km^2) in 2020. Similarly, bare land decreased from 9.6% (223.4 km^2) to 9.3% (216.4 km^2) during 1985–2000, reaching 5.5%

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(127.6 km^2) in 2020. Human settlements increased in area from 7.0% (163.3 km^2) to 8.9% (207.0 km^2) between 1985 and 2000, and to 11.7% (271.8 km^2) in 2020. Grassland cover abruptly decreased from 5.3% (123.2 km^2) in 1985 to 1.3% (31.4 km^2) in 2000, but increased to 2.8% (64.1 km^2) in 2020. The relative size of water cover, mostly Lake Hashenge, has been similar since 1985 (Fig. 2). Overall, LULC changes from 1985 to 2020 demonstrated that settlement and farmland increased by 66.5% and 22.7% respectively. Contrastingly, grassland showed a 47.9% reduction, while bare land declined by 42.9% and forest cover by 36.3%.

Discussion

We documented range extensions for 55 bird taxa in the region, 13 (23.6%) of them first records for Tigray, suggesting that the geographic ranges of some species are broader than previously thought. For example, our House Sparrow records must be considered in the context of its recent expansion into the north-east and north-west, together with small pockets in central and southern Ethiopia (Gedeon *et al*. 2015, 2017, Buechley *et al*. 2022). Pygmy Falcon, Three-banded Courser, Eastern Grey Woodpecker, Horsfield's Bush Lark, African Stonechat, Rüppell's Starling, Chestnut Sparrow, and White-headed and Red-billed Buffalo Weavers were previously recorded in eastern Ethiopia and the Rift Valley (Ash & Atkins 2009, Redman *et al*. 2011, BirdLife International 2023), but hitherto not from Tigray.

White-breasted Cormorant was the only new record for Tigray at the highland lake. In contrast to Alemayehu *et al*. (2017), we detected no other congenerics there. Importantly, two endemics, Rouget's Rail *Rougetius rougetii* and Blue-winged Goose *Cyanochen cyanoptera*, previously recorded in the area (Tilahun *et al*. 1996, Ash & Atkins 2009) are now locally extinct, having been neither reported by Alemayehu *et al*. (2017) nor during our study in 2018–20. Grazing pressure (Alemayehu *et al*. 2017) could be a factor in their disappearance.

We confirmed that the Ethiopian endemic *Calandrella blanfordi erlangeri* is widely distributed from Hintalo and Enderta highlands to the southern Tigray highlands abutting the DAF plateaux belt of Hugumbirda and Gra-Kahsu State Forest and Lake Hashenge. Hitherto nominate *C. b. blanfordi* had been tentatively assumed to occur in the highlands of our study area (tetrad 31b), whilst tetrads 31a and 31c were thought to be occupied by *erlangeri* (Ash & Atkins 2009). However, we encountered *C. b. erlangeri* only in grazing land and farmland around Hashenge in tetrad 31b. According to our observations in 2017–18, *C. b. erlangeri* also occurs in plateau grassland of Dessa'a Forest Reserve, Atsbi (Kal Amin, Golgol Naele and Ruba Feleg) and Dera highlands, *c*.240 km north of our study area, in agreement with Ash & Atkins (2009). However, we did not investigate the potential co-occurrence of the taxa in Tigray.

In our three-year study, of the 17 newly recorded taxa, 14 (82.4%) were in the lowlands, three (17.6%) in highland areas. All of the new records were made in disturbed habitats, suggesting a degree of tolerance of at least some anthropogenic disturbance. Our results are thus in accord with other reports (Wang *et al*. 2022) that suggest human-dominated landscapes support high avifaunal diversity (Aerts *et al*. 2008), especially in structurally complex farmland (Otieno *et al*. 2011, Gove *et al*. 2013, Marcacci *et al*. 2022). As found by Gove *et al*. (2008) and Buechley *et al*. (2015) small-scale mixed plantations of coffee and khat also harbour high species diversity in our study area.

Based on LULC dynamics, key drivers of habitat modification at the expense of native grassland and intact forest habitats are settlements, farmland and bare land (79.8%). Moreover, the increase in grassland cover during 2000–20 may be due to replacement of native grass species with invasive weeds (e.g. *Parthenium hysterophorus*). Such changes could

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have a profound impact on the area's biodiversity. Thus, without serious conservation interventions, human-induced habitat modifications could gradually affect species diversity. The development of ecotourism in the region relies on speciose wildlife.

Recommendations for future studies.—We provide baseline data from an ornithologically poorly known area of Ethiopia. Our extended monitoring underscores the value of such work, as most of our 'new' species records were multiple, suggesting that they were not one-off sightings of 'vagrants' or 'rarities'. Moreover, spatiotemporal documentation of bird species should avoid both false negatives as well as false positives, but does necessitate robust effort in terms of time, budget, field equipment and expertise, including trained field assistants.

Acknowledgements

This research was part of a large-scale project funded by Mekelle University (CRPO/CoDANR/001/2010). We thank Kasa Darge, Ofla district natural resource expert and the scouts of Hugumbirda and Gra-Kahsu State Forest for their support in the field. We also thank our field assistants and colleagues, and are grateful for the help of district administrators, experts and farmers in the highlands and in the Raya Valley. Three reviewers and the editor made constructive comments on a previous version.

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Supplementary Information. Bird taxa recorded from southern Tigray.

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Description of the eggs and nest, with notes on the breeding ecology of Hellmayr's Pipit *Anthus hellmayri dabbenei* in Chile

by Francisco Rivas, Heraldo V. Norambuena, Catalina Grandón Díaz, Sophie N. Seitz & Esteban Peña Bello

Received 13 April 2023; revised 2 September 2023; published 4 December 2023

http://zoobank.org/urn:lsid:zoobank.org:pub:A29E7BF6-4AA4-4C6E-9C5A-0049AAA2501B

Summary.—We report new ecological data for the poorly known migratory subspecies of Hellmayr's Pipit *Anthus hellmayri dabbenei* in Chile, describing four nests, eggs and some other aspects of the breeding biology. One nest was found in Bulnes, Ñuble region, in late October 2013, with three additional nests discovered between December 2019 and January 2020 on a grass-covered hill in Los Sauces, Araucanía region, in a previously harvested field. Eggs were oval, white to cream-white, with olive-brown speckling forming a 'cap'. Adults fed the nestlings almost entirely on grasshoppers (Orthoptera: Acrididae), averaging 0.8 deliveries per minute (range 0–3 deliveries per minute). The max. gap between deliveries was 31 minutes.

Hellmayr's Pipit *Anthus hellmayri*, which is represented in Chile by the subspecies *dabbenei* (Hellmayr 1932, Goodall *et al*. 1946), is one of three species of *Anthus* in the country. Peruvian Pipit *A. peruvianus* (monotypic) occurs in Arica, in the far north of Chile (del Hoyo *et al.* 2020) and Correndera Pipit *A. correndera* is represented by *A. c. calcaratus* in eastern Antofagasta and *A. c. correndera* from Atacama southwards (Tyler 2020, Norambuena *et al*. 2021). Previous observations suggested that *A. h. dabbenei* prefers tall dry grassland with scattered bushes (Raimilla *et al*. 2012), whereas a Brazilian study showed that a population of *A. h. hellmayri* selected grassland that had experienced wildfire within a year, but was much less abundant in grassland affected by fire longer ago, suggesting that they tended to avoid tall, dense grasses (Chiarani *et al*. 2020). In the austral summer *A. h. dabbenei* is patchily distributed between 37°S to 46°S in Chile (Hellmayr 1932, Raimilla *et al*. 2012, 2013) and at 36–50°S in Argentina (Ridgely & Tudor 1989, Tyler 2004), being present in southern Bolivia and northern Argentina (probably at least as far as Córdoba and Entre Ríos) in May (Hellmayr 1932, Ridgely & Tudor 1989, Pearman & Areta 2020. The migration routes and site fidelity of migrants still need to be assessed using modern techniques such as geolocators. Basic natural history information is still lacking for many Neotropical *Anthus*; for example, the nests of Peruvian Pipit *A. peruvianus* and Paramo Pipit *A. bogotensis* have been described only recently (Arcco *et al*. 2020, van Els *et al*. 2022). Despite its broad distribution, until now just one nest of *A. hellmayri* had been reported in Chile (Norambuena 2018).

Temperate grasslands are among the most altered biomes on earth (Heidenreich 2009, Jacobson *et al*. 2019) with factors as diverse as afforestation and climate change impacting these ecosystems worldwide (Brennan 2005). Understanding the home range size and habitat preferences of a species is important when monitoring their populations (Strasser *et al*. 2019). Land use change on former grassland in central Chile might be a threat to local Hellmayr's Pipit populations, as is true elsewhere for several grassland birds that cannot persist in suitable but fragmented habitat (Herkert 1994, Vickery *et al*. 1994). Here, we describe the breeding habitat and some aspects of the breeding biology of *A. h. dabbenei* in Chile.

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Field work and Methods

Nests were found in two areas: Bulnes in Ñuble region and Los Sauces in Araucanía region (Fig. 1). Bulnes was visited on 31 October 2013 and Los Sauces from 15 December 2019 through 15 January 2020. Bulnes was characterised by grassland habitat (height *c.*40–50 cm) with isolated shrubs. Vegetation in Los Sauces was characterised by grassland of variable height, with dry and low grasses (*c.*15–30 cm) dominating slopes and greenish, taller grasses (*c.*40–55 cm) the hollows. Sweet-briar *Rosa eglanteria* was sparsely distributed throughout the area. The site was rich in arthropods, mainly orthopterans (Acrididae) and some small Tettigoniidae (*Conocephalus* sp.). To locate nests, we conducted parallel transects with three observers spaced 5 m apart and checked the locations where birds flushed from the grass. All nest and egg measurements were taken using callipers precise to 0.1 mm.

To determine feeding rates by the adults, we deployed an autonomous recording unit (Audiomoth 1.0.0, Open Acoustic Devices, 2018) 10 cm from one of the nests for three days. The recording cycle was as follows: 24-hour/day, 0-second sleep duration and 60-second recording duration. The recorder uses the last two seconds of each one-minute cycle to write the file to the microSD card. To assess the presence of some insects we used a sample rate of 48 kHz. The gain setting was fixed between the 'Low' and 'Med' presets which avoids signal clipping when birds vocalise close to the recorder and minimises non-target sounds in the recordings. We inspected the recordings using Adobe Audition (Adobe CC 2017) in spectrogram view, then recorded the date and time for each begging call detected. To assess prey composition and test the association between deliveries and begging calls, we installed a trail camera (Campark T70) 30 cm from two of the nests (N2 and N4) for five hours each. When two or more begging calls were separated by ≥5 seconds in the same sound file, we

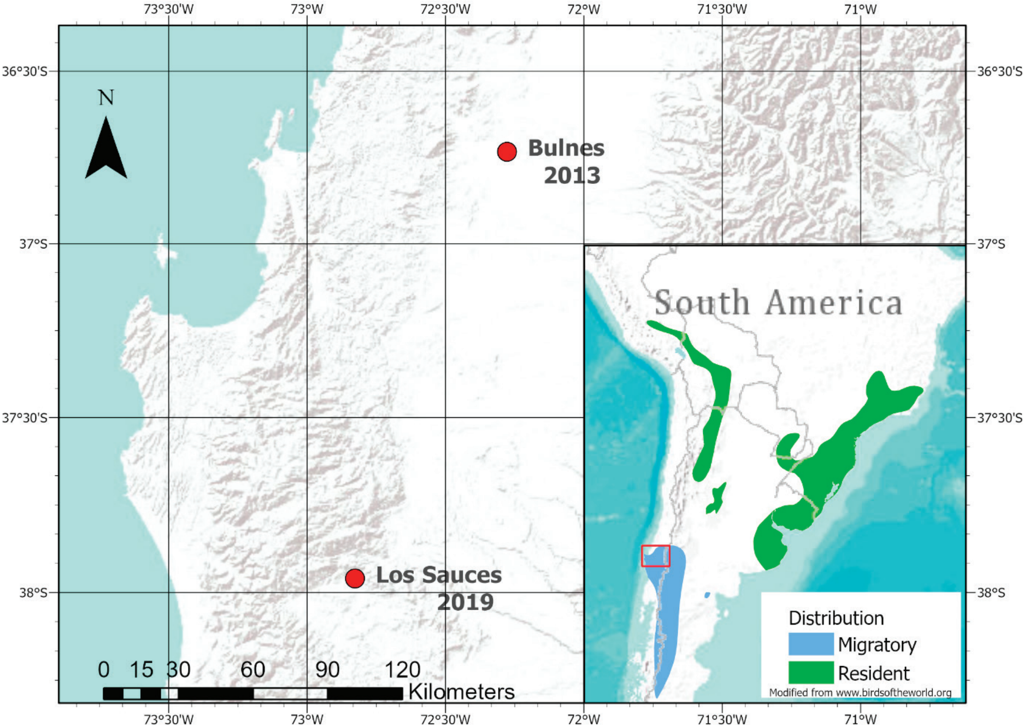

Figure 1. Location of the two nest sites of Hellmayr's Pipit *Anthus hellmayri dabbenei* in central Chile.

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Figure 2. Nests of Hellmayr's Pipit *Anthus hellmayri dabbenei* in central Chile: (A) N1, Bulnes, with three nestlings *c.*8 days old; (B) N2, Los Sauces, with three nestlings *c.*10 days old; (C) N3, Los Sauces, with three eggs; (D) N4, Los Sauces, with four nestlings *c.*12 days old (A: Heraldo V. Norambuena, B–D: Francisco Rivas)

treated these as independent feeding events, whereas calls separated by <5 seconds were considered the same feeding event, as this was the min. interval between deliveries detected using the trail camera.

Results and Discussion

Like other subspecies, *A. h. dabbenei* constructs a cup of grass, but its dimensions are slightly smaller. In Argentina, Colombo (2020) described that the nests of *A. h. hellmayri* had a mean external diameter of 8.63 ± 0.09 cm (range 6.5–10.53 cm), mean internal diameter 6.39 ± 0.08 cm (range 4.88–8.05 cm) and mean depth 3.99 ± 0.07 cm (range 2.7–5.5 cm). In Brazil, a nest of *A. h. brasilianus* had an external diameter of 8 cm, internal diameter 6 cm, and depth 4 cm (Lombardi *et al*. 2010). The quantitative data of our findings are summarised in Table 1. The first nest (N1) was found on 31 October 2013, at Bulnes. It was hidden in the grass and held three nestlings (Fig. 2A). To ascertain the species involved, we waited for the adults to return to the nest. After a few minutes an adult approached with an insect and made territorial flights over the nest area; it was identified as *A. hellmayri* by its plumage.

On 15 December 2019 FR, CGD, SNS & EPB visited Los Sauces and observed 16 adults. On the same day, we found an active nest (N2) with five eggs (the surviving nestlings are shown in Fig. 2B). The number of eggs in this nest corresponds to the max. clutch size reported to date (Colombo 2022). The nest was cup-shaped but covered by a dome of dry

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TABLE 1
Location, orientation and measurements of the four nests of Hellmayr's Pipit *Anthus hellmayri dabbenei* in central Chile described in this paper.

Nest	Location	Coordinates	Orientation	No. of eggs	No. hatched	Hatching date	Fledging date	Nest diameter	Nest depth
N1	Bulnes	36°44′09″S, 72°16′40″W	SW	-	3	24 Oct 2013	-	7.0 cm	3.5 cm
N2	Los Sauces	37°57′37″S, 72°49′42″W	ESE	5	3	26 Dec 2019	7–9 Jan 2020	6.0 cm	3.7 cm
N3	Los Sauces	37°57′37″S, 72°49′36″W	WNW	3	-	-	-	6.2 cm	4.1 cm
N4	Los Sauces	37°57′37″S, 72°49′35″W	ESE	-	4	1 Jan 2020	15 Jan 2020	6.0 cm	3.9 cm

grass stems, slightly inclined towards the entrance. These long stems were clustered by an agricultural machine during a previous harvest, as verified from satellite images taken the previous year (Google Earth, 14 February 2019). The eggs were photographed but no measurements were taken. They were creamy white speckled olive-brown throughout, but with a slight 'capped' effect, similar to those reported by Lombardi *et al*. (2010) in Brazil.

We visited the site again on 29 December 2019 and found another nest (N3), 45 m from N2, with three eggs: 20.55 ± 0.29 × 15.31 ± 0.2 mm (Fig. 2C). These measurements are slightly larger (by 0.44 × 0.58 mm) than the means reported by Salvador (2015) for *A. h. hellmayri* in north-west Argentina. The nest had an asymmetrical structure, with the lower edge facing the entrance and a reduced dome compared to N1 and N2. The same day we found three grey down-covered chicks in N2.

On 6 January 2020, we found the fourth nest (N4), 35 m from N3, with four nestlings (Fig. 2D) partially covered with grey down feathers. Their palate had yellowish choanal papillae. Again, the nest was cup-shaped and roofed with dry stems. To estimate the age of the nestlings we followed the guide for *A. spragueii* by Jongsomjit *et al*. (2007). Estimated hatching dates are shown in Table 1.

On 9 January 2020 N2 was empty. On 15 January 2020 N4 was empty and no eggs had hatched in N3, which had been abandoned by the adults; we confirmed this by watching the nest for five hours, during which time no adults approached it. We found a spider *Latrodectus thoracicus* using the nest to store prey and build a web across the cup. *L. thoracicus* was common in the grass mounds used by the pipits to nest.

Based on camera monitoring, we assessed that both members of the pair participated in provisioning food, confirming observations in Brazil (Sick 1997). All of the identified prey (n = 16) were grasshoppers (Orthoptera: Acrididae), although it is probable that they also feed the nestlings with *Conocephalus vitticollis* (Orthoptera: Tettigoniidae), a small conehead whose presence in the site was confirmed via Passive Acoustic Monitoring (PAM) analysis, and other small arthropods. After analysing the sonograms of our acoustic recordings, we noted a decrease in feeding rates at noon and during heavy winds. The largest interval between feeding events was 38 minutes, between 08.24 h and 09.02 h. The adults provided a mean 0.8 deliveries per minute.

In general terms, the breeding phenology of *A. h. dabbenei* is like that reported for Correndera Pipit in central Chile (Norambuena *et al*. 2017) but may show some variation depending on the arrival of pairs post-migration. For example, pairs incubating in late October is similar to the phenology of Correndera Pipit in Patagonia, which is also migratory to some extent, with the result that nesting can be delayed (Norambuena *et al*.

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2017). In Aysén (43–49°S), territorial *A. h. dabbenei* have been reported in December and January (Raimilla *et al*. 2013). The seasonal difference between the nest found in 2013 and those in 2019 may indicate that some pairs are double-brooded. Another possibility is that egg laying occurs within a three-month window, as observed in Sprague's Pipit *A. spragueii* (Maher 1973, Sutter *et al*. 1996) and Ochre-breasted Pipit *A. nattereri* (Fraga 2001). We infer that the breeding season in south-central Chile starts in September–October with nest construction and egg laying, and ends around mid January when the last nestlings fledge.

Both of the two successful nests at this site were oriented east, consistent with findings for *A. spragueii* (Sutter 1997). The failed nest was the only one oriented west-southwest, in line with studies that have found a significant correlation between mean nest orientation and latitude in several ground-nesting passerines (Burton 2007). At middle latitudes nests facing east, rather than west, may warm more rapidly in the morning and are better protected from solar radiation in the afternoon (Nelson & Martin 1999). The coloration and size of the eggs are consistent with the observations of de la Peña (2013) and Lombardi *et al*. (2010), who reported nests in Argentina and Brazil, respectively.

The relatively short distance between the different nests found at Los Sauces and our failure to find more nests in nearby areas suggest that the species might possess a facultative semi-colonial breeding strategy, perhaps driven by agricultural pressure and limited habitat availability (Raimilla *et al*. 2012). Pairs left the nesting area in the first days after the young fledged the nest, probably to forage in long-grass areas, behaviour also observed in Argentine populations (J. I. Areta *in litt*. 2019). Diet was consistent with that described for *A. spragueii*, which feeds almost entirely on arthropods in the breeding season (Harris 1933b, Maher 1973).

More research is needed to better understand the breeding habitat requirements of *A. h. dabbenei* and how its populations respond to agricultural pressure. We recommend local stakeholders develop plans to protect its breeding habitat by designing harvest schedules that enable the birds to use remaining mounds for nesting.

Acknowledgements

We acknowledge the local farmers in Los Sauces for allowing us to enter their collective property and monitor the nests, and two referees for their comments on the submitted version of the manuscript.

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ISSN-2513-9894 (Online)

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New breeding information on Brazilian birds. 2: Columbidae and Cuculidae

by Anita Studer & Marco Aurelio Crozariol

Received 2 May 2023; revised 26 August 2023; published 4 December 2023

http://zoobank.org/urn:lsid:zoobank.org:pub:F18E740A-0FD6-40F4-B1B5-716E0F0DD94F

Summary.—This is the second in a series of articles about the breeding biology of Brazilian birds based on field work in various regions of the country since the 1980s. The data cover various aspects of breeding biology, such as seasonality, nest architecture, materials and measurements, clutch size, egg colour, size and shape, incubation and nestling periods, and parental care. Many data are presented scientifically for the first time. Overall, we present information concerning 316 nests of 15 species of Columbidae and five species of Cuculidae: Scaled Pigeon *Patagioenas speciosa* (two nests, with the first detailed measurements), Picazuro Pigeon *P. picazuro* (22 nests), Pale-vented Pigeon *P. cayennensis* (four nests), Plumbeous Pigeon *P. plumbea* (one nest), Ruddy Pigeon *P. subvinacea* (three nests, with the first nest and egg measurements for the species), Ruddy Quail-Dove *Geotrygon montana* (33 nests), White-tipped Dove *Leptotila verreauxi* (40 nests), Grey-fronted Dove *L. rufaxilla* (two nests), Eared Dove *Zenaida auriculata* (18 nests), Long-tailed Ground Dove *Uropelia campestris* (three nests, providing the first breeding data for the species), Common Ground Dove *Columbina passerina* (two nests), Plain-breasted Ground Dove *C. minuta* (four nests), Ruddy Ground Dove *C. talpacoti* (43 nests), Scaled Dove *C. squammata* (16 nests), Picui Ground Dove *C. picui* (nine nests), Guira Cuckoo *Guira guira* (21 nests), Greater Ani *Crotophaga major* (four nests, with the first confirmed nest and egg measurements from Brazil), Smooth-billed Ani *C. ani* (76 nests), Striped Cuckoo *Tapera naevia* (12 events, including four new hosts), and Squirrel Cuckoo *Piaya cayana* (one nest).

We continue our series of publications with new breeding information on Brazilian birds. For introduction, objectives and methodology, see Studer & Crozariol (2022). Note: when describing nesting materials in this series, 'petiole' includes the mid-rib of the leaf. In this second paper, we present breeding data for 20 species: Scaled Pigeon *Patagioenas speciosa* (*n* = 2 nests), Picazuro Pigeon *P. picazuro* (*n* = 22), Pale-vented Pigeon *P. cayennensis* (*n* = 4), Plumbeous Pigeon *P. plumbea* (*n* = 1), Ruddy Pigeon *P. subvinacea* (*n* = 3), Ruddy Quail-Dove *Geotrygon montana* (*n* = 33), White-tipped Dove *Leptotila verreauxi* (*n* = 40), Grey-fronted Dove *L. rufaxilla* (*n* = 2), Eared Dove *Zenaida auriculata* (*n* = 18), Long-tailed Ground-Dove *Uropelia campestris* (*n* = 3), Common Ground Dove *Columbina passerina* (*n* = 2), Plain-breasted Ground Dove *C. minuta* (*n* = 4), Ruddy Ground Dove *C. talpacoti* (*n* = 43), Scaled Dove *C. squammata* (*n* = 16), Picui Ground Dove *C. picui* (*n* = 9), Guira Cuckoo *Guira guira* (*n* = 21), Greater Ani *Crotophaga major* (*n* = 4), Smooth-billed Ani *C. ani* (*n* = 76), Striped Cuckoo *Tapera naevia* (*n* = 12), and Squirrel Cuckoo *Piaya cayana* (*n* = 1).

Family Columbidae.—A family of very broad distribution, being absent only from Antarctica and northernmost parts of the Northern Hemisphere. Columbidae inhabit very varied environments, from arid regions to humid tropical forests and urban areas, where some species are well known to the general human population (Gibbs *et al*. 2001). It is a diverse family, with 49 genera and 348 species worldwide (Winkler *et al*. 2020), and some

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famous extinctions, including the Dodo *Raphus cucullatus* and Passenger Pigeon *Ectopistes migratorius*. In South America, 52 species are known (Remsen *et al*. 2020), of which 23 occur in Brazil (Pacheco *et al*. 2021).

SCALED PIGEON *Patagioenas speciosa*

Occurs from southern Mexico to Paraguay and north-east Argentina (Bodrati *et al*. 2010, Baptista *et al*. 2020a). In Brazil, it occurs in forests across most of the country but is rare or absent in the south and in most of the drought polygon (*sensu* Krol *et al*. 2004), with the Atlantic Forest population disjunct from those of the Cerrado and Amazonia (Sick 1997).

Reproductive information is still rare, from both outside (Schomburgk 1848, Penard & Penard 1908, Belcher & Smooker 1936, Friedmann & Smith 1955, Skutch 1964, Wetmore 1968, Haverschmidt 1972, Haverschmidt & Mees 1994, Aguilar 1996, Guevara *et al*. 2010) and inside Brazil (Ihering 1900, Snethlage 1935a, Pinto 1953, Sick 1997, Marini *et al*. 2010).

We describe two nests found in the municipality of Quebrangulo, Alagoas, active on 9 April 1991 and 12 April 1992, coinciding with the start of the local rainy season. Breeding data from the Atlantic Forest biome appear to have been completely lacking previously. In central Brazil, nests have been found in September / October (Marini *et al*. 2010) and in Pará in December (Snethlage 1935a). In Central America, the season is February–May (Skutch 1964, Wetmore 1968), although there is a record of nest construction in July (Skutch 1964). In northern South America, records range from May in Colombia (Hilty & Brown 1986), February–April and July–August in Venezuela (Friedmann & Smith 1955, Aguilar 1996), January–April, June and September–November in Suriname (Penard & Penard 1908, Haverschmidt 1972, Haverschmidt & Mees 1994), and March–April in Trinidad & Tobago (Belcher & Smooker 1936).

Both sexes brought materials to construct the nest (Fig. 1), which was formed of sticks and supported basally by a tangle of vines or branches near the crown of a tree. One nest was 7 m above ground in the crown of an *Ouratea pycnostachys* (Ochnaceae) and the other 12 m above ground in the top of a *Vochysia dardanoi* (Vochysiaceae). One nest had external diameter 28 cm, internal diameter 20 cm, external height 15 cm, internal height 7 cm, and weighed 30 g after the young had fledged. The other had external diameter 30 cm, internal diameter 18 cm, external height 12 cm and internal height 6 cm. We found only one previous report of nest size, which was *c*.20 cm in diameter (Wetmore 1968), making ours the first detailed measurements for the species. Skutch (1964) indicated that the largest stick in a nest measured 25.4 cm long and 0.47 cm in diameter at the thickest end. The nests in Alagoas were sited higher than previously indicated in the literature, except those in Trinidad & Tobago, which were at 9–12 m (Belcher & Smooker 1936) and two (of ten) nests found in Costa Rica were at 15–18 m (Skutch 1964). Although the species usually inhabits the forest canopy, its nests tend to be sited in the lower strata, even in anthropogenically degraded areas (Skutch 1964). In central Brazil, three nests were at 1.1–3.0 m (Marini *et al*. 2010), with others at 1.5 m in Ecuador (Guevara *et al*. 2010), 3 m in Venezuela (Friedmann & Smith 1955), 4 m in Pará (Snethlage 1935a) and 0.6–4.5 m in Costa Rica (Skutch 1964). In Venezuela, Aguilar (1996) even mentioned nests on the ground. We observed that lianas appear to be an important nest site (also see Skutch 1964), although nests can be constructed in *Pteridium aquilinum* ferns in recently degraded areas (Skutch 1964, Aguilar 1996). The nests we found can be considered 'low cup/base' type; some are so fragile they barely support the eggs (Skutch 1964) and they may even fall out (Aguilar 1996).

A single-egg clutch appears typical in this species (Snethlage 1935a, Skutch 1964, Haverschmidt 1972, Haverschmidt & Mees 1994, Aguilar 1996, Sick 1997). However, nests

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Figure 1 (left). Pair of Scaled Pigeon *Patagioenas speciosa* at a nest, Quebrangulo, Alagoas, Brazil, April 1998 (NORDESTA collection)

Figure 2 (right). Scaled Pigeon *Patagioenas speciosa* squab in nest, Quebrangulo, Alagoas, Brazil, April 1998 (NORDESTA collection)

found in Ecuador, Trinidad & Tobago and central Brazil indicate that two eggs may be common in some regions (Belcher & Smooker 1936, Guevara *et al*. 2010, Marini *et al*. 2010). The two nests in Alagoas each held one egg; they were white, oval to long-oval in shape, and measured 37.7 × 25.6 mm and 35.8 × 24.9 mm. They were somewhat smaller than most eggs reported in the literature, especially in width (Ihering 1900, Penard & Penard 1908, Belcher & Smooker 1936), but similar to those described by Wetmore (1968) and larger than most eggs described for Suriname (Haverschmidt & Mees 1994). The egg mentioned by Snethlage (1935a) is at the Museu Paraense Emílio Goeldi, Belém (MPEG.OVO 0287); it measures 40.1 × 28.0 mm. We were unable to elucidate the incubation period.

The only nestling observed in Alagoas hatched covered in dense, pale grey down. The legs and bill were black, the gape red and the palate dark grey. As it grew, brown feathers first began to emerge on its wings (Fig. 2). On fledging, after 14 days, it had brown feathers on the head, back and wings, a pale grey breast and belly, and no markings on the nape. The fledging period agrees with that in Costa Rica (Skutch 1964) and 15 days in Venezuela (Aguilar 1996) while Gibbs *et al*. (2001) mentioned 16–17 days. Both adults provisioned the nestling and during this period they vocalised less frequently. According to Skutch (1949), adults remove the nestlings' faeces in the period after hatching.

On 16 April 1992 the second nest, with a two-day-old nestling, was observed between 06.50 and 10.10 h. The female arrived at 07.10 h, fed the nestling for a few minutes and then brooded it for *c*.60 minutes. At 08.12 h, the male arrived at the nest and the pair engaged in a ceremonial display for *c*.2 minutes, involving both individuals opening their wings and preening each other's neck. No vocalisations were heard. Thereafter, the female remained at the nest for a few minutes, then flew off. The male fed the nestling, then after a few minutes commenced to brood. At 09.00 h, the female returned and the adults remained side by side in the nest for 70 minutes until the observations ceased.

The species has been known in north-east Brazil since the 17th century (Teixeira 1992). Our observations in this region were made in what is now a biological reserve. The species has persisted despite massive forest loss in north-east Brazil.

PICAZURO PIGEON *Patagioenas picazuro*

This species occurs in Argentina, Bolivia and over most of Brazil south of the Amazon, with recent records in Peru (Sick 1997, Ugarte 2019, Baptista *et al*. 2020b). This pigeon has benefitted from deforestation and expansion of agriculture, spreading and increasing, sometimes even alarmingly so (Willis & Oniki 1987, Alvarenga 1990, Willis 1991, Silveira 2013).

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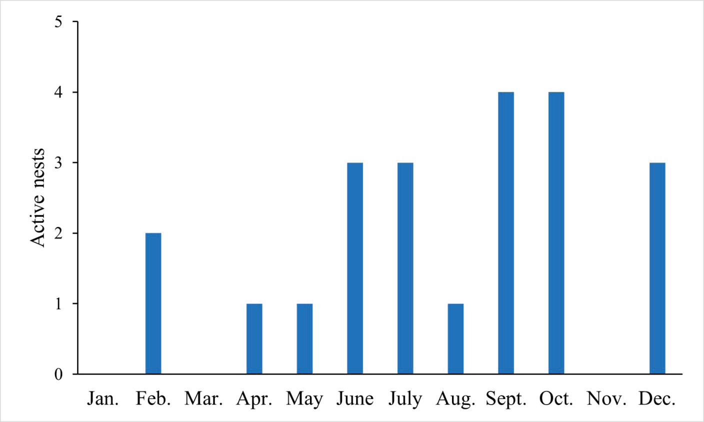

Figure 3. Number of active nests by month (based on date of discovery) of Picazuro Pigeon *Patagioenas picazuro* at Arcos (n = 21), Minas Gerais, and Caseara (n = 1), Tocantins, Brazil.

Although one of the commonest pigeons in Brazil, little is known of its natural history, characterised by the very brief résumé of information in Baptista *et al*. (2020b). Although much was omitted in the latter publication, knowledge of the species' breeding is still very incomplete, especially given that it now nests in large urban areas, like São Paulo (Silveira 2013). We are aware of comparatively few data on the species' nesting outside (Wetmore 1926, Dinelli 1929, Goodwin 1964, Carman 1971, Wilson 1977, Azpiroz 2001, Di Giacomo 2005, de la Peña 2019) and in Brazil (Ihering 1900, Santos 1938, Britto 1950, Belton 1984, Sick 1997, Oniki & Willis 2000, Pereira *et al*. 2009, Marini *et al*. 2010, Crozariol & Indiani 2010, Vitorino & Souza 2013).

We describe observations at 22 nests of *P. picazuro*, found sporadically between 1988 and 2010 in Arcos, Minas Gerais (n = 21) and Caseara, Tocantins (n = 1). Nests were found in almost every month of the year (Fig. 3), agreeing with earlier work (Marini *et al*. 2010, de la Peña 2019), in part because the same pair can lay several clutches across the course of the year (Willis & Oniki 1987, Di Giacomo 2005). However, it would be interesting to compare such behaviour between urban and rural environments.

We observed that both pair members build the nest. Only one was in a forested area; the rest were all in open areas. Forks, branches and tangles of vines were used as supports, with nests usually well hidden among foliage or vines. Of the 22 nests, 17 (77.3%) were in trees taller than 4 m, e.g., a *Eucalyptus* sp. (Myrtaceae) and *Bowdichia virgilioides* (Fabaceae), and five (22.7%) in bushes no taller than 3 m. The height of nests above ground averaged 4.1 ± 1.5 m (n = 19) (Table 1). Nests were always supported basally, being of the 'low cup/base' type (Figs. 4–5). The material used in eight nests was found, on the outside, to comprise solely thornless and budless twigs (n = 6), together with thin roots (n = 1) or petioles and leaf veins (n = 1); inside, we found only small twigs (n = 5), only petioles and leaf veins (n = 2) or leaf veins and petioles mixed with lianas (n = 1). One nest was constructed over six days. Four nests measured: external diameter 23.8 ± 1.5 cm (range 22–25 cm); internal diameter 14 ± 1.2 cm (13–15 cm); external height 6.3 ± 4.7 cm (3–13 cm) and internal height 1.9 ± 0.6 cm (1.0–2.5 cm) (Table 1). The use of *Eucalyptus* sp. for breeding has already been reported (Carman 1971, Wilson 1977, de la Peña 2019), whilst Marini *et al*. (2010) found nests mainly in exotic plants, which indicates the species' ability to adapt to modified environments. Others have found the male alone to collect the nest materials, passing them to the female, who then builds the nest (Vitorino & Souza 2013).

In all the nests that had eggs, we observed just one egg (n = 15), although a second egg was observed in one case. Eggs were white, ovaloid and measured 38.3 ± 1.9 × 27.5 ± 0.8 mm; mass 13.8 ± 2.2 g (n = 6) (Table 2). The incubation period was 18–19 days in two nests. Some

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TABLE 1
Measurements of Picazuro Pigeon *Patagioenas picazuro* nests found in the wild in Brazil. NM = not measured.

Locality	**External height (cm)**	**Internal height (cm)**	**External diameter (cm)**	**Internal diameter (cm)**	**Mass (g)**	**Height above ground (m)**
Caseara/TO	NM	NM	NM	NM	NM	2.5
Arcos/MG	NM	NM	NM	NM	NM	2.4
Arcos/MG	NM	NM	NM	NM	NM	NM
Arcos/MG	NM	NM	NM	NM	NM	8.2
Arcos/MG	NM	NM	NM	NM	NM	4.4
Arcos/MG	NM	NM	NM	NM	NM	2.4
Arcos/MG	NM	NM	NM	NM	NM	NM
Arcos/MG	3	1	22	15	NM	3.3
Arcos/MG	NM	NM	NM	NM	NM	5.1
Arcos/MG	NM	NM	NM	NM	NM	3.6
Arcos/MG	3	2	25	13	NM	3.9
Arcos/MG	13	2	23	13	NM	4.6
Arcos/MG	6	2.5	25	15	150	3.1
Arcos/MG	NM	NM	NM	NM	NM	4.0
Arcos/MG	NM	NM	NM	NM	NM	1.7
Arcos/MG	NM	NM	NM	NM	NM	3.8
Arcos/MG	NM	NM	NM	NM	NM	3.5
Arcos/MG	NM	NM	NM	NM	NM	4.5
Arcos/MG	NM	NM	NM	NM	NM	5.2
Arcos/MG	NM	NM	NM	NM	NM	6.6
Arcos/MG	NM	NM	NM	NM	NM	NM
Arcos/MG	NM	NM	NM	NM	NM	4.5
Mean ± SD	**6.3 ± 4.7**	**1.9 ± 0.6**	**23.8 ± 1.5**	**14 ± 1.2**	**150 ± 0**	**4.1 ± 1.5**
Min.–max.	**3–13**	**1.0–2.5**	**22–25**	**13–15**	**150**	**1.7–8.2**

Figure 4 (left). Nestling Picazuro Pigeon *Patagioenas picazuro* being fed in the nest, Arcos, Minas Gerais, Brazil, September 2001 (NORDESTA collection)

Figure 5 (right). Adult and nestling Picazuro Pigeon *Patagioenas picazuro* in the nest, Arcos, Minas Gerais, Brazil, September 2001 (NORDESTA collection)

literature has reported two eggs (Ihering 1900, Dinelli 1929, Marini *et al*. 2010), but more than one egg is not common. Willis & Oniki (1987) reported five successive clutches between September and February at one nest. Eggs in Argentina (Di Giacomo 2005, de la Peña 2019) average slightly larger than those found in Brazil by us and Marini *et al*. (2010). Di Giacomo (2005) indicated an incubation period of 17 days, whereas Marini *et al*. (2010) reported 14 days.

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TABLE 2

Measurements of Picazuro Pigeon *Patagioenas picazuro* eggs found in Arcos, Minas Gerais, Brazil.

Date found	Clutch	Mass (g)	Length (mm)	Width (mm)
24 Jul 1989	1	15	37.6	27.7
15 Sep 1988	1	17	40.8	27.6
20 Jul 1993	1	12	39.8	27.7
22 Sep 1990	1	14	38.8	28.7
18 Sep 1992	1	14	37.2	26.7
17 Aug 1994	1	10.8	35.5	26.6
Mean ± SD	**1 ± 0**	**13.8 ± 2.2**	**38.3 ± 1.9**	**27.5 ± 0.8**
Min.–max.	**1**	**10.8–17.0**	**35.5–40.8**	**26.6–28.7**

In two nests, the chicks remained 16 and 20 days, respectively. They hatched with dark grey skin covered by a sparse but tufty beige down. The bill, throat and legs were dark grey; iris dark brown. After one week, the skin on the head becomes paler grey and reddish. The wing feathers were finely edged beige with white fringes to the coverts. The nestling period was similar to that in Argentina (Di Giacomo 2005), but Marini *et al*. (2010) mentioned a mean period of 12.9 ± 2.4 days ($n = 8$).

In the presence of a nestling, the adult occasionally gives a short, muffled, guttural sound. Usually discreet when arriving or leaving the nest, but when an intruder approaches the adults fly noisily, beating their wings together, and sometimes throw themselves to the ground pretending to be injured in a well-known distraction behaviour. A nest with an egg at Arcos, Minas Gerais, was predated after 11 days by a Curl-crested Jay *Cyanocorax cristatellus*. Two other nests, with nestlings three and ten days old, were predated by an Aplomado Falcon *Falco femoralis*. Di Giacomo (2005) mentioned egg predation by Purplish Jay *Cyanocorax cyanomelas*, and Oniki & Willis (2000) mentioned adults ducking down in the nest in the presence of Plush-crested Jay *C. chrysops*, suggesting that *Cyanocorax* may be important predators of the species' eggs. Aplomado Falcon had been observed predating an adult *P. picazuro*, as well as Roadside Hawk *Rupornis magnirostris* preying on fledglings and juveniles (Sazima & Hipolito 2017).

On 26 September 2001, at Arcos, Minas Gerais, a nest containing a 12-day-old nestling was watched between 07.30 and 11.30 h. At 07.55 h an adult in a neighbouring tree arrived silently, landing three times in quick succession before reaching the nest. The nestling pushed its head under the motionless adult's belly. At 08.45 h, the nestling began to preen its feathers under the adult, which occasionally stood up without changing position. At 09.45 h, the adult started to feed the nestling, which stuck its bill into a corner of the adult's (Fig. 4). The liquid food was regurgitated by vigorous vertical movements of the head, and the feed lasted *c*.3 minutes. Subsequently, after a pause, the nestling held itself erect, immobile, with its bill close to the adult's for *c*.1 minute. After a short time, feeding resumed. The intervals lasted *c*.10 minutes in total. Small flies constantly swarmed around the adult's head between each session, clustering in its nostrils and eyes, but it remained motionless (Fig. 5) and apparently impassive. After *c*.30 minutes, the chick begged for food again, rubbing its head against the adult's breast, and feeding eventually recommenced. After a few more minutes, at *c*.11.15 h the chick begged again. This time, the adult did not resume feeding and flew off *c*.15 minutes later when observations were terminated.

Picazuro Pigeon is poorly studied. It is particularly interesting to understand how a species can invade even urban environments in such a short period of time. MAC has been monitoring its populations in rice fields in the Paraíba Valley, in the municipality of Tremembé, where the species was first recorded in São Paulo state (Willis & Oniki 1987,

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Alvarenga 1990). By 2005 it was already forming large flocks in the region. Willis & Oniki (1987) drew attention to the possibility of negative impacts on other species due to the expansion of *P. picazuro*. Indeed, *P. picazuro* and Eared Dove *Zenaida auriculata* are by far the most abundant species in the region today, whereas Pale-vented Pigeon *P. cayennensis*, formerly the commonest pigeon in the Tremembé rice fields, is now rare.

PALE-VENTED PIGEON *Patagioenas cayennensis*

Occurs from Mexico to Argentina, being well distributed in open areas especially in South America, and is currently even found in large cities (Chalkowski 2020). Although Sick (1997) indicated that the species is distributed throughout Brazil, it is rare in the Caatinga. Its breeding biology is still poorly known (Penard & Penard 1908, Belcher & Smooker 1936, Hellebrekers 1942, Friedmann & Smith 1950, Haverschmidt 1955a, Skutch 1964, Russell 1964, Wetmore 1968, Goodwin 1973, Haverschmidt 1975, ffrench 1980, Haverschmidt & Mees 1994, Di Giacomo & López Lanús 1998, Greeney & Gelis 2008, Hayes 2014, de la Peña 2019), especially in Brazil, where data are even more fragmentary (Ihering 1900, Snethlage 1935a, Belton 1984, Sick 1997, Crozariol & Indiani 2010, Marini *et al*. 2010, Lopes *et al*. 2013, Nacinovic 2018).

Observations were made at four nests found between 1989 and 2004 at Arcos, Minas Gerais ($n = 3$) and Alto Parnaíba, Maranhão ($n = 1$). Nests were found in March, June and September in Minas Gerais, and in June in Maranhão. Our data are insufficient to define the species' breeding season in the region. Snethlage (1935a) mentioned March in Pará, Marini *et al*. (2010) October in central Brazil, Lopes *et al*. (2013) September in Minas Gerais, and Belton (1984) collected a male in breeding condition in late October in Rio Grande do Sul. Nacinovic (2018), however, indicated that it nests year-round in the lowlands of the municipality of Rio de Janeiro, with a peak in April–September. This is likely to be true over much of the species' range in the country.

Nests were sited in open areas, in trees taller than 4 m. The pair builds in forks or tangles of vines, or clumps of vegetation (Figs. 6–8) at a mean height of 3.9 ± 1.8 m above ground ($n = 3$) (Table 3). One nest was in an Arecaceae, probably an *Astrocaryum* (Fig. 7). An adult was observed breaking off small branches of *Psidium guajava* (Myrtaceae) and carrying them to the nest. During nest construction, adults remain in the nest, fluttering their wings and making faint, hoarse sounds. Mainly thin twigs were used to construct nests, both inside and outside, but grasses and leaves were also used. The nest is a shallow cup of the 'low cup/base' type. Two nests measured: external diameter 23.0 ± 4.2 cm (range 20–26 cm), internal diameter 9.5 ± 2.1 cm (8–11 cm), external height 10 cm and internal height 3.5 ± 0.7 cm (3–4 cm) (Table 3). One of the nests contained 103 sticks, of which 60 measured 10–15 cm, 42 were 16–25 cm, and one stick measured 35 cm. Nests were similar to those described in the literature; however, Greeney & Gelis (2008) mentioned two very low nests in Ecuador, sited just above the surface of water.

TABLE 3

Measurements of Pale-vented Pigeon *Patagioenas cayennensis* nests found in Arcos, Minas Gerais, Brazil. NM = not measured.

Nest	**External height (cm)**	**Internal height (cm)**	**External diameter (cm)**	**Internal diameter (cm)**	**Height above ground (m)**
1	10	3	20	11	3.6
2	NM	NM	NM	NM	2.2
3	10	4	26	8	5.8
Mean ± SD	**10 ± 0**	**3.5 ± 0.7**	**23 ± 4.2**	**9.5 ± 2.1**	**3.9 ± 1.8**
Min.–max.	**10**	**3–4**	**20–26**	**8–11**	**2.2–5.8**

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Figure 6 (top). Adult Pale-vented Pigeon *Patagioenas cayennensis* in the nest, Alto Parnaíba, Maranhão, Brazil, November 2003 (NORDESTA collection)

Figure 7 (bottom left). Adult and nestling Pale-vented Pigeon *Patagioenas cayennensis* in the nest, Alto Parnaíba, Maranhão, Brazil, January 2000 (NORDESTA collection)

Figure 8 (bottom right). Adult Pale-vented Pigeon *Patagioenas cayennensis* feeding a nestling, Alto Parnaíba, Maranhão, Brazil, November 2003 (NORDESTA collection)

Nests we found held one egg (*n* = 2). These were entirely white and long oval-shaped. Two eggs at Arcos measured: 36.6 × 26.1 mm, mass 11 g, and 39.2 × 27.4 mm, 15 g. These measurements are within the known range (Belcher & Smooker 1936, Hellebrekers 1942), although Haverschmidt (1955a) and Skutch (1964) mentioned smaller eggs in Suriname and Central America, respectively.

Single-egg clutches seem most common in this species (Belcher & Smooker 1936, ffrench 1980, Haverschmidt & Mees 1994), although two eggs have been reported (Penard & Penard 1908, de la Peña 2019), including in Brazil (Snethlage 1935a) and seem very common in Paraguay, as of 15 nests observed, all had two eggs (Hayes 2014). Unfortunately, we were unable to determine incubation and nestling periods.

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On 12 November 2003, in Alto Parnaíba, we observed a nest with a nestling *c*.7 days old between 07.40 and 09.40 h. A feeding session was seen at 09.00 h when an adult arrived silently. The nestling immediately started pecking at the adult's breast and neck until it managed to insert its bill into the adult's gape (Fig. 8) and was fed for seven minutes. After a short break, the adult preened itself, then the nestling and fed it again for another six minutes.

PLUMBEOUS PIGEON *Patagioenas plumbea*

A widespread species, from Colombia to northern Argentina including over most of Brazil, apart from the north-east (Sick 1997, Baptista *et al*. 2020c). Breeding data are minimal (Ihering 1900, Goodwin 1973, Sick 1997, Gibbs *et al*. 2001) and Baptista *et al*. (2020c) erroneously reported 'No information available'. A single nest was found on 16 October 2002 in the municipality of Arcos, Minas Gerais. It was constructed using only smooth twigs, sited 2.8 m above ground in a forested environment, and was of the 'low cup/base' type. Unfortunately, the nest was predated, precluding further observations.

RUDDY PIGEON *Patagioenas subvinacea*

Occurs in forested environments from Costa Rica to Bolivia, and in most of Amazonian Brazil (Sick 1997, Baptista *et al*. 2020d). Like the preceding species, it is poorly known in terms of ecology, and its breeding biology is almost entirely unknown (Haverschmidt & Mees 1994, Gibbs *et al*. 2001, Baptista *et al*. 2020d).

Observations at three nests found in 2010 and 2011 in the municipality of Caseara, Tocantins, were made. One was discovered on 20 October 2010 and the other two, with eggs, on 10 January 2011. We are unaware of any previous breeding data from Brazil. However, the season is indicated as June and July in Costa Rica, April and August in Colombia, and September onwards in Peru (Gibbs *et al*. 2001). In Suriname, a nest with a nestling was seen on 17 May and a male had enlarged testes in January (Haverschmidt & Mees 1994).

Two nests in Tocantins were in semi-open habitat and one in forest. They were sited relatively low, 1.7 ± 1.3 m ($n = 3$) above ground or water. Two were in shrubs 45 cm and 1.6 m above the water surface, and another 3.1 m above ground in a tree >4 m tall. Nests were constructed entirely of smooth twigs taken from the same trees where the nests were sited. One nest had external diameter 7 cm, internal diameter 5 cm, external height 2 cm and internal height 1.5 cm. It was tiny, only slightly larger than its egg (see below), basally supported, and can be classified as a 'simple/platform' or 'low cup/base' type. Ours seem to be the first available nest measurements for the species.

Two nests whose contents could be observed held one egg each, in accord with the prior literature (Gibbs *et al*. 2001, Baptista *et al*. 2020d). The eggs were all white, pyriform-shaped and measured 40.9 × 28.7 mm and 41.5 × 28.9 mm. To our knowledge, these are the first egg measurements for the species. Given that the eggs were almost the same size as the internal diameter of the nest we measured, it could hardly hold two eggs. Both nests were unsuccessful: one was destroyed seven days after being found, possibly predated, and the other had a nestling *c*.5 days old on 18 January. However, on 19 January, the rains intensified and when the nest was visited on 21 January the water had risen 50 cm above it. The nestling had grey skin with dense yellowish down on its back, and the head, eyes and tarsus were grey, with pinkish nails.

On 18 January 2011, we monitored the nest with the nestling between 07.00 and 11.00 h. The nestling was healthy and asleep on arrival. It stayed motionless until 08.30 h when an adult arrived, and soon started feeding it. The nestling stuck its bill into the adult's.

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The feeding session lasted *c*.4.5 minutes. Thereafter, the adult brooded the nestling for 15 minutes, then flew off, and did not return during the observation period.

RUDDY QUAIL-DOVE *Geotrygon montana*

A forest pigeon of mostly terrestrial habits, this *Geotrygon* has the most extensive distribution of any of the genus, occurring from Mexico and the West Indies to north-east Argentina (Gibb *et al*. 2001, Kuecker *et al*. 2020). It is found over almost all of Brazil, but is rare or absent in much of the north-east (Pacheco & Whitney 1995, Sick 1997).

Despite its inconspicuous behaviour, there are many descriptions of breeding outside Brazil (Gosse 1847, Penard & Penard 1908, Beebe *et al*. 1917, Osgood & Conover 1922, Belcher & Smooker 1936, Bond 1941, Hellebrekers 1942, Skutch 1949, 1964, 1981, Haverschmidt 1955a, Wetmore 1968, Willis & Eisenmann 1979, Haverschmidt & Mees 1994, Peris *et al*. 1995, Greeney 1999, Rivera-Milán 2001, Greeney *et al*. 2004, Raine 2007, Almirón *et al*. 2012, Bodrati & Salvador 2013a, Cadena-Ortiz & Buitrón-Jurado 2015, Hruska *et al*. 2016, de la Peña 2019). In Brazil, data are few (Goeldi 1894, Ihering 1900, Snethlage 1935a, Pinto 1953, Oniki & Willis 1983, Belton 1984, Sick 1997, Stratford 2004, Buzzetti & Silva 2008, Lima *et al*. 2019).

Observations were made at 33 nests of *G. montana*, found between 1986 and 2020, in the municipality of Quebrangulo, Alagoas. The breeding season was relatively well demarcated here, with active nests from December until June, with peaks in March and especially April (Fig. 9), coinciding with the rainy season (Agência Nacional de Águas 2009). Penard & Penard (1908) mentioned that the species breeds in the dry period in northern South America, while Skutch (1949) indicated that nesting occurs after the onset of rains in Costa Rica, with a peak in June in Puerto Rico (Rivera-Milán 1996) and during the wet and early dry periods in Ecuador (Cadena-Ortiz & Buitrón-Jurado 2015). In Brazil, in the north of the country, active nests have been found in October–May (Oniki & Willis 1983, Stratford 2004, Lima *et al*. 2019) including November in Serra dos Carajás, Pará (G. M. Kirwan *in litt*. 2023), while in Serra dos Órgãos, Rio de Janeiro, Goeldi (1894) found an active nest in November. In the same month, Belton (1984) collected a male with 'greatly enlarged testes' in the far south of the country. It is still necessary to unravel how the species' migrations (see Stouffer & Bierregaard 1993) match the breeding season.

All nests were in dense forest and, on average, 1.5 ± 0.9 m (0.2–3.8 m) above ground ($n = 33$) (Table 4). Sites tended to be tangles of vegetation or places where the nest was primarily supported from the base. Nests were found amid clumps ($n = 2$), on broken tree stumps ($n = 3$), amid lianas ($n = 5$) or piles of branches and leaves accumulated on bushes

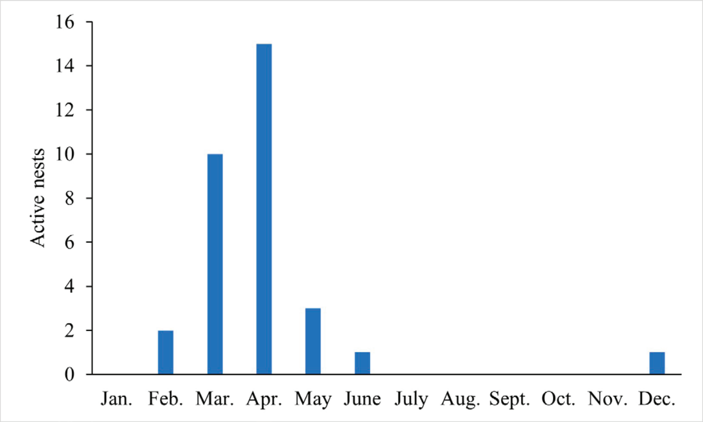

Figure 9. Number of active nests by month (based on date of discovery) of Ruddy Quail-Dove *Geotrygon montana* at Quebrangulo, Alagoas, Brazil.

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TABLE 4
Measurements of Ruddy Quail-Dove *Geotrygon montana* nests found in Quebrangulo, Alagoas, Brazil. NM = not measured.

Nest	**External height (cm)**	**Internal height (cm)**	**External diameter (cm)**	**Internal diameter (cm)**	**Mass (g)**	**Height above ground (m)**
1	NM	NM	NM	NM	110	3.7
2	5	2	18	11	NM	1.7
3	NM	NM	NM	NM	50	1.2
4	NM	NM	NM	NM	NM	1.5
5	NM	1.5	18	7	NM	1.1
6	7	3	22	10	NM	1.1
7	NM	NM	22	10	80	3.7
8	NM	NM	15	7	35	0.2
9	4	2	17	10	NM	1.2
10	6	4	29	10	57	3.5
11	6	4	32	11	NM	1.8
12	4	4	22	9	60	0.7
13	11	3	12	8	NM	1.3
14	10	3	20	13	NM	0.65
15	14	4	22	12	NM	1.2
16	8	2	16	9	NM	1.2
17	NM	NM	NM	NM	NM	1.2
18	5	3	22	15	NM	1.1
19	NM	NM	NM	NM	NM	1.9
20	7	2	23	10	30	1.9
21	10	4	25	8	25	1.3
22	11	3	20	8	NM	1.9
23	NM	NM	NM	NM	NM	2.5
24	5	2	15	10	40	3.8
25	NM	NM	NM	NM	NM	0.55
26	NM	NM	NM	NM	NM	1.7
27	NM	NM	NM	NM	120	1.6
28	7.5	3	15	13	23	1.1
29	NM	NM	NM	NM	40	0.6
30	NM	NM	NM	NM	NM	1.1
31	NM	NM	NM	NM	NM	1.5
32	NM	NM	NM	NM	NM	0.45
33	NM	NM	NM	NM	NM	0.8
Mean ± SD	**7.5 ± 2.9**	**2.9 ± 0.9**	**20.3 ± 5**	**10.1 ± 2.1**	**55.8 ± 32.1**	**1.5 ± 0.9**
Min.–max.	**4–14**	**1.5–4.0**	**12–32**	**7–15**	**23–120**	**20–3.8**

or trees (*n* = 22). They were usually fragile, could be classified as a 'simple/platform' or 'low cup/base' and measured on average: external diameter 20.3 ± 5 cm (range 12–32 cm; *n* = 19), internal diameter 10.1 ± 2.1 cm (7–15 cm; *n* = 19), external height 7.5 ± 2.9 cm (4–14 cm; *n* = 16), internal height 2.9 ± 0.9 cm (1.5–4.0 cm; *n* = 17), and weighed 55.8 ± 32.1 g (23–120 g; *n* = 12) (Table 4). One nest measured 22 × 18 cm in external diameter. The materials used in 19 nests were as follows (externally): various twigs and dry leaves (*n* = 6), dry leaves and petioles (*n* = 5), only sticks and twigs (*n* = 3), only dry leaves (*n* = 1), dry leaves and unidentified plant materials (*n* = 1), various small twigs, dry leaves and petioles (*n* = 1), twigs, dry leaves and lianas (*n* = 1), and thorny twigs and dry leaves (*n* = 1). Internally, constituents

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Figure 10 (top left). Eggs of Ruddy Quail-Dove *Geotrygon montana* in a nest, Quebrangulo, Alagoas, Brazil, April 1992 (NORDESTA collection)

Figure 11 (top right). Adult and nestling Ruddy Quail-Dove *Geotrygon montana*, Quebrangulo, Alagoas, Brazil, April 1991 (NORDESTA collection)

Figure 12 (bottom left). Adult Ruddy Quail-Dove *Geotrygon montana* feeding a nestling. Quebrangulo, Alagoas, Brazil, April 1991 (NORDESTA collection)

Figure 13 (bottom right). Ruddy Quail-Dove *Geotrygon montana* nestlings, Quebrangulo, Alagoas, Brazil, April 1986 (NORDESTA collection)

were dry leaves (*n* = 11), twigs and dry leaves (*n* = 3), green and dry leaves (*n* = 3) and dry leaves and petioles (*n* = 2). Thus, the most frequent type of material throughout the nest changes little, but they appear different. Externally, dry leaves appeared in 84.2% of nests, followed by twigs (57.9%) and petioles (31.6%). In contrast, internally dry leaves dominated, being present in 100% of nests, and the most used nest material. As for proportions of the materials, two nests were analysed, albeit without separating the external and internal parts. One comprised 71 leaves and 95 sticks, and the other 63 leaves and 123 sticks (ranging in length from 7–45 cm). Green leaves may be added to the nest throughout the period. Although we are unaware of more detailed descriptions of materials used, our observations agree with previous data (Beebe *et al*. 1917, Snethlage 1935a, Belcher & Smooker 1936, Skutch 1949, 1964, Wetmore 1968, Oniki & Willis 1983, Greeney 1999, Greeney *et al*. 2004, Bodrati & Salvador 2013a).

Almost all clutches were of two eggs (*n* = 19) (Fig. 10); just one nest had a single egg. Eggs are oval or ovaloid, whitish with a salmon-beige tinge (*n* = 190; Séguy 1936). On average, eggs measured 27.6 ± 1.2 × 21.2 ± 0.7 mm (*n* = 38); mass 6.3 ± 1.1 g (*n* = 37) (Table 5). Clutch size, coloration and egg measurements agree with the literature (Beebe *et al*. 1917, Snethlage 1935a, Skutch 1949, 1964, Wetmore 1968, Oniki & Willis 1983, Haverschmidt & Mees 1994, Stratford 2004). Interestingly, the eggs are not white, unlike most other members of the family, with some variation in coloration (Bodrati & Salvador 2013a).

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TABLE 5
Measurements of Ruddy Quail-Dove *Geotrygon montana* eggs found in Quebrangulo, Alagoas, Brazil. NM = not measured.

Date found	**Clutch**	**Mass (g)**	**Length (mm)**	**Width (mm)**
27 Mar 1995	2	5.0	27.7	21.1
		5.0	27.2	21.5
27 Apr 1993	2	4.6	27.7	20.5
		5.2	28.8	20.5
4 May 1992	2	6.3	28.3	21.6
		6.4	29.4	21.1
29 Apr 1991	1	5.0	26.0	20.0
14 Apr 1992	2	5.8	27.7	21.1
		5.5	27.2	21.0
6 Feb 1991	2	6.0	27.0	21.1
		6.0	27.2	21.8
5 Apr 1987	2	5.7	25.8	20.0
		6.6	26.9	21.1
6 Apr 1996	2	6.1	26.6	21.6
		6.9	27.7	21.6
28 Mar 1986	2	5.4	25.5	21.0
		NM	NM	NM
21 Mar 1986	2	6.0	27.4	21.8
		5.8	28.0	21.5
28 Jan 1990	2	8.0	28.0	22.1
		8.0	28.7	21.9
29 Apr 1991	2	6.5	25.2	21.0
		6.0	27.2	20.6
3 Dec 1997	2	6.0	28.8	20.5
		9.9	29.0	21.2
6 Jun 2008	2	7.5	28.1	21.7
		7.5	27.2	20.3
20 Apr 1998	2	6.7	30.1	21.3
		NM	27.7	21.2
12 Mar 1998	2	6.3	25.9	20.6
		6.5	27.6	21.2
25 Mar 1998	2	6.8	29.5	21.9
		6.8	28.7	22.0
12 Apr 1998	2	7.5	29.4	21.8
		7.0	28.8	21.4
12 May 1999	2	5.0	26.9	20.2
		5.4	26.5	20.1
26 Apr 1999	2	6.2	29.1	22.9
		5.3	26.1	22.5
Mean ± SD	**2 ± 0.2**	**6.3 ± 1.1**	**27.6 ± 1.2**	**21.2 ± 0.7**
Min.–max.	**1–2**	**4.6–9.9**	**25.2–30.1**	**20–22.9**

Both adults were observed incubating, but males seemed to take the greater role, perhaps because, as Skutch (1949) found, males tend to brood most of the day, being

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replaced by the female in the afternoon and night. The incubation period at two nests was 11 and 13 days, respectively, similar to Skutch (1949), who indicated 10–11 days. The skin of hatchlings is black-violaceous with dense fuzzy yellow down, and a spiky appearance. The bill is black with the tip showing protuberances; eyes and gape grey-black. Juveniles have grey plumage on the head, and the wing feathers are brown fringed with beige. The pair feeds their young by regurgitating a liquid substance, 'pigeon milk', from their crops.

Juveniles fledged at 11 days ($n = 3$), 12 days ($n = 2$), 13 days ($n = 2$) or 14 days ($n = 1$). They usually landed on the ground and remained motionless, camouflaged by the dry leaf litter where they were fed by the adults. After some hours, sometimes one or even two days, they begin to climb and explore the surrounding vegetation. Skutch (1949) mentioned one nestling leaving the nest when frightened at eight days of age. At three other nests, the young left at 11 days old and were already able to fly well. In the nest, one adult remains with the nestling (Fig. 11) until it begs for food, inserting its bill into that of the adult (Fig. 12).

On 10 April 1986, in Quebrangulo, Alagoas, between 07.30 and 08.30 h, a nest with two nestlings, *c*.5 days old, was watched (Fig. 13). The female arrived in silent flight. The two nestlings vigorously grasped the female's bill, each seizing a corner of it. The female immediately began to regurgitate the liquid; after a pause of *c*.45 seconds, the adult lowered her head, settled and again regurgitated the milky liquid, with the two nestlings inserting their bills into the female's. The nestlings begged constantly, following the adult's every move, to which the adult responded by vigorously shaking its body. The female remained another five minutes cleaning the nest, collecting some faeces, then flew away silently. Six feeding sessions occurred over just four minutes. At the same nest, when the chicks were *c*.7 days old, the adults started provisioning various wild fruits. Clouds of mosquitoes attacked the chicks, especially their naked heads. The chicks, constantly agitated, shook themselves in an effort to reduce the discomfort. Skutch (1949: 10) and Oniki & Willis (1983) also observed these insects attacking nestlings.

More recently, at another nest, also in Quebrangulo, not included in our analyses, adult behaviour in the face of a predation event was witnessed. This nest was being monitored by camera on 24 March 2023 and had two eggs. At 11.05 h, an adult was present in the nest and at 14.08 h it began to exhibit a peculiar behaviour, keeping both wings open and almost vertical, typical of Columbidae defending their space against other individuals. In this case, however, it presaged the approach of a large, green snake, possibly a *Chironius* sp. As it continued, the adult became increasingly agitated, standing upright, with raised wings. Eventually, the snake almost touched the adult, which had not left the nest, until at 14.10 h the *G. montana* struck the snake with its wing, causing the latter to retreat. Soon after, however, the snake approached again, this time adopting a threatening posture, attacking the adult at 14.11 h, causing it to depart in flight, apparently unharmed. The snake proceeded to predate the eggs. The adult returned to the empty nest at 15.32 h and raised its right wing for a few moments; however, whether the snake was still present in the environs is unknown (see https://youtube/LKZjxh9j930).

WHITE-TIPPED DOVE *Leptotila verreauxi*

Inhabits varied environments, from humid to dry forests, fragmented habitats or near urban areas (Gibbs *et al*. 2001, Giese *et al*. 2020). The 12 currently accepted subspecies (*sensu* Giese *et al*. 2020) occur over a broad distribution, ranging from Argentina to the southern USA (Gibbs *et al*. 2001, Giese *et al*. 2020). In the north of this range, especially Texas, its breeding biology is probably best known (Rowley 1962, Boydston & DeYoung 1987, Hayslette *et al*. 2000, Hall *et al*. 2018, Giese *et al*. 2020). However, robust data are also available for Central America (Stone 1918, Belcher & Smooker 1936, Dickey & van Rossem 1938, Skutch 1964,

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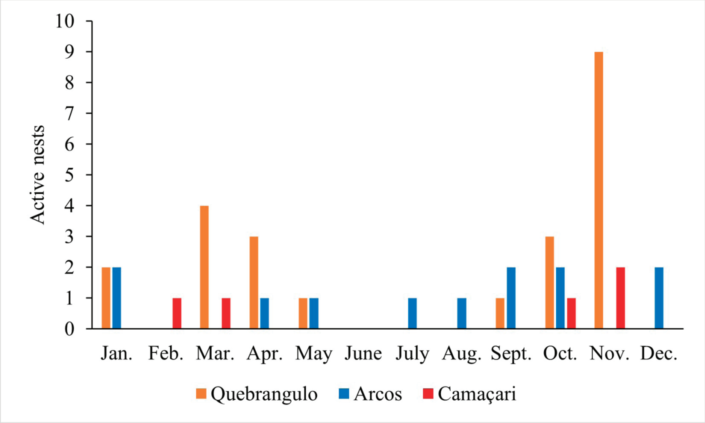

Figure 14. Number of active nests by month (based on date of discovery) of White-tipped Dove *Leptotila verreauxi* at Quebrangulo (*n* = 23), Alagoas, Arcos (*n* = 12), Minas Gerais, and Camaçari (*n* = 5) Bahia, Brazil.

1981, Wetmore 1968, Bulgarella & Heimpel 2015) and South America (Allen 1905, Osgood & Conover 1922, Hellebrekers 1942, Haverschmidt 1972, Ingels 1976, Zapata 1977, Fraga 1983, Haverschmidt & Mees 1994, Azpiroz 2001, Di Giacomo 2005, Knowlton 2010, Hayes 2014, de la Peña 2019). However, for Brazil, information is much less detailed (Ihering 1900, Dias da Rocha 1911, Mitchell 1957, Oniki & Willis 1983, Belton 1984, Sick 1997, Almeida *et al*. 2012, Lopes *et al*. 2013, Nacinovic 2018).

We describe observations at 40 nests of *L. verreauxi*, found between 1984 and 2018 at Quebrangulo, Alagoas (*n* = 23), Arcos, Minas Gerais (*n* = 12), and Camaçari, Bahia (*n* = 5). Active nests were found in every month of the year, except June, mainly between September and April (Fig. 14). There was just one case of the same nest being reused in a different season. Some authors have indicated that the species seems to breed throughout the year in some countries (Dickey & van Rossem 1938, Wetmore 1968, ffrench 1980, de la Peña 2019). In Brazil, the same seems to be true in regions such as Rio de Janeiro (Nacinovic 2018), but there may be some variation. In the Pantanal, for example, vocalisations decrease dramatically in January–February (Pérez-Granado & Schuchmann 2020). However, we do not know the species' seasonality in the region.

Nests were small, 'low cup/base' type, sited 2.6 ± 1.3 m above ground (*n* = 39) (Table 6). They were in forest (*n* = 20), the open (*n* = 11), semi-open (*n* = 6) or edges and clearings (*n* = 3). Nests were found in shrubs below 3 m (*n* = 20) or above 4 m (*n* = 12), in addition to isolated cases such as nests on stumps (*n* = 1), in herbaceous clumps (*n* = 1), amid vines (*n* = 1) piles of leaves (*n* = 1), under ledges of ravines (*n* = 1) and on the edge of cliffs, both rock (*n* = 1) (Fig. 15) and earth (*n* = 1). On average, nests measured: external diameter 15.2 ± 4.0 cm (range 9–21 cm; *n* = 19), internal diameter 8.5 ± 2.5 cm (2–13 cm; *n* = 16), external height 6.0 ± 2.3 cm (3–11 cm; *n* = 11), and internal height 2.9 ± 1.2 cm (1–6 cm; *n* = 13), weighing 38.6 ± 21.4 g (8–60 g; *n* = 5) (Table 6). Nests can be elongated; two measured 12 × 19 cm and 13 × 15 cm in external diameter, respectively. The characteristics of the nest sites and nest measurements agree with previous work (Allen 1905, Dickey & van Rossem 1938, Skutch 1964, Wetmore 1968, Di Giacomo 2005). However, few complete measurements and descriptions are available, especially for Brazil. The material used in 20 nests was (externally): various thin twigs (*n* = 10), petioles alone (*n* = 4), twigs and petioles (*n* = 1), small twigs and dry leaves (*n* = 1), twigs, petioles, lianas and green leaves (*n* = 1), dry grass and thin roots (*n* = 1), petioles and thin roots (*n* = 1) and twigs and unidentified plants (*n* = 1). Internally, they comprised: only petioles (*n* = 7), only twigs (*n* = 4), only feathers (*n* = 2), only dry leaves (*n* = 1), petioles and small twigs (*n* = 1), petioles and lianas (*n* = 1), twigs and dry grasses (*n* = 1), dry grasses and thin roots (*n* = 1), petioles and thin roots (*n* = 1) and petioles and dry leaves (*n* = 1). Thus,

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Figure 15 (left). White-tipped Dove *Leptotila verreauxi* nestlings in a nest on a stony bank, Quebrangulo, Alagoas, Brazil, October 1989 (NORDESTA collection)

Figure 16 (right). Adult and nestlings of White-tipped Dove *Leptotila verreauxi* in a nest, Arcos, Minas Gerais, Brazil, October 1996 (NORDESTA collection)

petioles and twigs predominate, with twigs mainly used externally. Petioles, which tend to be thinner and more flexible, are primarily found in the inner part. Skutch (1964) seems to have been, until now, the only author to report the number of materials used in a nest, which comprised 350 items. The materials used to construct one nest totalled 143 items: 23 twigs of 0–10 cm, 34 twigs of 10–22 cm, 40 grass stalks, 20 strands of smooth, thin liana of which the longest was 84 cm, eight strands of tendril-shaped liana, four small, dried leaves, two grass stems, two small white feathers and ten parts of broken dry leaves. The many different types of habitats used for nesting by this species (see Giese *et al*. 2020) probably contribute to its survival and illustrate its adaptability.

The clutch was almost always two eggs (*n* = 24), with just one nest having a single egg. Eggs were oval (*n* = 12) or elliptical (*n* = 6), white, usually with traces of limestone on the shell. On average, eggs measured 29.8 ± 1.3 × 22.5 ± 0.7 mm (*n* = 49); mass 7.4 ± 0.7 g (*n* = 45) (Table 7). Clutches are of two eggs elsewhere too (Skutch 1964, Wetmore 1968). Eggs tend to be smaller and lighter in northern populations (e.g., Skutch 1964, Wetmore 1968, Haverschmidt 1972) compared to those in the south (e.g., Fraga 1983, de la Peña 2019). Incubation in three nests lasted 13, 14 and 16 days, whereas the literature mainly indicates 14 days (Skutch 1964, Fraga 1983, Oniki & Willis 1983).

In five nests monitored, nestlings remained 11, 12, 15, 16 and 17 days before fledging. In the literature the fledging period is reported as 11–17 days (Skutch 1964, Fraga 1983, Oniki & Willis 1983, Di Giacomo 2005). On hatching, chicks have dark purple skin, bill and legs, sparse grey down, dark brown irides, and a yellowish throat. Larger nestlings have greyish-brown plumage, pale brown wing-coverts, a purplish-grey bill and legs, and brown irides (Fig. 16). We observed that both adults build the nest, incubate, and feed the nestlings. Observations in Texas indicated that the female attends the nest during the night and early morning, while the male does so for the rest of the day (Hall *et al*. 2018).

At Camaçari, Bahia, where there are many hunters, nests tended to be more frequently abandoned, even those with well-grown chicks. However, in some areas, the species seems to be a 'risk-taker'. In September 1995, at Arcos, an adult continued to incubate its eggs even when a tractor was ploughing a few metres away.

On 16 September 1996, also at Arcos, an adult left a nest with two eggs when it was approached, flew to the ground, and feigned a wing injury. Such behaviour was also observed twice in Alagoas. Skutch (1964: 233), who described this behaviour in detail, mentioned that 'they give some of the most prolonged, vigorous, and convincing distraction displays I have ever witnessed'.

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TABLE 6

Measurements of White-tipped Dove *Leptotila verreauxi* nests found in the wild in Brazil. NM = not measured.

Locality	**External height (cm)**	**Internal height (cm)**	**External diameter (cm)**	**Internal diameter (cm)**	**Mass (g)**	**Height above ground (m)**
Quebrangulo/AL	NM	NM	NM	NM	NM	2.7
Quebrangulo/AL	NM	NM	NM	NM	NM	1.5
Quebrangulo/AL	NM	NM	10	8	NM	NM
Quebrangulo/AL	7	3	18	8	NM	3.1
Quebrangulo/AL	NM	NM	18	NM	50	3.4
Quebrangulo/AL	NM	NM	10	8	NM	5.7
Quebrangulo/AL	7	3	18	8	NM	3.8
Quebrangulo/AL	NM	NM	16	9	NM	3.4
Quebrangulo/AL	4	2	11	9	NM	1.6
Quebrangulo/AL	4	3	15	8	NM	4.6
Quebrangulo/AL	NM	NM	18	NM	50	4.6
Quebrangulo/AL	NM	NM	NM	NM	NM	2.2
Quebrangulo/AL	NM	NM	NM	NM	NM	3.8
Quebrangulo/AL	3	NM	9	2	60	2.7
Quebrangulo/AL	NM	NM	NM	NM	NM	4.8
Quebrangulo/AL	NM	NM	NM	NM	NM	1.8
Quebrangulo/AL	NM	NM	NM	NM	NM	1.9
Quebrangulo/AL	7	2	19	9	25	2.2
Quebrangulo/AL	NM	NM	NM	NM	NM	1.6
Quebrangulo/AL	NM	NM	NM	NM	NM	0.75
Quebrangulo/AL	NM	NM	NM	NM	NM	2.2
Quebrangulo/AL	NM	NM	NM	NM	NM	4.5
Quebrangulo/AL	NM	NM	NM	NM	NM	1.8
Arcos/MG	NM	NM	NM	NM	NM	1.6
Arcos/MG	NM	NM	NM	NM	NM	1.2
Arcos/MG	11	3	20	10	8	2.7
Arcos/MG	NM	NM	NM	NM	NM	1.2
Arcos/MG	NM	NM	NM	NM	NM	1.1
Arcos/MG	5	4	10	8	NM	3.0
Arcos/MG	8	3	17	9	NM	3.1
Arcos/MG	NM	2.5	14	10	NM	1.7
Arcos/MG	5	3	20	12	NM	3.4
Arcos/MG	NM	NM	NM	NM	NM	1.6
Arcos/MG	NM	NM	NM	NM	NM	0.7
Arcos/MG	NM	NM	NM	NM	NM	0.8
Camaçari/BA	NM	1	13	NM	NM	2.2
Camaçari/BA	5	2	21	13	NM	3.2
Camaçari/BA	NM	NM	NM	NM	NM	3.3
Camaçari/BA	NM	6	12	5	NM	5.2
Camaçari/BA	NM	NM	NM	NM	NM	2.3
Mean ± SD	**6.0 ± 2.3**	**2.9 ± 1.2**	**15.2 ± 4.0**	**8.5 ± 2.5**	**38.6 ± 21.4**	**2.6 ± 1.3**
Min.–max.	**3–11**	**1–6**	**9–21**	**2–13**	**8–60**	**0.7–5.7**

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TABLE 7
Measurements of White-tipped Dove *Leptotila verreauxi* eggs found in the wild in Brazil. NM = not measured.

Locality	Date found	Clutch	Mass (g)	Length (mm)	Width (mm)
Quebrangulo/AL	1 Nov 1990	2	7.4	30.0	22.7
			7.8	29.2	23.4
Quebrangulo/AL	19 Nov 1990	2	7.7	29.4	22.0
			7.7	29.4	21.8
Quebrangulo/AL	16 Jan 1991	2	6.5	28.8	21.9
			6.5	29.2	21.7
Quebrangulo/AL	25 Nov 1990	2	8.0	29.4	23.1
			8.0	29.3	22.7
Quebrangulo/AL	1 Mar 1991	2	7.5	30.8	22.0
			7.5	30.3	22.1
Quebrangulo/AL	19 Nov 1989	2	7.0	28.6	22.1
			7.0	28.8	22.1
Quebrangulo/AL	30 Oct 1989	2	8.0	28.2	23.7
			9.0	28.9	23.3
Quebrangulo/AL	19 Nov 1989	2	6.5	31.4	22.5
			7.0	31.9	23.6
Camaçari/BA	08 Feb 1984	2	7.1	28.7	21.9
			7.3	28.9	21.8
Arcos/MG	1 Jan 1989	2	NM	30.9	22.7
			NM	30.9	23.3
Quebrangulo/AL	1 Nov 1989	2	8.0	28.2	23.7
			9.0	28.9	23.3
Camaçari/BA	24 Nov 1993	2	6.4	27.1	21.1
			6.6	28.0	21.2
Quebrangulo/AL	19 Nov 1989	2	6.5	31.4	22.5
			7.0	31.9	23.6
Quebrangulo/AL	11 Mar 1990	2	7.0	29.8	21.9
			8.0	31.0	21.7
Quebrangulo/AL	27 Mar 1992	2	6.0	27.7	21.8
			6.0	28.0	21.4
Camaçari/BA	17 Oct 1992	2	7.0	28.2	22.3
			7.5	28.1	23.2
Quebrangulo/AL	24 Mar 2008	2	7.0	29.9	21.5
			7.2	30.8	21.5
Arcos/MG	5 Apr 2004	2	8.1	30.4	22.9
			8.1	30.3	22.7
Camaçari/BA	14 Nov 1992	2	NM	32.9	22.2
			NM	30.5	22.4
Arcos/MG	5 Oct 1996	2	7.1	31.8	22.7
			6.5	30.4	22.2
Quebrangulo/AL	22 Oct 1998	2	8.2	30.3	22.6
			8.0	29.6	22.6
Arcos/MG	10 Sep 1996	2	7.6	29.7	22.7
			7.8	31.6	22.7
Arcos/MG	18 Sep 1996	2	8.5	30.6	23.3
			7.6	29.4	23.9
Arcos/MG	26 Aug 1998	2	7.8	32	22.2
			7.6	30.5	22.5
Camaçari/BA	16 Mar 1985	1	6.6	29.6	22.2
Mean ± SD		**2 ± 0.2**	**7.4 ± 0.7**	**29.8 ± 1.3**	**22.5 ± 0.7**
Min.–max.		**1–2**	**6–9**	**27.1–32.9**	**21.1–23.9**

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On 4 February 2001, at Quebrangulo, a feeding session at a nest with a five-day-old chick was observed during 06.20–11.15 h. At 06.20 h, an adult was on the nest but flew off on our arrival. At 08.10 h, both adults sang nearby and at 08.35 h one adult sang from the ground below the nest, whereupon the nestling started to move and call in the nest; the adult remained on the ground and sang until 09.05 h. At 09.50 h, an adult flew directly to the nest and fed the nestling for 11 minutes. During the entire feeding period, the nestling remained with its bill inside the adult's and only withdrew it when there was no more food. The adult stayed another five minutes with the chick, then sang and flew off. From 10.30 to 11.00 h, the two adults sang both from afar and around the nest, and the nestling responded. At 11.15 h, a green snake, *Philodryas olfersii*, arrived, grabbed the chick by the wing, and dragged it from the nest. They fell to the ground and the snake slithered away with the nestling in its mouth. In Argentina, only birds and mammals have been observed as nest predators of this species (de la Peña 2019).

The species' breeding success appears low. Of 33 nests, only six were successful, with at least one chick fledging (18% of the nests). The others were abandoned or predated. At Arcos, a nest in which two eggs had disappeared on 19 April 2004 was reoccupied, apparently by the same pair, and held two eggs on 3 May, which also disappeared on 11 May. In two studies in Texas, one indicated that 'The probability of an egg surviving from the beginning of incubation to fledging was 0.53 [%]' (Boydstun & DeYoung 1987). The other mentioned that the mean success rate at the egg stage was 69.4% and at the nestling stage 89.6% (Hayslette *et al*. 2000), much higher than we observed.

GREY-FRONTED DOVE *Leptotila rufaxilla*

This species and the previous one are the only *Leptotila* in Brazil (Baptista *et al*. 2020e, Pacheco *et al*. 2021). It is more closely tied to forest than White-tipped Dove, preferring humid regions, although it commonly uses secondary or partially degraded areas (Sick 1997, Gibbs *et al*. 2001). The species occurs from Venezuela to Argentina and virtually throughout Brazil, but is absent or uncommon in most of the Caatinga and part of the Cerrado (Sick 1997, Baptista *et al*. 2020e).

Compared to the previous species, much less is known about the breeding ecology, with most publications containing only anecdotal information, from both outside (Penard & Penard 1908, Chubb 1916, Young 1928, Belcher & Smooker 1936, Hellebrekers 1942, Haverschmidt 1972, Ingels 1976, ffrench 1980, Tostain 1989, Haverschmidt & Mees 1994, Bodrati & Salvador 2013b, Bulgarella & Heimpel 2015, Rivero *et al*. 2018, de la Peña 2019) and inside Brazil (Euler 1900, Ihering 1900, Snethlage 1935a, Pinto 1953, Oniki 1978, Oniki & Willis 1983, Belton 1984, Sanaiotti & Cintra 2001, Maurício *et al*. 2013, Nacinovic 2018, Lima *et al*. 2021).

Two nests of *L. rufaxilla* were found in 2010 at Caseara, Tocantins, on 28 October and 10 November, close to the water at the edge of the Rio Coco's riparian forest, a tributary of the Rio Araguaia. They were of the 'low cup/base' type, supported on tangles of vines and constructed externally of dry leaves, twigs and vines, and internally lined with pieces of dry leaves and grass. One was 1.3 m above ground and had external diameter 12 cm, internal diameter 9 cm, external height 9 cm and internal height 1 cm, weighing 45 g. The eggs in both nests were predated shortly after the first egg was laid; thus, clutch size was unknown. Eggs were white, elliptical and measured 29 × 21.2 and 28.2 × 19.9 mm, respectively.

The species tends to breed at the start of, and during, the rainy season (Lima *et al*. 2021), agreeing with our observations. The nest and eggs also agreed with the literature (Oniki & Willis 1983, Bodrati & Salvador 2013b, Lima *et al*. 2021). Although the species is common in

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forest habitats, nests are frequently located near clearings, roads and in plantations (Oniki & Willis 1983, Lima *et al*. 2021), which may explain why a riverbank was chosen.

EARED DOVE *Zenaida auriculata*

Inhabits open landscapes, natural or anthropogenic, and is an abundant species widely distributed across much of South America, including some islands (Sick 1997, Port & Fisch 2015, Baptista *et al*. 2020f). In Brazil, it occurs throughout, but is rarer or absent in the best-forested parts of Amazonia (Sick 1997, Ortúzar-Ferreira *et al*. 2022). Although it endures hunting pressure in some regions, the species has benefitted from deforestation and increased grain supply from agriculture (Silva & Guadagnin 2018, Ortúzar-Ferreira *et al*. 2022).

Eared Dove's ecology is relatively well known, including its breeding (e.g., Wetmore 1926, Belcher & Smooker 1936, Daguerre 1936, Bond 1941, Hellebrekers 1942, Marchant 1960, Bucher & Nores 1973, Murton *et al*. 1974, Bucher & Gómez 1977, Bucher & Orueta 1977, Carman 1979, Wiley 1991, Azpiroz 2001, Di Giacomo 2005, Cisnero-Heredias 2006, Segura *et al*. 2016, de la Peña 2019, Maldonado *et al*. 2020), with abundant data from Brazil (Ihering 1900, Dias da Rocha 1911, Ihering 1935, Pinto 1949, Aguirre 1972, 1976, Bucher 1982, Belton 1984, Antas 1987a, Sick 1997, Donatelli 2000, Scherer *et al*. 2006, Buzzetti & Silva 2008, Ramos & Maria 2012, Lopes *et al*. 2013, Guaraldo & Gussoni 2015, Braz & Silva 2017).

We made observations at 18 nests of *Z. auriculata* found between 1990 and 2008 at Arcos, Minas Gerais, in almost every month of the year (Fig. 17). However, the species' extensive distribution and its partially migratory behaviour result in different regional breeding periods (Gibbs *et al*. 2001, Baptista *et al*. 2020f). Interesting observations were made in Argentina via gonad and testosterone analysis, with no changes in testis size noted across the year, although blood plasma and testosterone levels increased during spring and summer (Maldonado *et al*. 2020).

Nests were all in open areas, in very varied situations, but usually well concealed in foliage. All were solitary and built, for example, on *Coffea arabica* coffee bushes (Rubiaceae; *n* = 6), in trees, especially thick-barked ones, e.g., *Stryphnodendron astringens* (Fabaceae; *n* = 1), *Dalbergia miscolobium* (Fabaceae; *n* = 1) and *Annona crassiflora* (Annonaceae; *n* = 1), atop a palm (*n* = 1), on the ground amid clumps of grasses (*n* = 3), amid lianas (*n* = 1), in a crevice on a cliff hidden by vegetation (*n* = 1) (Fig. 18), atop a closed, long, pensile nest of Rufous-fronted Thornbird *Phacellodomus rufifrons* (*n* = 1) and under a farm building roof (*n* = 1), at a mean height of 2.4 m above ground (*n* = 16) (Table 8). The nests, 'low cup/base'

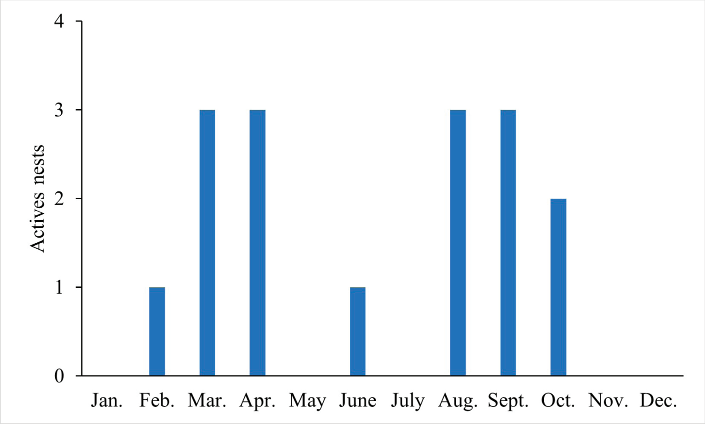

Figure 17. Number of active nests by month (based on date of discovery) of Eared Dove *Zenaida auriculata* at Arcos, Minas Gerais, Brazil.

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Figure 18. Adult Eared Dove *Zenaida auriculata* in nest in a crevice in a cliff, São Roque de Minas, Minas Gerais, Brazil, December 2001; it was predated before it could be measured and was not included in any of our analyses (NORDESTA collection)

TABLE 8

Measurements of Eared Dove *Zenaida auriculata* nests found in Arcos, Minas Gerais, Brazil. NM = not measured.

Nest	External height (cm)	Internal height (cm)	External diameter (cm)	Internal diameter (cm)	Mass (g)	Height above ground (m)
1	6.0	2.0	14	8.0	33	3.6
2	2.0	NM	12	9.0	NM	6.8
3	6.0	2.0	15	8.0	18	2.2
4	6.0	2.5	14	7.5	21	2.6
5	NM	NM	NM	NM	NM	NM
6	NM	NM	NM	NM	NM	NM
7	NM	NM	NM	NM	NM	1.8
8	NM	1.0	12	6.0	NM	7.2
9	4.5	2.5	18	6.5	9	1.4
10	4.0	2.5	19	4.0	16	1.3
11	NM	NM	NM	NM	NM	0.8
12	NM	NM	NM	NM	NM	0.6
13	NM	NM	NM	NM	NM	1.8
14	NM	NM	NM	NM	56	1.2
15	7.0	1.5	18	8.0	50	3.1
16	3.0	0.5	16	10.0	NM	0.8
17	10.0	4.0	15	7.0	70	0.8
18	7.0	4.0	15	8.0	50	2.5
Mean ± SD	**5.6 ± 2.3**	**2.3 ± 1.1**	**15.3 ± 2.3**	**7.5 ± 1.6**	**35.9 ± 21.3**	**2.4 ± 2.0**
Min.–max.	**2–10**	**0.5–4.0**	**12–19**	**4–10**	**9–70**	**0.6–7.2**

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TABLE 9

Measurements of Eared Dove *Zenaida auriculata* eggs found in Arcos, Minas Gerais, Brazil. NM = not measured.

Date found	Clutch	Mass (g)	Length (mm)	Width (mm)
20 Aug 1993	2	5.7	27.7	20.5
		5.7	28.3	21.0
21 Oct 1990	2	5.6	27.3	21.6
		6.1	29.4	21.6
25 Aug 1993	2	7.2	28.8	22.2
		7.4	30.0	22.0
28 Sep 1993	2	6.5	27.7	21.1
		6.5	28.0	21.0
3 Mar 2004	2	7.0	28.4	21.9
		7.2	29.1	21.6
24 Aug 2002	2	6.7	27.7	21.6
		6.7	27.7	21.6
3 Mar 2004	1	6.5	28.1	21.5
27 Apr 2004	2	6.3	27.4	22.0
		NM	27.5	22.4
2 Jan 2005	2	6.1	29.2	20.7
		NM	29.1	20.7
Mean ± SD	**1.9 ± 0.3**	**6.5 ± 0.6**	**28.3 ± 0.8**	**21.5 ± 0.6**
Min.–max.	**1–2**	**5.6–7.4**	**27.3–30.0**	**20.5–22.4**

type, measured on average: external diameter 15.3 ± 2.3 cm (range 12–19 cm; *n* = 11), internal diameter 7.5 ± 1.6 cm (4–10 cm; *n* = 11), external height 5.6 ± 2.3 cm (2–10 cm; *n* = 10) and internal height 2.3 ± 1.1 cm (0.5–4.0 cm; *n* = 10); mass 35.9 ± 21.3 g (9–70 g; *n* = 9) (Table 8). The following materials were used in the external part of nests: only fine roots (*n* = 2), only twigs (*n* = 1), twigs and petioles (*n* = 1), fine roots and unidentified plants (*n* = 1), twigs and dry grass (*n* = 1) and fine roots, dried leaves and lianas (*n* = 1). The interiors contained: only fine roots (*n* = 3), only twigs (*n* = 1), twigs with dried grass (*n* = 1) and twigs with dry leaves (*n* = 1). One nest weighing 20 g contained 45 branches, and 30 grass stems 4–20 cm long. Although our observations were of solitary nests, in some regions the species forms substantial 'colonies' of thousands of individuals, nesting on the ground (Ihering 1935, Aguirre 1976, Bulcher 1982, Donatelli 2000), sometimes laying the eggs directly on the substrate (Donatelli 2000). In the past, these 'colonies' were harvested for eggs and adults to be sold in cities (Ihering 1935, Pinto 1949, Aguirre 1976).

Like our observations of the species breeding on a nest of *Phacellodomus*, Wetmore (1926) also mentioned a nest built on top of that of an oscine passerine. Pinto (1949) reported that such behaviour is common, but he may have relied on Wetmore. Nevertheless, that the species has been observed usurping a nest of Creamy-bellied Thrush *Turdus amaurochalinus* (Segura *et al.* 2016) demonstrates an unusual interest in the nests of other species. Although Pinto (1949) indicated that the behaviour of nesting on the ground or on vegetation can be related to different populations, in some regions the species uses various niches (Marchant 1960, Antas 1987), which agrees with our observations and demonstrates the species' remarkable plasticity, permitting it to nest in agricultural and urban areas (Donatelli 2000, Ramos & Maria 2012, Guaraldo & Gussoni 2015, Dardanelli *et al*. 2016).

A clutch almost always comprised two eggs (*n* = 8); just one nest contained one egg (Table 9). Eggs were white and long elliptical in shape; they measured 28.3 ± 0.8 ×

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21.5 ± 0.6 mm (*n* = 17); mass 6.5 ± 0.6 g (*n* = 15) (Table 9). Clutch size and egg size agree with the previous literature (Ihering 1900, 1935, Belcher & Smooker 1936, Marchant 1960, Bucher 1982, Donatelli 2000, Di Giacomo 2005, Guaraldo & Gussoni 2015). Eggs may become darker due to soiling (Donatelli 2000).

The incubation period was 15 days (*n* = 1) or 16 days (*n* = 1). Previous authors have indicated 14 days (Marchant 1960, Donatelli 2000, Di Giacomo 2005, Scherer *et al*. 2006). Nestlings fledged after 11 days (*n* = 1), 12 (*n* = 1), 14 (*n* = 2), 15 (*n* = 1) and 18 days (*n* = 1). Donatelli (2000) mentioned that although the nestling is feathered at 14 days fledging only occurs when nearly 30 days old, but this is clearly at variance with other reports, which indicated a period of 12–16 days (Di Giacomo 2005, Scherer *et al*. 2006).

At one nest, hatching was asynchronous, with one chick emerging on 27 September 2006 and the other on 1 October. However, both fledged on the same day, the younger chick at 14 and the older when 18 days old. A six-day-old nestling had thin, sparse, beige down covering the skin, which is dark grey. The bill is greyish with hints of pink and a black tip. The gape is pale pink and the tongue is darker, tending towards wine-red.

On 3 December 2001, we observed a nest with two nestlings about seven days old, from 07.30 to 09.30 h. During this time, the adults visited twice; one fed the nestlings and remained in the nest, while the other adult stayed on a nearby branch and vocalised softly. We found a nestling on 14 December 1995 parasitised by larvae of a fly *Philornis* sp. (Diptera, Muscidae) under both wings. Parasitism by *Philornis* was already documented in Argentina (e.g., Couri 2009, Salvador & Bodrati 2013).

LONG-TAILED GROUND DOVE *Uropelia campestris*

One of the least known Columbidae in South America (Goodwin 1959, Gibbs *et al*. 2001, Baptista *et al*. 2020g), it occurs mainly in Brazil, in semi-open cerrado, and Bolivia (Sick 1997). Its breeding is completely unknown (Sick 1997, Gibbs *et al*. 2001, Baptista *et al*. 2020g). The following appear to be the first breeding data for the species.

Two nests of *U. campestris* were found on 5 and 15 September 2006 at Poconé, Mato Grosso, with a third found by V. Piacentini on 21 January 2023, also at Poconé (16°24′25.5″S, 56°40′12.5″W). Furthermore, we analysed all 969 images available on WikiAves (https://www.wikiaves.com.br/wiki/rolinha-vaqueira) on 7 April 2023 and specimens held at the Museu Paraense Emílio Goeldi (MPEG), Belém, on 8 March 2023.

Excluding evident duplicates, in WikiAves we found five records of pairs copulating (WA698593—14 June 2012, Aquidauana, Mato Grosso do Sul; WA3320060—31 March 2019, Ponte Alta do Bom Jesus, Tocantins; WA2079672—3 April 2016, Mateiros, Tocantins, WA1566491—1 January 2015, Uruana de Minas, Minas Gerais; WA1344877—10 April 2014, Formoso, Minas Gerais); one of a fledging, still with a short tail (WA2900691—24 February 2018, Curvelo, Minas Gerais); an empty nest (WA5313358—29 May 2021, Arraias, Tocantins); and three photographs of the same nest, with adult incubating, and with one and then two eggs (WA5314067—4 June 2022, WA5313342—3 June 2022, WA5313343—4 June 2022, Arraias, Tocantins).

Ten specimens with breeding data are held at MPEG: 48504, female, gonad 6 × 4 mm, 1 August 1992, Santana do Araguaia, Pará; 48503, male, gonad 6 × 4 mm, 23 June 1992, Santana do Araguaia; 34376, male, gonad 2.2 × 2.2 mm, 5 February 1982, Soure, Ilha de Marajó, Pará; 34377, female, gonad 2.7 × 3.1 mm, 2 February 1982, Soure; 22632, female, with egg in oviduct measuring 23 mm, 9 July 1964, Cachoeira do Arara, Ilha de Marajó; 57509, male, 3 × 2 mm, 11 November 2003, Manicoré, Amazonas; 57508, female, gonad 10 × 5 mm, 11 November 2003, Manicoré; 57507, male, 8 × 4 mm, 11 November 2003, Manicoré; 14112,

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Figure 19 (top left). Adult Long-tailed Ground Dove *Uropelia campestris* in a nest, Poconé, Mato Grosso, Brazil, September 2006 (NORDESTA collection)

Figure 20 (top right). Adult Long-tailed Ground Dove *Uropelia campestris* feeding nestlings, Poconé, Mato Grosso, Brazil, September 2006 (NORDESTA collection)

Figure 21 (bottom left). Adult Long-tailed Ground Dove *Uropelia campestris* in a nest, Poconé, Mato Grosso, Brazil, September 2006; note accumulation of nestling faeces on sides of nest (NORDESTA collection)

Figure 22 (bottom right). Eggs of Long-tailed Ground Dove *Uropelia campestris* in nest, Poconé, Mato Grosso, Brazil, January 2023 (Vítor Piacentini)

female, gonad 4.6 × 3.4 mm, 23 March 1958, Aragarças, Goiás; 15318, male, 3.9 × 2.3 mm, 23 August 1958, Aragarças.

These limited data suggest that the species breeds year-round in Brazil. In the Pantanal, copulation was observed in June, with our observations of active nests in September and January at the start and middle of the rainy season. In the Cerrado of Minas Gerais, Goiás and Tocantins, breeding seems to occur from January until July at least, i.e., mainly during the rainy season or at the end of the rains. In Amazonia, in Pará and Amazonas, breeding occurs between June and November, at the end of the rains.

One of our nests was constructed of material from the supporting substrate, a clump of grasses with long leaves reminiscent of *Typha* sp. (Typhaceae) (Figs. 19–21) and was in a marshy area. Another was also of grasses with long leaves, on an unidentified bush, in an open area. Measurements of these two nests were: external diameter 12 and 15 cm, internal diameter 8 and 9 cm, external height 11 and 15 cm and internal height (both) 3 cm, and were 1.4 and 1.55 m above ground. The nest found by V. Piacentini (Fig. 22) was on a closed *Curatella americana* (Dilleniaceae) shrub which had regrown after being cut. It was *c.*50 cm above ground and was estimated to be *c.*10 cm in external diameter. All were of the 'low cup/base' type.

All nests contained two white, ovaloid eggs (Fig. 22). At Poconé, two eggs measured 22.2 × 16.3 mm, mass 3.1 g, and 20.1 × 15.5 mm, mass 3 g. On 11 September 2006, one of these

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Figure 23. Young male Long-tailed Ground Dove *Uropelia campestris* at Museu Paraense Emílio Goeldi, Belém (MPEG 14111); ventral, lateral and dorsal views (M. A. Crozariol)

nests had two chicks, *c*.3–4 days old, and was observed between 07.00 and 09.00 h. Adults visited but it was impossible to know if just one or both individuals did so. The nestlings pecked vigorously at the adult's bill for food (Fig. 20). Faeces accumulate in the nest as the nestling grows (Fig. 21).

A young male specimen at MPEG (14111), collected on 19 May 1958 at Aragarças, Goiás, is in juvenile plumage (Fig. 23). It is generally paler in colour than the adult. The wing patches are somewhat smaller and duller, of a brownish hue, almost lacking the glistening purple of the adult. The mantle, rump and uppertail-covert feathers possess narrow cream-coloured tips, which are paler than the rest of the feathers.

COMMON GROUND DOVE *Columbina passerina*

One of the smallest Columbidae, this species occurs from the USA to northern South America, including many islands in the Caribbean (Weisz *et al*. 2007, Bowman 2020). In Brazil, it is widely distributed across Amazonia, also most of the coastal north-east and south as far as Espírito Santo (Sick 1997). Its population has increased, and its range has expanded due to agricultural development and deforestation (Gibbs *et al*. 2001).

Although Bowman (2020) presented a detailed review of our knowledge of the species' breeding biology, most information came from North America, outside of which information is limited (Lloyd 1897, Allen 1905, Penard & Penard 1908, Chubb 1916, Young 1925, 1928, Belcher & Smooker 1936, Dickey & Rossem 1938, Bond 1941, Hellebrekers 1942, Friedmann & Smith 1950, Bourne 1957, Skutch 1964, Haverschmidt 1972, Valdés & Cruz 1990, Rivera-Milán 1996, 2001, Bosque *et al*. 2018, Segovia-Vega *et al*. 2019), especially in Brazil, where data are primarily historical and anecdotal (Ihering 1900, Dias da Rocha 1911, Snethlage 1935a, Lamm 1948, Pinto 1953, Oniki & Willis 1983, Sick 1997).

We found two nests of *C. passerina* in 1981 at Altamira, municipality of Santo Estevão, Bahia. They were active on 4 and 10 February, a dry period of the year with irregular

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TABLE 10
Measurements of Common Ground Dove *Columbina passerina* eggs found in Altamira, Bahia, Brazil. NM = not measured.

Date found	Clutch	Mass (g)	Length (mm)	Width (mm)
10 Feb 1981	2	NM	20	15.0
		NM	21	15.5
4 Feb 1981	2	2.7	20	15.5
		2.7	19	16.0
Mean ± SD	**2 ± 0**	**2.7 ± 0.0**	**20 ± 0.8**	**15.5 ± 0.4**
Min.–max.	**2**	**2.7**	**19–21**	**15–16**

rainfall in the region. In the southern USA, the species nests almost year-round, but primarily in April–September (Bowman & Woolfenden 1997, Bowman 2020), apparently related to food availability and perhaps opportunistically (Gibbs *et al*. 2001, Bosque *et al*. 2018). In most of its range, the species seems to breed all year (Dickey & Rossem 1938, Gibbs *et al*. 2001).

Nests were on an unidentified bush and a grass clump in an open area. They had a basket shape, were supported at the bottom, and were 'simple/platform' or 'low cup/base' types. One was constructed almost entirely of thin roots with some feathers in the lining, whilst the other was formed externally of smooth twigs and petioles, and lined with dry grass and some feathers. One was 70 cm above ground and measured: external diameter 6 cm, internal diameter 4.5 cm; the other had external diameter 7 cm, internal diameter 6 cm, external height 3 cm and internal height 2 cm. Because the nest is basically an accumulation of materials, it is difficult to distinguish a border to it. Our observations agree with those in the literature (Pinto 1953, Oniki & Willis 1983, Segovia-Vega *et al*. 2019). However, neither of those we found was on the ground, a characteristic apparently common in some regions (see Oniki & Willis 1983).

Each nest held two white, oval eggs, which measured 20 ± 0.8 × 15.5 ± 0.4 mm ($n = 4$); mass 2.7 ± 0.0 g ($n = 2$) (Table 10), i.e., within the known range for the species (Snethlage 1935a, Oniki & Willis 1983, Bosque *et al*. 2018, Segovia-Vega *et al*. 2019). Pinto (1953) mentioned slightly larger eggs, and Dias da Rocha (1911) more rounded ones, measuring 19.5–21.5 × 19–20 mm. Both nests were predated a few days after being found, when still with eggs. In Cuba, nest failures occurred mainly at this stage (Segovia-Vega *et al*. 2019).

PLAIN-BREASTED GROUND DOVE *Columbina minuta*

C. minuta has a large but disjunct distribution, from southern Mexico to north-east Argentina (Gibbs *et al*. 2001, Weisz *et al*. 2007, Baptista *et al*. 2020h). In Brazil, it is known from most states, but is absent or rare in the south (Sick 1997). The species' breeding biology is poorly known, although data are available from several countries (Young 1925, 1928, Belcher & Smooker 1936, Skutch 1964, Wetmore 1968, Bosque *et al*. 2004, Bosque & Pacheco 2019, de la Peña 2019) including Brazil (Ihering 1900, Dias da Rocha 1911, Antas 1987b, Lima *et al*. 2010, Lopes *et al*. 2013, Nacinovic 2018).

We made observations at four nests of *C. minuta* found in August and September 1993 in Quebrangulo, Alagoas. Elsewhere, the species tends to nest year-round, albeit in larger numbers in some seasons, depending on environmental variables (Gibbs *et al*. 2001, Nacinovic 2018, Baptista *et al*. 2020h).

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TABLE 11
Measurements of Plain-breasted Ground Dove *Columbina minuta* nests found at Quebrangulo, Alagoas, Brazil. NM = not measured.

Nest	External diameter (cm)	Internal diameter (cm)	External height (cm)	Internal height (cm)	Height above ground (m)
1	5.0	4.0	3.0	2.0	3.7
2	6.0	4.0	4.0	2.0	2.6
3	6.0	4.5	4.5	2.5	2.9
4	5.5	4.0	2.5	1.5	1.5
Mean ± SD	**5.6 ± 0.5**	**4.1 ± 0.3**	**3.5 ± 0.9**	**2 ± 0.4**	**2.7 ± 0.9**
Min.–max.	**5–6**	**4.0–4.5**	**2.5–4.5**	**1.5–2.5**	**1.5–3.7**

TABLE 12
Measurements of Plain-breasted Ground Dove *Columbina minuta* eggs found at Quebrangulo, Alagoas, Brazil.

Date found	Clutch	Mass (g)	Length (mm)	Width (mm)
27 Aug 1993	2	2.5	21.1	17.2
		2.8	21.1	16.2
27 Sep 1993	2	3.2	23.3	18.7
		3.4	22.2	17.2
27 Sep 1993	2	2.7	20.9	16.1
		2.6	20.9	16.1
27 Sep 1993	2	3.3	21.1	17.2
		3.1	21.1	16.6
Mean ± SD	**2 ± 0**	**3 ± 0.3**	**21.5 ± 0.9**	**16.9 ± 0.9**
Min.–max.	**2**	**2.5–3.4**	**20.9–23.3**	**16.1–18.7**

Nests were of the 'simple/platform' or 'low cup/base' type and sited in the lower part of shrubs in open areas. Three were 1.5, 2.6 and 2.9 m above ground in *Erythrina mulungu* (Fabaceae), with the highest at 3.7 m in *Sarcomphalus joazeiro* (Rhamnaceae); mean 2.7 ± 0.9 m (*n* = 4) (Table 11). *Erythrina* is used for building fences in this region, but their trunks eventually sprout, creating a favourable environment for the species to nest along roadsides. Mean measurements of the four nests were: external diameter 5.6 ± 0.5 cm (range 5–6 cm), internal diameter 4.1 ± 0.3 cm (4.0–4.5 cm), external height 3.5 ± 0.9 cm (2.5–4.5 cm) and internal height 2.0 ± 0.4 cm (1.5–2.5 cm) (Table 11). They were constructed externally of thin roots (*n* = 1) or petioles (*n* = 1), internally only of petioles (*n* = 1), petioles with dry leaves (*n* = 1) or petioles with thin roots (*n* = 1). Thus, petioles were an important constituent of the nests, which were similar to descriptions in the literature, although like the previous species it can also nest on the ground (Wetmore 1968, Antas 1987b, Lopes *et al*. 2013, Nacinovic 2018).

Two white, ovaloid eggs were laid per nest. On average, they measured 21.5 ± 0.9 × 16.9 ± 0.9 mm; mass 3.0 ± 0.3 g (*n* = 8) (Table 12), and they resembled descriptions in the literature (Ihering 1900, Dias da Rocha 1911, Belcher & Smooker 1936, Wetmore 1968, Lima *et al*. 2010, Lopes *et al*. 2013). According to Baptista *et al*. (2020h), the eggs of *C. m. minuta* (the only subspecies in Brazil; Pacheco *et al*. 2021) tend to be larger than those of *C. m. elaeodes* (see Wetmore 1968), agreeing with our observations.

The nestling period in one nest was 12 days, whereas others have stated that it is 13–14 days (Baptista *et al*. 2020h). Three of the four nests, all in *Erythrina mulungu*, were predated *c*.10 days after discovery by an unidentified rodent, a green snake, *Philodryas olfersii*, and a

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Roadside Hawk *Rupornis magnirostris*. Lyra-Neves *et al*. (2007) mentioned that the species flees the nest in the face of Common Marmoset *Callithrix jacchus*.

RUDDY GROUND DOVE *Columbina talpacoti*

One of the most abundant Columbidae in the Americas, this species occurs in a wide variety of habitats, including urban areas, from the southern USA to Argentina and throughout Brazil (Sick 1997, Hart 2020). It benefits from deforestation and agricultural production (Gibbs *et al*. 2001, Hart 2020). There are many publications on the species' breeding outside (Lloyd 1897, Allen 1905, Penard & Penard 1908, Beebe *et al*. 1917, Stone 1918, Wetmore 1926, 1968, Belcher & Smooker 1936, Hellebrekers 1942, Hostos 1946, Haverschmidt 1953, Skutch 1956, 1983, Vanegas 1996, Bosque *et al*. 2004, Tejera *et al*. 2004, Di Giacomo 2005, Hayes 2014, Bulgarella & Heimpel 2015, Bosque & Pacheco 2019, de la Peña 2019) and in Brazil (Euler 1900, Ihering 1900, Dias da Rocha 1911, Snethlage 1935a, Santos 1938, Pinto 1953, Mitchell 1957, Oniki & Willis 1983, Belton 1984, Cintra 1988, Cintra & Cavalcanti 1997, Sick 1997, Saracura 2005, Vasconcelos & Vasconcelos 2007, Marini *et al*. 2010, Almeida *et al*. 2012, Almeida & Anjos-Silva 2015, Nacinovic 2018, Santos *et al*. 2022). However, most observations are anecdotal, with relatively few nest and egg descriptions.

We found 43 nests of *C. talpacoti* between 1981 and 2010 in Quebrangulo (*n* = 22), Alagoas, Arcos (*n* = 17) and Inhumas (*n* = 2), Minas Gerais, and Camaçari (*n* = 2), Bahia. Taken together, these records indicate the species nests throughout the year. However, nests were active mainly in October–February at Arcos and April–July at Quebrangulo (Fig. 24). Elsewhere, the species also tends to nest all year, albeit possibly with greater activity in some seasons, depending on the availability of food (Haverschmidt 1953, Cintra 1988, Cintra & Cavalcanti 1997, Hart 2020). The same female may lay several eggs over the course of a few months (Haverschmidt 1953, Cintra 1988).

Both adults build the nest. Except one nest in a marshy area, all were in open fields. Most were in shrubs or trees 3 m or less tall (*n* = 26), or on human constructions (*n* = 10) and trees taller than 4 m (*n* = 6), usually among clumps of branches, lianas, or on beams in buildings. Nests were on average 2.4 ± 1.0 m above ground (*n* = 43) (Table 13) and were of the 'low cup/base' type. In October 1996, a nest was found under the roof of a house, 1 m from an active nest of Scaled Dove *C. squammata*. Materials used in construction were very variable externally: only petioles (*n* = 4), only dry grass (*n* = 3), only smooth twigs (*n* = 2), only fine roots (*n* = 2), only pieces of wood (*n* = 2), only plastic (*n* = 1), dry grass and smooth twigs (*n* = 1), dry grass and herbaceous stalks (*n* = 1), dry grass and dry leaves (*n* = 1), dry grass and fine roots (*n* = 1), dry grass and inflorescences (*n* = 1), fine roots and twine (*n* = 1),

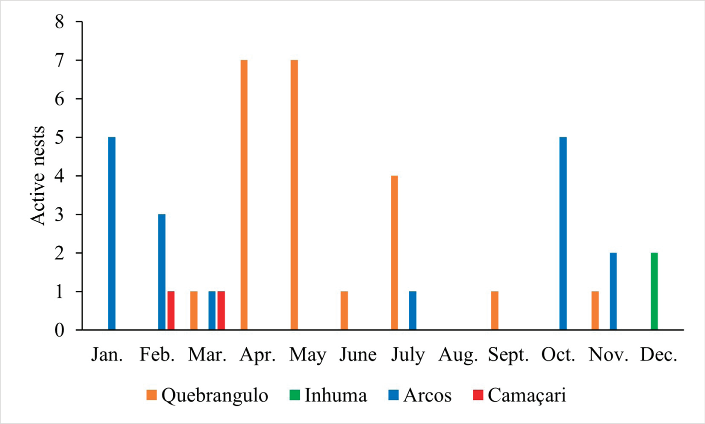

Figure 24. Number of active nests by month (based on date of discovery) of Ruddy Ground Dove *Columbina talpacoti* at Quebrangulo (*n* = 22), Alagoas, Arcos (*n* = 17) and Inhumas (*n* = 2), Minas Gerais, and Camaçari (*n* = 2), Bahia.

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Figure 25 (top). Adult female Ruddy Ground Dove *Columbina talpacoti* feeding nestlings, Quebrangulo, Alagoas, Brazil, May 2010; note large number of faeces produced by the nestlings (NORDESTA collection)

Figure 26 (bottom). Pair of Ruddy Ground Doves *Columbina talpacoti* with nestling, Arcos, Minas Gerais, Brazil, December 1996 (NORDESTA collection)

fine roots, lianas and plant fibres (*n* = 1), dry leaves and twines (*n* = 1) and petioles and lianas (*n* = 1). Internally they comprised the following: only dry grass (*n* = 8), only dry leaves (*n* = 3), pieces of wood and dry leaves (*n* = 2), dry grass and thin roots (*n* = 2), only thin roots (*n* = 1), only petioles (*n* = 1), smooth twigs and petioles (*n* = 1), smooth twigs and feathers (*n* = 1), dry grass and herbaceous stalks (*n* = 1), dry grass and dry leaves (*n* = 1), dry grass, dry leaves and thin roots (*n* = 1), thin roots, lianas and plant fibres (*n* = 1) and thin roots, lianas and petioles (*n* = 1). Thus, externally dry grass (24.2% of nests), petioles (15.2%) and fine roots (15.2%) were the most used materials, whilst internally dry grass (34.2%), dry leaves (18.4%) and fine roots (15.8%) dominated.

Nests measured: external diameter 9.4 ± 2.6 cm (range 5–15 cm; *n* = 19), internal diameter 6.2 ± 1.7 cm (4–10 cm; *n* = 19), external height 5.3 ± 2.1 cm (3–11 cm; *n* = 18), internal height 2.6 ± 1.7 cm (1–9 cm; *n* = 19); mass 13 ± 5.5 g (6–20 g; *n* = 7) (Table 13). The same nest, which was successful in November 2000, was reused in January 2001. Because the adults do not remove the nestlings' faeces, a thick layer of droppings tends to accumulate on the nest rims (Fig. 25). The considerable variation in nest sites, material used, and measurements are within the ranges reported in the literature (Wetmore 1926, Haverschmidt 1953, Skutch 1956, Oniki & Willis 1983, Marini *et al*. 2010, Hart 2020). Cintra (1988) reported that most of the 218 nests he found were constructed of *Urochloa* [*Brachiaria*] *plantaginea* (Poaceae), drawing a parallel with the dry grass that was most important in the nests we found. Man-made materials are rarely reported in the species' nests (e.g., Skutch 1956, Cintra 1988, Gibbs *et al*. 2001, Marini *et al*. 2010, de la Peña 2019, Hart 2020), even in urban areas (e.g., Tejera *et al*. 2004), but the species is known to use such materials (Batisteli *et al*. 2019). The accumulation of faeces has also long been known (Ihering 1900, Skutch 1956, Oniki & Willis 1983).

All clutches comprised two (*n* = 34) white, elliptical (*n* = 9) or oval (*n* = 6) eggs. They measured on average 22.6 ± 1.4 × 16.9 ± 0.6 mm (*n* = 68); mass 3.2 ± 0.4 g (*n* = 62) (Table 14). Clutch size and measurements agree with the literature (Haverschmidt 1953, Skutch 1956, Oniki & Willis 1983, Cintra 1988).

Incubation, undertaken by the pair, occupied 12 (*n* = 3) or 13 days (*n* = 1) as described in the literature (Haverschmidt 1953, Skutch 1956, Oniki & Willis 1983, Cintra 1988). The nestling period was 11 (*n* = 1 nest), 12 (*n* = 1) or 13 days (*n* = 1), also within the range reported in the literature (Haverschmidt 1953, Skutch 1956, Cintra 1988). Oniki & Willis (1983) mentioned the shortest period, just eight days. The nestlings hatch with a fine, sparse, beige down covering their dark grey body, and are tended by both adults (Fig. 26). The fledglings have similar plumage to the adults, only a little paler.

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TABLE 13

Measurements of Ruddy Ground Dove *Columbina talpacoti* nests found in the wild in Brazil. NM = not measured.

Locality	External height (cm)	Internal height (cm)	External diameter (cm)	Internal diameter (cm)	Mass (g)	Height above ground (m)
Quebrangulo/AL	NM	NM	NM	NM	NM	1.6
Quebrangulo/AL	NM	NM	NM	NM	NM	2.2
Quebrangulo/AL	NM	NM	NM	NM	NM	2.6
Quebrangulo/AL	NM	1.0	8	6.0	NM	3.5
Quebrangulo/AL	4	1.5	12	7.0	NM	3.3
Quebrangulo/AL	NM	NM	NM	NM	NM	1.6
Quebrangulo/AL	3	1.0	9	5.0	6	2.8
Quebrangulo/AL	NM	NM	NM	NM	NM	2.3
Quebrangulo/AL	NM	NM	NM	NM	NM	1.7
Quebrangulo/AL	NM	NM	NM	NM	NM	3.4
Quebrangulo/AL	NM	NM	NM	NM	NM	1.6
Quebrangulo/AL	11	9.0	6	4.0	NM	3.7
Quebrangulo/AL	NM	NM	NM	NM	NM	2.1
Quebrangulo/AL	3	2.0	5	4.0	NM	1.7
Quebrangulo/AL	7	3.0	5	4.0	NM	2.2
Quebrangulo/AL	NM	NM	NM	NM	NM	3.4
Quebrangulo/AL	NM	NM	NM	NM	NM	3.6
Quebrangulo/AL	NM	NM	NM	NM	NM	4.5
Quebrangulo/AL	4	1.5	8	4.5	NM	2.6
Quebrangulo/AL	5	3.0	11	7.0	14	2.2
Quebrangulo/AL	5	3.5	12	7.5	13	1.8
Quebrangulo/AL	NM	NM	NM	NM	NM	0.8
Inhumas/MG	NM	NM	NM	NM	NM	1.1
Inhumas/MG	NM	NM	NM	NM	NM	1.2
Arcos/MG	NM	NM	NM	NM	NM	1.1
Arcos/MG	NM	NM	NM	NM	NM	2.5
Arcos/MG	NM	NM	NM	NM	NM	0.4
Arcos/MG	4	2.0	13	9.0	NM	3.7
Arcos/MG	3	2.0	8	6.5	20	1.1
Arcos/MG	NM	NM	NM	NM	NM	3.9
Arcos/MG	NM	NM	NM	NM	NM	2.4
Arcos/MG	NM	NM	NM	NM	NM	2.7
Arcos/MG	NM	NM	NM	NM	NM	1.1
Arcos/MG	9	3.0	8	5.0	9	2.8
Arcos/MG	6	3.0	10	7.0	20	3.1
Arcos/MG	5	2.0	9	6.0	9	3.5
Arcos/MG	6	2.0	11	7.0	NM	3.4
Arcos/MG	6	2.0	9	7.0	NM	1.1
Arcos/MG	NM	NM	NM	NM	NM	3.8
Arcos/MG	6	2.0	10	5.0	NM	2.3
Arcos/MG	5	3.0	15	10.0	NM	2.1
Camaçari/BA	3	2.0	10	5.6	NM	1.8
Camaçari/BA	NM	NM	NM	NM	NM	1.4
Mean ± SD	**5.3 ± 2.1**	**2.6 ± 1.7**	**9.4 ± 2.6**	**6.2 ± 1.7**	**13.0 ± 5.5**	**2.4 ± 1**
Min.–max.	**3–11**	**1–9**	**5–15**	**4–10**	**6–20**	**0.4–4.5**

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TABLE 14
Measurements of Ruddy Ground Dove *Columbina talpacoti* eggs found in the wild in Brazil. NM = not measured.

Locality	**Date found**	**Clutch**	**Mass (g)**	**Length (mm)**	**Width (mm)**
Quebrangulo/AL	26 May 1988	2	3.8	23.0	17.7
			3.9	23.6	17.3
Quebrangulo/AL	16 Apr 1986	2	3.1	23.2	16.6
			3.5	24.2	16.9
Arcos/MG	2 Jan 1989	2	NM	21.6	17.2
			NM	21.5	16.6
Inhumas/MG	14 Dec 1981	2	2.75	24.6	17.0
			2.75	24.8	17.0
Quebrangulo/AL	8 May 1989	2	3.9	21.6	16.5
			4.1	23.0	16.4
Camaçari/BA	22 Feb 1982	2	NM	24.6	17.2
			NM	23.3	17.9
Quebrangulo/AL	22 Jun 1990	2	NM	23.8	17.3
			NM	24.0	17.5
Camaçari/BA	15 Mar 1985	2	3.5	23.5	17.2
			3.3	23.0	17.0
Quebrangulo/AL	3 Apr 1985	2	3.4	23.9	17.2
			3.2	23.5	17.4
Quebrangulo/AL	7 Apr 1985	2	3.2	23.0	16.7
			3.55	24.2	17.2
Quebrangulo/AL	19 Apr 1985	2	3.5	23.0	17.2
			3.4	23.2	17.1
Quebrangulo/AL	15 May 1986	2	3.5	21.7	17.4
			3.1	21.0	16.7
Quebrangulo/AL	4 May 1986	2	3.0	21.8	17.0
			2.8	21.8	16.0
Quebrangulo/AL	4 May 1986	2	3.2	23.0	16.6
			3.0	21.6	16.9
Arcos/MG	8 Feb 1996	2	3.2	22.3	17.4
			3.2	21.0	17.2
Quebrangulo/AL	17 Sep 1990	2	3.6	24.4	17.0
			3.2	23.4	16.0
Arcos/MG	2 Feb 1997	2	2.9	22.7	16.9
			2.6	22.4	16.7
Arcos/MG	7 Feb 1996	2	2.8	23.3	16.6
			3.1	23.3	17.2
Arcos/MG	31 Oct 1996	2	2.5	23.3	17.2
			2.8	22.6	17.2
Arcos/MG	15 Nov 1996	2	3.0	22.1	17.2
			3.3	23.4	17.2
Arcos/MG	20 Jan 1996	2	3.4	23.0	17.5
			3.5	23.4	17.4
Quebrangulo/AL	15 Apr 2008	2	3.0	20.0	15.7
			3.2	22.0	15.8
Quebrangulo/AL	16 Apr 2008	2	3.8	21.2	16.6
			4.0	22.1	16.4
Arcos/MG	1 Mar 1991	2	3.6	23.8	17.2

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			3.2	23.3	16.6
Arcos/MG	20 Jan 1996	2	3.2	24.0	17.2
			3.1	26.0	17.0
Arcos/MG	23 Jan 1996	2	3.7	23.8	17.5
			3.2	22.6	17.2
Quebrangulo/AL	8 Jul 1993	2	3.2	23.3	18.7
			3.4	22.2	17.2
Quebrangulo/AL	8 Jul 1993	2	2.5	21.1	17.2
			2.8	21.1	16.2
Quebrangulo/AL	9 Jul1993	2	2.4	19.4	15.9
			2.3	20.9	15.9
Quebrangulo/AL	9 Jul 1993	2	2.2	21.1	16.1
			2.7	19.4	15.9
Quebrangulo/AL	1 Mar 1991	2	3.6	23.8	17.2
			3.2	23.3	16.6
Arcos/MG	29 Oct 1993	2	3.1	22.7	17.2
			3.2	21.1	17.2
Arcos/MG	29 Oct 1993	2	2.4	19.4	15.9
			3.3	20.9	15.9
Arcos/MG	29 Oct 1993	2	3.3	21.1	17.2
			3.3	21.1	16.5
Mean ± SD		**2 ± 0**	**3.2 ± 0.4**	**22.6 ± 1.4**	**16.9 ± 0.6**
Min.–max.		**2**	**2.2–4.1**	**19.4–26.0**	**15.7–18.7**

A nest with two five-day-old chicks was monitored on 30 November 1996 between 07.00 and 08.40 h, at Arcos, Minas Gerais. The pair visited the nest together on three occasions, each adult feeding the nestlings for 2–3 minutes, regurgitating crop milk directly into their bills. Cintra (1988) indicated that the young remain with their parents for *c*.25 days after fledging and might reach maturity at three months.

One nest, in a *Morus nigra* (Moraceae) bush, and which was being reused, was predated at the egg stage by Rufous-fronted Thornbird *Phacellodomus rufifrons*. Five *P. rufifrons* attacked the nest and ate the eggs, leaving only the shells. Also at Arcos, on 29 October 1996, at a nest of Pileated Finch *Coryphospingus pileatus* with two eggs, we observed *P. rufifrons* eject one egg from the nest and eat the other. In this case, the *P. rufifrons* flew off with the empty shell. We have found no other cases of *P. rufifrons* predating bird eggs, only the suspected destruction of a nest belonging to a Yellow-browed Tyrant *Satrapa icterophrys* (Cruz & Andrews 1989). Other birds, although not the only nest predators of *C. talpacoti* (see Tejera *et al*. 2004, Santos-Filho *et al*. 2021), do seem to be the most important ones. Skutch (1956) mentioned Fiery-billed Aracari *Pteroglossus frantzii*, and Cintra (1988) Curl-crested Jay *Cyanocorax cristatellus*, American Kestrel *Falco sparverius*, Aplomado Falcon *F. femoralis* and Roadside Hawk *Rupornis magnirostris* as nest predators.

SCALED DOVE *Columbina squammata*

This species draws attention both for its vocalisations and the noise its wings make in flight, which recalls a rattlesnake (Amorim & Dias 2019, 2021). It has two disjunct populations, one in northern South America, in Colombia and Venezuela, and another in northern Argentina and most of Brazil outside Amazonia (Sick 1997, Silva 2006, Baptista *et al*. 2020i). It inhabits open areas commonly impacted by human activity. While the species' breeding in the wild is not yet known, most publications are based on observations made in Brazil (Ihering 1900, Dias da Rocha 1911, Lamm 1948, Britto 1950, Lordello 1954, Eston 1993, Sick 1997, Saracura

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Figure 27 (top). Adult Scaled Dove *Columbina squammata* in nest, Camaçari, Bahia, Brazil, March 2014; note use of anthropogenic material in lower part of nest (NORDESTA collection)

Figure 28 (bottom left). Adult Scaled Dove *Columbina squammata* feeding nestlings, Camaçari, Bahia, Brazil, May 2002; note accumulation of faeces on edge of nest (NORDESTA collection)

Figure 29 (bottom right). Scaled Dove *Columbina squammata* eggs in a nest, Arcos, Minas Gerais, Brazil, April 1990 (NORDESTA collection)

2005, Marini *et al*. 2010), with a few from elsewhere (Harrison 1961, Rivera-Milán 1996, Bosque *et al*. 2004, Bosque & Pacheco 2019, de la Peña 2019).

Observations were made at 16 nests found between 1984 and 2014 at Arcos, Minas Gerais (*n* = 13) and Camaçari, Bahia (*n* = 3), between January and September, primarily in January–March (69% of nests). In Colombia, nesting occurs in March–April and in Venezuela during January–October, with an apparent pause in July–August (Gibbs *et al*. 2001). Like other small Columbidae, it probably breeds year-round in Brazil (Gibbs *et al*. 2001), albeit perhaps with increased activity during periods of more abundant food.

Nests were found in open areas on shrubs (*n* = 11), trees (*n* = 3) (Fig. 27) or under the roofs of buildings (*n* = 2). We identified nests on the following plants: *Solanum lycocarpum* (Solanaceae) (*n* = 3), *Mangifera indica* (Anacardiaceae) (*n* = 2), *Citrus* sp. (Rutaceae) (*n* = 1),

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TABLE 15
Measurements of Scaled Dove *Columbina squammata* nests found in the wild in Brazil. NM = not measured.

Locality	External height (cm)	Internal height (cm	External diameter (cm)	Internal diameter (cm)	Mass (g)	Height above ground (m)
Arcos/MG	NM	NM	NM	NM	NM	1.6
Arcos/MG	NM	NM	NM	NM	NM	1.2
Arcos/MG	NM	NM	NM	NM	NM	1.3
Arcos/MG	2	1.0	7	5.0	NM	3.4
Arcos/MG	4	2.0	8	7.5	22	2.6
Arcos/MG	NM	NM	NM	NM	NM	1.9
Arcos/MG	8	3.0	10	6.0	15	1.6
Arcos/MG	NM	NM	NM	NM	NM	2.4
Arcos/MG	6	2.0	8	5.0	NM	1.1
Arcos/MG	NM	NM	NM	NM	NM	1.8
Arcos/MG	NM	NM	NM	NM	NM	2.5
Arcos/MG	3	1.5	8	4.5	NM	1.8
Arcos/MG	3	1.0	9	8.0	10	5.6
Camaçari/BA	NM	1.5	11	5.0	NM	1.8
Camaçari/BA	NM	NM	NM	NM	NM	1.5
Camaçari/BA	5	2.0	11	6.0	NM	3.2
Mean ± SD	**4.4 ± 2.1**	**1.8 ± 0.7**	**9.0 ± 1.5**	**5.9 ± 1.3**	**15.7 ± 6.0**	**2.2 ± 1.1**
Min.–max.	**2–8**	**1–3**	**7–11**	**4.5–8.0**	**10–22**	**1.1–5.6**

TABLE 16
Measurements of Scaled Dove *Columbina squammata* eggs found in the wild in Brazil.

Locality	Date found	Clutch	Mass (g)	Length (mm)	Width (mm)
Arcos/MG	27 Apr 1990	2	3.5	25.9	16.6
			3.0	24.8	17.2
Camaçari/BA	15 Feb 1984	2	3.8	23.3	17.4
			3.7	23.0	17.5
Camaçari/BA	8 Mar 1984	2	3.7	23.0	17.5
			3.8	23.3	17.4
Arcos/MG	2 Mar 1991	2	4.3	26.0	18.3
			4.1	25.0	18.0
Arcos/MG	2 Mar 1991	2	4.3	26.0	18.3
			4.1	25.0	18.0
Arcos/MG	27 Jan 2004	2	3.8	24.0	17.4
			4.0	24.4	17.5
Arcos/MG	4 Feb 1996	2	3.3	24.3	17.0
			3.6	25.0	17.2
Mean ± SD		**2 ± 0**	**3.8 ± 0.4**	**24.5 ± 1.1**	**17.5 ± 0.5**
Min.–max.		**2**	**3.0–4.3**	**23–26**	**16.6–18.3**

Morus sp. (Moraceae) (*n* = 1), *Sarcomphalus joazeiro* (Rhamnaceae) (*n* = 1), *Vitis* sp. (Vitaceae) (*n* = 1) and *Musa* sp. (Musaceae) (*n* = 1). They were on average 2.2 ± 1.1 m above ground (*n* = 16) (Table 15) and were of the 'low cup/base' type. The nests were externally constructed using: only smooth twigs (*n* = 2), only roots (*n* = 1), roots and thorny twigs (*n* = 1), grasses and roots (*n* = 1) and grasses, roots and feathers (*n* = 1); internally they comprised: only roots (*n* = 1), roots and grass inflorescences (*n* = 1) and mainly grasses and feathers (*n* = 3). Overall, the nest is poorly elaborated. Nests measured: external diameter 9.0 ± 1.5 cm (range

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7–11 cm; *n* = 8), internal diameter 5.9 ± 1.3 cm (4.5–8.0 cm; *n* = 8), external height 4.4 ± 2.1 cm (2–8 cm; *n* = 7), internal height 1.8 ± 0.7 cm (1–3 cm; *n* = 8); mass 15.7 ± 6.0 g (10–22 g; *n* = 3) (Table 15). They were similar to descriptions in the literature (Eston 1993, Gibbs *et al*. 2001). As the nestlings develop, many faeces can accumulate in the nest (Fig. 28).

The pair builds the nest. Sticks are often brought by one adult but inserted and adjusted by the other already in the nest. Eston (1993) reported that males bring the materials, and the female arranges them. Construction was completed in three days at some nests, but took up to eight days in less favourable weather. A three-day construction period was also indicated by Eston (1993).

All clutches contained two (*n* = 7 nests) white, oval eggs (Fig. 29). Eggs measured 24.5 ± 1.1 × 17.5 ± 0.5 mm; mass 3.8 ± 0.4 g (*n* = 14) (Table 16). Egg size matches that known for the species (Eston 1993).

Incubation, undertaken by the pair, lasted 14 days, in accord with the literature (Lordello 1954, Eston 1993). In one nest, the nestlings fledged when 15 days old. Periods of just ten days have been reported (Lordello 1954), but the fledging period is usually 12–16 days (Eston 1993, Gibbs *et al*. 2001). On hatching, the young have dark grey skin covered with a thin, sparse beige down; the gape and legs are black. The young tended to remain in their parents' territory for an extended period after fledging, but we never saw them assist with subsequent broods, in common with previous reports (Eston 1993).

At Camaçari, Bahia, on 3 May 2002 from 06.20 to 08.00 h, a nest on the horizontal branch of a *Mangifera indica* (Anacardiaceae), *c*.2.5 m above ground, with two nestlings *c*.7 days old, was observed. Only one adult fed the nestling, for a few minutes, but stayed in the nest about an hour. It flew off as soon as the other adult arrived, announcing its presence by singing twice on the edge of the nest. After *c*.10 minutes it fed the nestlings for a few minutes. Finally, it brooded the chicks, until our observations ceased.

PICUI GROUND DOVE *Columbina picui*

Occurs in central and southern South America, from Peru to southern Argentina, including a population west of the Andes in Chile (Pearson 1975, Baptista *et al*. 2020j). In Brazil, it occurs from Rio Grande do Sul to Ceará and from Mato Grosso do Sul to Acre, but is absent from most of Amazonia (Sick 1997). Its range has expanded due to deforestation (Sick 1997, Blamires *et al*. 2002). Although common, and even considered a pest in some regions (Sick 1997), studies of the species' breeding are few, both outside (Fiebig 1921, Devincenzi 1925, Castellanos 1931, Masramón 1977, Wilson 1977, Mahler & Kempenaer 2002, Di Giacomo 2005, Altamirano *et al*. 2009, Marín 2009, de la Peña 2019) and in Brazil (Ihering 1900, Belton 1984, Lima et *al*. 2010, Almeida *et al*. 2012, Valério *et al*. 2012, Lopes *et al*. 2013).

Observations were made at nine nests found between 1981 and 2007 at Quebrangulo (*n* = 5), Alagoas; Altamira (*n* = 3) and Jeremoabo (*n* = 1), Bahia. Nests were active in July at Quebrangulo, December at Jeremoabo and February at Altamira. In Argentina, although Di Giacomo (2005) mentioned that it nests in August–March, gonadal analysis indicated that the species could breed year-round (Altamirano *et al*. 2009) as confirmed by de la Peña (2019). In Chile, the species breeds in September–October and November–January (Marín 2009).

Nests were built by the pair, in open areas, on trees and shrubs, e.g., *Citrus* sp. (Rutaceae), <3 m tall (*n* = 4), in thickets (*n* = 2), on the ground between thickets (*n* = 1), on the cactus *Cereus jamacaru* (Cactaceae) (*n* = 1) or supported on the bark of a roadside stump, on average 1.1 ± 0.7 m above ground (0.0–2.2 m; *n* = 9) (Table 17). The 'low cup/base' type nest is constructed in the fork of small branches, and is sometimes so fragile that the contents are visible from below. One nest had external diameter 7 cm and internal diameter 4.5 cm,

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TABLE 17

Measurements of Picui Ground Dove *Columbina picui* nests found in the wild in Brazil. NM = not measured.

Locality	External height (cm)	Internal height (cm)	External diameter (cm)	Internal diameter (cm)	Height above ground (m)
Quebrangulo/AL	NM	NM	NM	NM	0.45
Quebrangulo/AL	NM	NM	NM	NM	0.9
Quebrangulo/AL	NM	NM	NM	NM	0.4
Quebrangulo/AL	NM	NM	NM	NM	NM
Quebrangulo/AL	NM	NM	NM	NM	0.65
Altamira/BA	NM	NM	NM	NM	1.6
Altamira/BA	NM	NM	7.0	4.5	1.8
Altamira/BA	NM	NM	NM	NM	1.6
Jeremoabo/BA	3.0	2.0	9.0	8.0	2.2
Mean ± SD	**3 ± 0**	**2 ± 0**	**8.0 ± 1.4**	**6.25 ± 2.5**	**1.2 ± 0.7**
Min.–max.	**3**	**2**	**7–9**	**4.5–8.0**	**0.4–2.2**

TABLE 18

Measurements of Picui Ground Dove *Columbina picui* eggs found in the wild in Brazil. NM = not measured.

Locality	Date found	Clutch	Mass (g)	Length (mm)	Width (mm)
Quebrangulo/AL	27 Jul 1993	2	3.3	21.1	17.2
			3.1	21.1	16.6
Altamira/BA	10 Feb 1981	2	3.3	23.5	16.5
			NM	22.5	15.8
Altamira/BA	10 Feb 1981	2	3.3	22.5	16.5
			3.6	24.5	16.5
Quebrangulo/AL	27 Jul 1993	2	2.6	20.9	16.1
			2.8	21.1	16.5
Quebrangulo/AL	27 Jul 1993	1	NM	NM	NM
Quebrangulo/AL	27 Jul 1993	2	2.5	21.1	16.7
			2.5	21.1	17.2
Quebrangulo/AL	27 Jul 1993	2	3.3	24.8	16.6
			3.2	23.3	16.6
Jeremoabo/BA	5 Dec 2007	2	NM	21.5	15.4
			NM	21.4	15.4
Mean ± SD		**1.9 ± 0.4**	**3.0 ± 0.4**	**22.2 ± 1.4**	**16.4 ± 0.6**
Min.–max.		**1–2**	**2.5–3.6**	**20.9–24.8**	**15.4–17.2**

and another external diameter 9 cm, internal diameter 8 cm, external height 3 cm and internal height 2 cm (Table 17). Only petioles (*n* = 3), dry grass (*n* = 2) and only herbaceous stems (*n* = 1) were used to build the outer part of nests. Internally, only feathers (*n* = 2), only dry leaves (*n* = 1), only fine roots (*n* = 1), dry grass with fine roots (*n* = 1) and dry grass with feathers (*n* = 1) were used. Adults do not remove the nestlings' excrement, which accumulates on the nest edges, as Di Giacomo (2005) also noted. Our data are similar to previous descriptions (Di Giacomo 2005, Marín 2009, de la Peña 2019). In Chile, the species prefers to nest on thorny plants (Marín 2009).

Except one nest with one egg, the other seven nests contained two white, elliptical eggs. They measured 22.2 ± 1.4 × 16.4 ± 0.6 mm (*n* = 14); mass 3 ± 0.4 g (*n* = 11) (Table 18), in agreement with the previous literature (Ihering 1900, Di Giacomo 2005, Lopes *et al.* 2013), although the mean of 76 eggs in Chile was somewhat larger (Marín 2009).

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We could not determine the incubation period. Hatchlings have yellowish-grey skin and sparse, beige down. The bill is greyish buff, and the gape pale pink with dark patches on the palate. Nestlings fledged at 17 (*n* = 1), 18 (*n* = 2) or 20 days (*n* = 2). Di Giacomo (2005) mentioned a shorter period in Argentina of 13–14 days, and, in Chile, Marín (2009) reported that hatching to fledging occupied just 10–11 days.

Family Cuculidae.—A cosmopolitan group, absent only from polar regions, Cuculidae inhabit mainly forested areas, although some species have colonised open landscapes, including human-modified ones. Despite being best known for its brood-parasitic behaviour, the family exhibits among the greatest variety of reproductive strategies among birds (Payne 2005, Erritzøe *et al*. 2012, Winkler *et al*. 2020b). A relatively diverse group with 33 genera and 147 species worldwide (Winkler *et al*. 2020b), 24 species occur in South America (Remsen *et al*. 2020) and 20 in Brazil (Pacheco *et al*. 2021).

GUIRA CUCKOO *Guira guira*

A common and widespread species, occurring from Amapá, northern Brazil, to southern Argentina, except forested areas, although its range has increased due to deforestation (Sick 1997, Erritzøe *et al*. 2012, Payne & Kirwan 2020). Because of the species' interesting social behaviours, many authors have studied its reproduction, both outside (Serié 1923a,b, Friedmann 1927, Smyth 1928, Pereyra 1935, Davis 1940a, Skutch 1966, Azategui 1975, Wilson 1977, Board & Perrott 1979, Salvador 1981, 2011, Martella *et al*. 1985, Jenny 1997, Azpiroz 2001, Voyles & Schmit 2004, Di Giacomo 2005, Darrieu *et al*. 2010, Hayes 2014) and in Brazil, especially central Brazil by Regina Macedo and collaborators (Euler 1900, Ihering 1900, Dias da Rocha 1911, Santos 1938, Belton 1984, Cavalcanti *et al*. 1991, Macedo 1992, 1994, 2015, Quinn et *al*. 1994, Sick 1997, Macedo & Bianchi 1997a,b, Melo & Macedo 1997, Macedo & Melo 1999, Cariello *et al*. 2002, 2006, Macedo *et al*. 2004a,b, Lima *et al*. 2011, Almeida *et al*. 2012, Tubelis & Sazima 2021).

Observations were made at 21 nests of *G. guira*, found between 1981 and 2019, at Quebrangulo, Alagoas (*n* = 10), Arcos, Minas Gerais (*n* = 7), Poconé, Mato Grosso (*n* = 3) and Altamira, Bahia (*n* = 1). Eggs were found throughout the year except June and July (Table 19), while the presence of nestlings in July indicates that breeding also occurs in this period, albeit possibly less frequently, as noted in the literature (Macedo 1992, Darrieu *et al*. 2010, Payne & Kirwan 2020).

Nests are usually built in the upper part of trees and shrubs, very well hidden in foliage and sometimes by epiphytic plants, such as bromeliads and vines. The following plant species were used as nesting substrates: *Calotropis procera* (Apocynaceae, *n* = 1), an unidentified palm (Arecaceae, *n* = 1), *Acrocomia aculeata* (Arecaceae, *n* = 1), *Jacaranda* sp. (Bignoniaceae, *n* = 2), *Trattinnickia burseraefolia* (Burseraceae, *n* = 1), *Crateva tapia* (Capparaceae, *n* = 1) covered by bromeliads, *Erythrina mulungu* (Fabaceae, *n* = 1) covered by bromeliads, *Machaerium acutifolium* (Fabaceae, *n* = 1), *Eucalyptus* sp. (Myrtaceae,

TABLE 19

The reproductive period of Guira Cuckoo *Guira guira* four different localities in Brazil. N = nestling, E = eggs. Each letter represents an active nest.

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Altamira/BA		E										
Quebrangulo/AL			N/E	NN/EEE	E				E			E
Arcos/MG	E							E	EE	EE	E	
Poconé/MT							N		N	E		

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TABLE 20
Measurements of Guira Cuckoo *Guira guira* nests found in the wild in Brazil. NM = not measured.

Locality	**External height cm)**	**Internal height (cm)**	**External diameter (cm)**	**Internal diameter (cm)**	**Mass (g)**	**Height above ground (m)**
Altamira/BA	NM	NM	NM	NM	NM	5.8
Arcos/MG	32	11	34	19	NM	3.1
Arcos/MG	29	11	42	19	750	5.5
Arcos/MG	NM	NM	NM	NM	NM	5.6
Arcos/MG	NM	NM	NM	NM	NM	4.5
Arcos/MG	NM	NM	NM	NM	NM	7.8
Arcos/MG	NM	NM	NM	NM	NM	2.9
Arcos/MG	NM	NM	NM	NM	NM	8.0
Poconé/MT	NM	7	40	15	2,000	5.7
Poconé/MT	NM	NM	NM	NM	NM	7.2
Poconé/MT	10	7	16	9	NM	2.6
Quebrangulo/AL	NM	NM	NM	NM	NM	3.1
Quebrangulo/AL	NM	NM	NM	NM	NM	4.5
Quebrangulo/AL	NM	NM	NM	NM	NM	2.2
Quebrangulo/AL	NM	NM	NM	NM	NM	8.0
Quebrangulo/AL	NM	NM	NM	NM	NM	5.3
Quebrangulo/AL	NM	NM	NM	NM	NM	2.5
Quebrangulo/AL	NM	NM	NM	NM	NM	3.3
Quebrangulo/AL	NM	NM	NM	NM	NM	4.5
Quebrangulo/AL	NM	NM	NM	NM	NM	2.5
Quebrangulo/AL	NM	NM	NM	NM	NM	4.7
Mean ± SD	**23.7 ± 11.9**	**9.0 ± 2.3**	**33 ± 11.8**	**15.5 ± 4.7**	**1,375 ± 883.9**	**4.7 ± 1.9**
Min.–max.	**10–32**	**7–11**	**16–42**	**9–19**	**750–2,000**	**2.2–8.0**

n = 1), *Eugenia dystenterica* (Myrtaceae, *n* = 1), *Nectandra lanceolata* (Myrtaceae, *n* = 1), a *Bougainvillea* sp. (Nyctaginaceae, *n* = 1) covered with lianas, in a clump of bamboo (Poaceae, *n* = 1), and *Sarcomphalus joazeiro* (Rhamnaceae) with lianas (*n* = 1) or bromeliads (*n* = 1). In Argentina, in Formosa province, *Copernicia alba* (Arecaceae) palms were the most frequently used plant (Di Giacomo 2005). Nests were on average 4.7 ± 1.9 m (*n* = 21) above ground (Table 20) and had a 'low cup/base' shape, measuring: external diameter 33 ± 11.8 cm (*n* = 4), internal diameter 15.5 ± 4.7 cm (*n* = 4), external height 23.7 ± 11.9 cm (*n* = 3) and internal height 9 ± 2.3 cm (*n* = 4); mass 1,375 ± 883.9 g (*n* = 2) (Table 20). Nests are voluminous and although externally they can appear poorly constructed, as if just an accumulation of sticks, internally there is a clear structure, with the material generally arranged in a circle. Externally, the species uses a variety of twigs (*n* = 3), twigs and dry leaves (*n* = 2), twigs and vines (*n* = 1), only vines (*n* = 1) and petioles and leaf veins (*n* = 1); internally the structure comprises green leaves (*n* = 3), green leaves and petioles (*n* = 1), twigs and dry leaves (*n* = 2), only dry leaves (*n* = 1) and only petioles (*n* = 1). It is common for the birds to insert new green leaves into the egg chamber throughout the incubation and nestling periods (Fig. 30), as already reported by others (Di Giacomo 2005). At Arcos, we observed adults breaking twigs directly from trees, rather than collecting them from the ground. Green leaves are also usually taken from trees near the nest, which is constructed by at least three individuals over 15 days. The nests we observed were overall much like those described previously (Davis 1940a, Sick 1997, Di Giacomo 2005, Erritzøe *et al*. 2012, Payne & Kirwan 2020).

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Figure 30 (top left). Guira Cuckoo *Guira guira* nestlings and eggs, Arcos, Minas Gerais, Brazil, January 2019; note green leaves lining bottom of nest, also patterned tongue and palate (NORDESTA collection)

Figure 31 (top right). Eggs of Guira Cuckoo *Guira guira*, one of the most beautiful eggs among birds, Quebrangulo, Alagoas, Brazil, October 2023; this nest was not included in the those analysed herein (NORDESTA collection)

Figure 32 (bottom left). Guira Cuckoo *Guira guira* bringing a *Tropidurus* gr. *torquatus* for its nestlings, Arcos, Minas Gerais, Brazil, September 2000 (NORDESTA collection)

Figure 33 (bottom right). A *Didelphis* sp. that had predated the eggs in a Guira Cuckoo *Guira guira* nest, Quebrangulo, Alagoas, Brazil, April 2003 (NORDESTA collection)

The nest of *G. guira* is communal. We found nests with 2–11 eggs, with a mean 6.3 ± 3.1 eggs per nest (*n* = 9) (Table 21). Due to some of the species' complex behaviours, such as evicting its own eggs and even infanticide (e.g., Macedo 1992, 1994, 2015), it is not straightforward to identify the contribution of each female to a clutch. Yolk protein electrophoresis analyses by Cariello *et al*. (2002) made it possible to determine that individual females contribute 1–3 eggs per nest. The species' eggs are among the most beautiful of all birds (Fig. 31), blue or blue-green but covered by a thin, rough white layer formed by vaterite, a polymorph of calcium carbonate (Board & Perrott 1979), distributed in a lace-like pattern all over the surface, leaving small irregular patches where the striking ground colour is visible. Eggs were oval, tending to elliptical, size 42 ± 2.2 × 32.2 ± 1.4 mm (*n* = 46); mass 22.6 ± 2.4 g (*n* = 41) (Table 21). Eggs from Argentina are somewhat smaller and lighter but otherwise within the known range (Di Giacomo 2005). The nest site may be reused over the years, as occurred at Arcos, where a group of 12 built their nest in a dense bamboo grove annually between 1975 and 1980.

The incubation period could be determined at just one nest, with three eggs, and was 13–15 days, similar to the report by Di Giacomo (2005), whereas, for Brazil, Macedo (1992) indicated a mean of only 10.1 days (*n* = 23). At Poconé, we found a nest on 28 October 2005 containing 11 eggs, all of which hatched over a period of eight days, and nine nestlings survived until 8 November. Asynchronous hatching indicates that incubation may begin

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TABLE 21
Measurements of Guira Cuckoo *Guira guira* eggs found in the wild in Brazil. NM = not measured.

Locality	**Date found**	**Clutch**	**Mass (g)**	**Length (mm)**	**Width (mm)**
Altamira/BA	8 Feb 1981	3	21.5	40.5	30.5
			23.5	41.5	32.5
			26.5	43.5	32.5
Arcos/MG	5 Oct 1990	4	26.0	44.0	34.8
			22.0	41.6	32.2
			23.0	43.7	32.2
			23.0	43.7	32.2
Arcos/MG	5 Nov 1990	9	23.0	39.4	33.3
			25.0	43.8	32.2
			23.5	42.7	31.6
			24.4	40.0	32.4
			24.0	42.2	32.2
			21.6	41.1	31.6
			26.4	45.5	33.0
			24.3	41.6	33.0
			20.3	38.3	30.5
Arcos/MG	24 Sep 2000	2	23.0	48.6	34.4
			NM	45.0	30.7
Quebrangulo/AL	24 Mar 1985	4	NM	43.0	32.7
			NM	43.0	32.8
			NM	39.4	32.5
			NM	46.0	33.4
Quebrangulo/AL	3 Sep 1999	8	24.4	38.6	32.6
			20.3	40.0	31.1
			20.2	40.0	32.2
			20.1	38.5	32.2
			20.1	39.0	32.1
			20.1	40.1	31.0
			20.3	42.1	30.0
			20.4	42.0	31.1
Quebrangulo/AL	13 Apr 2000	7	22.5	40.8	31.6
			23.0	40.4	31.2
			26.5	42.9	33.2
			24.0	41.9	31.5
			22.5	43.2	29.9
			21.0	40.6	29.6
			21.0	39.6	30.3
Quebrangulo/AL	10 Apr 2003	9	30.2	44.7	35.5
			20.7	43.6	34.4
			26.1	41.4	34.6
			20.4	43.6	32.3
			20.5	41.1	33.9
			20.5	42.4	33.7
			20.3	40.5	31.0
			20.1	44.7	31.2
			20.5	42.4	33.4
Poconé/MT	28 Apr 2003	11	NM	NM	NM
Mean ± SD		**6.3 ± 3.1**	**22.6 ± 2.4**	**42.0 ± 2.2**	**32.2 ± 1.4**
Min.–max.		**2–11**	**20.1–30.2**	**38.3–48.6**	**29.6–35.5**

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before laying is complete, which is unsurprising in a communal nest. However, of 28 nests monitored in Brazil, hatching was synchronous in 75% (Macedo 1992). Macedo *et al*. (2004) also indicated that females that lay first tend to devote more time to incubating compared to females that lay later.

Post-hatching, chicks have pinkish skin, becoming dark grey within a few days. The eye is surrounded by greenish-grey skin, and the bill is dark grey with a buff tip. The tongue and palate are red, adorned by white structures that form complex patterns, protruding arches and triangles with ridges, sometimes interspersed by a few black lines, especially on the tongue (Fig. 30). These patterns are already known in some species of Cuculidae including *G. guira* (Sick 1997, Erritzøe *et al*. 2012). Feathers initially have a filamentous, hair-like, pale-coloured appearance, making the neonates seem very different (Fig. 30). These modified neo-natal feathers are known as trichoptiles and are present in Falconiformes, Cuculiformes and Rallidae (see Ilyashenko 2006).

The nestling period varied from 13 to 17 days (*n* = 4). However, in a nest with eight young that were seven days old, built on an *Erythrina mulungu* tree heavily covered with bromeliads, three of the young left the nest to hide among the bromeliads, returning to the nest later. A similar event occurred in a nest next to a tangle of vines; when the nestlings were *c*.7 days old they began to move among the vines. Finally, in a nest near a house, all the nestlings fledged simultaneously at 17 days of age. Other authors have reported a similar period and have mentioned that nestlings 5–7 days old can already leave the nest and explore the environs (Macedo 1992, Di Giacomo 2005), but fledging typically occurs around 15 days (Macedo 1992).

On 17 February 2019, at Arcos, a nest with three eight-day-old chicks was observed from 07.00 to 10.00 h. Three different adults arrived at 10–20-minute intervals with small lizards and various insects, such as Orthoptera, Mantodea and Lepidoptera (larvae and adults). The offspring called constantly, but the adults were mainly silent and vocalised only when further away from the nest. One of the adults acted as sentinel, given the presence of some Curl-crested Jays *Cyanocorax cristatellus* in a neighbouring tree.

Also at Arcos, on 28 September 2000, a nest containing four five-day-old chicks was studied from 08.30 to 11.00 h. Two adults arrived with insects, and four others were close by. After feeding the chicks, they all flew off together to forage, vocalising frequently. They returned together, remaining quiet around the nest, bringing whole insects such as Cicadidae, Diptera, Coleoptera, adult Lepidoptera, a segment of snake, a lizard and an amphibian. At 09.05 h, an adult arrived with a lizard *Tropidurus* gr. *torquatus* almost as large as the nestlings, which failed to swallow it (Fig. 32). The adult did not break the food but insisted on offering it whole to the nestlings another seven times over a total of 18 minutes without success. A second adult arrived and the individual with the *Tropidurus* moved to a nearby branch; after the second adult left, it returned to the nest and offered the lizard to the young five more times, again without success. Eventually, the bird swallowed the prey itself, then brooded the young. At 09.45 h, it flew from the nest carrying an unhatched egg in its bill.

The diet of *G. guira* is varied (Soave *et al*. 2008, Erritzøe *et al*. 2012) and includes two species of *Tropidurus*, including *T. torquatus* (Oliveira *et al*. 2022). Macedo (1994) found that 6.8% of prey items delivered to nestlings were lizards, with the bulk being invertebrates—90.3%—especially Orthoptera.

On 15 August 2014, during 07.00–11.00 h, at Quebrangulo, we observed a nest in a *Bougainvillea* sp. with eight nestlings, three in the nest and five outside exploring the environs. A group of nine adults arrived five times at 30–40-minute intervals, usually

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together, some with insects, others without prey. The group was noisy, vocalising before arrival and departure.

The only predation event we observed was at Quebrangulo on 13 April 2003. On 10 April, we found a nest with nine eggs amid a vine tangle near the crown of a *Sarcomphalus joazeiro*. When we returned on 13 April, two opossums *Didelphis* sp. were sleeping inside the nest, having consumed the eggs (Fig. 33). A nest of *G. guira* was usurped by Tropical Screech Owl *Megascops choliba* (Claudino *et al*. 2012).

GREATER ANI *Crotophaga major*

Similar to the next species, but larger, pale-eyed, and always associated with aquatic habitats, from Panama to Argentina, including throughout Brazil (Sick 1997, Erritzøe *et al*. 2012, Riehl 2020). Like other social species of Cuculidae, its breeding behaviour is relatively well known, but almost exclusively based on observations outside Brazil (Hartert & Venturi 1909, Penard & Penard 1910, Young 1925, Belcher & Smooker 1936, Davis 1941, Hellebrekers 1942, Wetmore 1968, Willis & Eisenmann 1979, ffrench 1980, Haverschmidt & Mees 1994, Lau *et al*. 1998, Di Giacomo 2005, Logue 2007, Greeney & Gelis 2008, Riehl & Jara 2009, Riehl 2010, 2012, Hauber *et al*. 2018). For Brazil, there is only anecdotal information, none including nest measurements (Euler 1900, Ihering 1900, Stone 1929, Sick 1997, Lopes *et al*. 2013, Nacinovic 2018, Tubelis & Sazima 2021) and the only egg measurement, presented by Ihering (1900), is from Nehrkorn (1899: 173), involving an egg from 'Amazonia' which may not have been from Brazil.

We made observations at four nests found in January and February between 2006 and 2010, at Poconé, Mato Grosso, at the peak of the wet season in the region. The breeding season in *C. major* tends to vary regionally, but is reported to be tied to the onset of the rains (Riehl 2020) or be spread across the rainy season (Di Giacomo 2005, Riehl & Jara 2009), probably because lakes and rivers are full ensuring more options for nest sites, which are usually placed above water (Lau *et al*. 1998, Greeney & Gelis 2008, Riehl & Jara 2009, Riehl 2020). However, egg laying tends to occur *c*.2 months after the onset of rains, even in nests completed a few weeks earlier (Riehl & Jara 2009).

Nests were constructed among dense, vine-covered shrubs in marshy areas, on average 2.3 m above ground (Table 22), within the range known for the species (Davis 1941, Lau *et al*. 1998). However, in Argentina, some nests were high, 6.0–8.5 m above ground (Di Giacomo 2005). Nests were either 'low cup/base' (*n* = 3) or 'high cup/base' (*n* = 1), external diameter 31.8 ± 7.1 cm (*n* = 4), internal diameter 16.3 ± 2.9 cm (*n* = 4), external height 18.5 ± 7.7 cm (*n* = 4) and internal height 9.7 ± 2.1 cm (*n* = 3); one dried nest weighed only 65 g (Table 22). They were constructed externally of twigs and branches covered in thorns and lined internally with dry leaves (*n* = 1), thorny twigs and dry leaves (*n* = 1) and thorny twigs, dry leaves and green leaves (*n* = 1), supported at the base (*n* = 3) or basally with some lateral

TABLE 22

Measurements of Greater Ani *Crotophaga major* nests found in the wild in Brazil. NM = not measured.

Nest	External height (cm)	Internal height (cm)	External diameter (cm)	Internal diameter (cm)	Mass (g)	Height above ground (m)
1	25	NM	24	16	65	3.1
2	14	12	28	13	NM	1.3
3	25	9	40	20	NM	3.1
4	10	8	35	16	NM	1.5
Mean ± SD	**18.5 ± 7.7**	**9.7 ± 2.1**	**31.8 ± 7.1**	**16.3 ± 2.9**	**65**	**2.3 ± 0.9**
Min - Max.	**10–25**	**8–12**	**24–40**	**13–20**	**65**	**1.3–3.1**

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Figure 34 (top left). Nest and eggs of Greater Ani *Crotophaga major*, Poconé, Mato Grosso, Brazil, February 2009; the eggshell becomes darker with time (NORDESTA collection)

Figure 35 (top right). Greater Ani *Crotophaga major* nestlings, Poconé, Mato Grosso, Brazil, February 2009 (NORDESTA collection)

Figure 36 (botom left). Greater Ani *Crotophaga major* adults commonly arrive in groups to feed the nestlings, Poconé, Mato Grosso, Brazil, February 2009 (NORDESTA collection)

Figure 37 (bottom right). Greater Ani *Crotophaga major*, Poconé, Mato Grosso, Brazil, February 2009, arriving at nest with food; above an orthopteran, and below an unidentified insect (NORDESTA collection)

supports (n = 1). Overall, our nest measurements agree with those reported in the literature (Riehl & Jara 2009).

Like other Cuculidae, *C. major* nests colonially, with several females laying in the same structure (Riehl 2020), so our observations refer to all eggs found in each nest and not to the eggs laid by individual females. We found six eggs in two nests and three nestlings in another, but do not know if there were more eggs in this last nest prior to hatching. Eggs were oval with a bluish-green ground and almost entirely covered by a white calcareous layer, vaterite (Board & Perrott 1979), which acquired a brownish tinge after a few days due to dirt (Fig. 34). Our egg data match previous knowledge (Davis 1941, Di Giacomo 2005); eggs vary significantly in mass and size, correlating with survival and laying sequence (Riehl & Jara 2009, Riehl 2010). Mean measurements of six eggs in one nest were 39.9 ± 3.3 × 32.4 ± 4 mm; mass 27.1 ± 6.5 g (Table 23). We were unable to determine the incubation period.

At two nests, the nestlings remained 12 days, but at another the young were already exploring the environs of the nest when seven days old, and fledged at nine days old. Di Giacomo (2005) indicated a fledging period of 12–13 days in Argentina, but noted that nestlings may vacate the nest if a human approaches when just six days old. In Panama, at five days old nestlings can escape the nest in response to alarm calls by the adults, some jumping into the water and climbing back to the nest once danger has passed (Riehl &

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TABLE 23
Measurements of Greater Ani *Crotophaga major* eggs found in the wild in Brazil. NM = not measured.

Egg	Mass (g)	Length (mm)	Width (mm)
1	25.1	41.2	30.1
2	23.2	42.3	34.8
3	25.1	40.1	34.8
4	40.3	33.4	25.2
5	25.0	41.2	34.1
6	24.0	41.3	35.4
Mean ± SD	**27.1 ± 6.5**	**39.9 ± 3.3**	**32.4 ± 4.0**
Min - Max.	**23.2–40.3**	**33.4–42.3**	**25.2–35.4**

Jara 2009). Chicks have dark purplish skin and, like other cuckoos, raised white-and-black markings on the palate and tongue. Their feathers, when still growing, are usually black (Fig. 35).

A nest with six chicks, *c*.3 days old, lost two young, probably to predation. Venezuelan nests showed no losses during the nestling stage, only when with eggs (Lau *et al*. 1998), consistent with the higher survival probability during the nestling stage reported in Panama (Riehl & Jara 2009).

On 29 February 2008 between 06.50 and 08.50 h, we observed a nest with four nestlings *c*.6 days old. The adults arrived alone (*n* = 8), in pairs (*n* = 7) (Fig. 36) or in trios (*n* = 5), at average intervals of five minutes. They were generally vocalising, to which the nestlings responded frequently. Among the prey, we identified: seven green lepidopteran caterpillars, nine Orthoptera (six green grasshoppers and three brown crickets) and three spiders (Fig. 37). On 7 February 2009 between 07.00 and 09.00 h, another nest with six chicks *c*.7 days old, attended by a group of four adults, was followed. We observed ten food deliveries and identified three green lepidopteran caterpillars and an anuran amphibian. One young was smaller, presumably having hatched last, indicating asynchronous hatching, which had been reported previously (Riehl & Jara 2009). Intriguingly, the smaller nestling received more food, including the amphibian. In Ecuador, adults have been observed bringing Mantodea, a spider and a tree-frog (*Hyla* sp.) (Greeney & Gelis 2008).

SMOOTH-BILLED ANI *Crotophaga ani*

Common in most of its distribution, from Florida, USA, the West Indies and Mexico to central Argentina, the Galápagos (where introduced) and throughout Brazil, inhabiting mainly open areas and benefitting from deforestation (Rosenberg *et al*. 1990, Sick 1997, Erritzøe et *al*. 2012, Quinn & Startek-Foote 2020). Like some other Cuculidae, its complex reproductive behaviour has stimulated many studies, especially outside Brazil (Penard & Penard 1910, Chubb 1916, Stone 1918, Young 1925, Smyth 1928, Belcher & Smooker 1936, Davis 1940b, Bond 1941, Hellebrekers 1942, Skutch 1966, Wetmore 1968, Köster 1971, Board & Perrott 1979, Willis & Eisenmann 1979, ffrench 1980, Loflin 1982, Haverschmidt & Mees 1994, Di Giacomo 2005, Greeney & Gelis 2008, Salvador 2011, Grieves *et al*. 2014, 2015, Hayes 2014, Bulgarella & Heimpel 2015, Robertson *et al*. 2017a,b). In Brazil, despite several prior publications on nesting, few have presented measurements of nests or eggs (Euler 1900, Ihering 1900, Dias da Rocha 1911, Snethlage 1935a, Santos 1938, Lamm 1948, Pinto 1953, Mitchell 1957, Sick 1962, Oniki & Willis 1983, Belton 1984, Sick 1997, Almeida *et al*. 2012, Almeida & Anjos-Silva 2015, Nacinovic 2018, Tubelis & Sazima 2021).

Observations were made at 76 nests found between 1981 and 2020, at Quebrangulo, Alagoas (*n* = 60), Arcos, Minas Gerais (*n* = 7), Poconé, Mato Grosso (*n* = 5), Altamira (*n* = 2)

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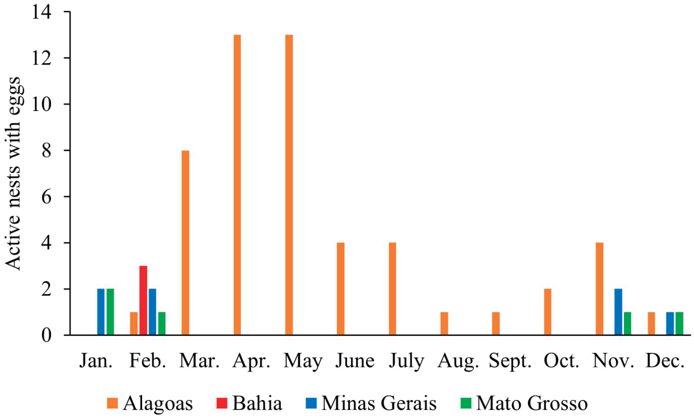

Figure 38. Number of active nests with eggs by month (based on date of discovery) of Smooth-billed Ani *Crotophaga ani*.

and Camaçari (*n* = 2), Bahia. Nests with eggs were found in all months of the year. However, in Bahia, Minas Gerais and Mato Grosso, nests were active only between November and February. At Quebrangulo, peak breeding was in March–April (Fig. 38), indicating that egg laying starts with the rains in these regions, similar to reports in Cuba (Davis 1940b). However, it may nest year-round in some areas (ffrench 1980, Nacinovic 2018).

We found 68.4% of nests in open areas with sparse trees (*n* = 52), but also in marshy areas (*n* = 21) and primary or secondary forest edges (*n* = 3). Some nests in marshy areas were above water. Most nests (*n* = 59) were below 3 m and the mean height above ground was 1.8 ± 1.2 m (*n* = 76) (Table 24). In some cases, the plants used as a base had thorns or sharp leaves. Plant species we were able to identify as nest supports were *Mangifera indica* (Anacardiaceae, *n* = 2), palms (Arecaceae, *n* = 2), bromeliads on *Crateva* sp. (Capparaceae, *n* = 1), *Costus spicatus* (Costaceae, *n* = 3), *Cyperus rotundus* (Cyperceae, *n* = 1), *Erythrina mulungu* (Fabaceae, *n* = 1), *Juncus* sp. (Juncaceae, *n* = 4), *Cenchrus* sp. (Poaceae, *n* = 2), *Paspalum virgatum* (Poaceae, *n* = 1), *Sarcomphalus joazeiro* (Rhamnaceae, *n* = 11), *Citrus* sp. (Rutaceae, *n* = 1) and *Cestrum axillare* (Solanaceae, *n* = 1). Some 94.7% of nests were supported only basally (*n* = 72), with a minority supported laterally (*n* = 2) or lacking total or partial support at the bottom (*n* = 2). One was inside a half-broken tree trunk where a large cavity had formed; bromeliads and other plants were growing inside, concealing the nest. Nests were almost all 'low cup/base' type, with relatively thick walls: external diameter 25.5 ± 5.1 cm (*n* = 15), internal diameter 12.9 ± 2.8 cm (*n* = 15), external height 13.3 ± 3 cm (*n* = 16) and internal height 6.4 ± 1.6 cm (*n* = 16); mass 152.6 ± 67.5 g (*n* = 5) (Table 24). Externally, various twigs (*n* = 39), twigs and vines (*n* = 1), twigs and petioles (*n* = 1), only petioles (*n* = 10), only dry leaves (*n* = 1) and dry leaves with thorny sticks (*n* = 1) were used as nest materials. Internally, the following were used: green leaves (*n* = 35), green leaves and stems (*n* = 5), green leaves and dry leaves (*n* = 4), green leaves and petioles (*n* = 1), only dry leaves (*n* = 4), only petioles (*n* = 1), only stems (*n* = 1), stems and unidentified plants (*n* = 1) and thorny twigs and unidentified plants (*n* = 1). Thus, externally smooth sticks predominated in 77.4% of nests, and internally green leaves were present in 84.9%. Green leaves are often renewed by the birds. We counted the materials used in a large nest of 2,500 g at Quebrangulo, which comprised 300 g of earth and 437 other items: twigs of 5–10 cm (*n* = 130), 10.1–15.0 cm (*n* = 121), 15.1–20.0 cm (*n* = 100), 20.1–30.0 cm (*n* = 40), 30.1–40.0 cm (*n* = 20), 40.1–50 cm (*n* = 24), 55 cm (*n* = 2) and 75 dry leaves. This information agrees with the literature (Euler 1900, Davis 1940b, Oniki & Willis 1983). Nests of *C. ani* can be sited next to wasp nests (Almeida & Anjos-Silva 2015).

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Figure 39 (top left). Nest and eggs of Smooth-billed Ani *Crotophaga ani*, Quebrangulo, Alagoas, Brazil, June 2003; the vaterite layer often covers the entire egg, affording the illusion that the eggs are white (NORDESTA collection)

Figure 40 (top right). Nest and eggs of Smooth-billed Ani *Crotophaga ani*, Quebrangulo, Alagoas, Brazil, March 1985; the eggs become scratched and worn over time, revealing the turquoise-blue ground colour (NORDESTA collection)

Figure 41 (bottom left). Nestlings and eggs of Smooth-billed Ani *Crotophaga ani*, Quebrangulo, Alagoas, Brazil, May 2020 (NORDESTA collection)

Figure 42 (bottom right). Like Greater Ani *Crotophaga major*, it is not rare for adult Smooth-billed Anis *Crotophaga ani* to arrive at their nests in groups to feed the nestlings, Quebrangulo, Alagoas, Brazil, July 2017 (NORDESTA collection)

Like the two previous species, *C. ani* nests communally. We could not determine the individual clutch of each female, but nests had on average 7.8 ± 4.5 eggs each (n = 24). Eggs closely resembled those of the previous species, with a bluish background and a whitish vaterite layer (Board & Perrott 1979) covering the entire surface. The vaterite often covers the entire egg, giving the illusion that the eggs are white (Fig. 39) but as they become scratched and worn with time, the turquoise-blue base can be revealed (Fig. 40). They are long-elliptical in shape. The mean size of eggs was 35.1 ± 1.9 × 25.7 ± 1.6 mm (n = 168); mass 12.4 ± 1.8 g (n = 161) (Table 25), in accord with the literature (Euler 1900, Ihering 1900, Dias da Rocha 1911, Davis 1940b, Oniki & Willis 1983, Di Giacomo 2005). Sick (1997) mentioned that a single nest can contain 50+ eggs including abandoned eggs from previous clutches.

It was difficult to calculate the incubation period because, in some nests, incubation started while eggs were still being laid. However, we estimated it to be between 12 and 15 days, agreeing with most literature (Davis 1940b, Di Giacomo 2005). Oniki & Willis (1983)

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TABLE 24

Measurements of Smooth-billed *Crotophaga ani* nests found in the wild in Brazil. NM = not measured.

Locality	**External height (cm)**	**Internal height (cm)**	**External diameter (cm)**	**Internal diameter (cm)**	**Mass (g)**	**Height above ground (m)**
Camaçari/BA	14	5.0	28	14	NM	3.1
Quebrangulo/AL	NM	NM	NM	NM	NM	1.8
Poconé/MT	11	8.0	29	14	180	1.8
Arcos/MG	NM	NM	NM	NM	NM	1.3
Arcos/MG	NM	NM	NM	NM	NM	1.5
Quebrangulo/AL	NM	NM	NM	NM	NM	3.5
Quebrangulo/AL	NM	NM	NM	NM	NM	3.5
Quebrangulo/AL	NM	NM	NM	NM	NM	1.5
Quebrangulo/AL	NM	NM	NM	NM	NM	3.6
Quebrangulo/AL	NM	NM	NM	NM	NM	1.5
Arcos/MG	NM	NM	NM	NM	NM	1.1
Quebrangulo/AL	NM	NM	NM	NM	NM	0.6
Quebrangulo/AL	NM	NM	NM	NM	NM	3.3
Altamira	NM	NM	NM	NM	NM	2.6
Quebrangulo/AL	NM	NM	NM	NM	NM	1.4
Altamira	10	6.5	21	13	NM	1.9
Quebrangulo/AL	NM	NM	NM	NM	NM	3.7
Quebrangulo/AL	NM	NM	NM	NM	NM	1.9
Quebrangulo/AL	12	6.5	25	10	NM	1.5
Quebrangulo/AL	NM	NM	NM	NM	NM	1.2
Quebrangulo/AL	NM	NM	NM	NM	NM	2.6
Camaçari/BA	NM	NM	NM	NM	NM	4.2
Quebrangulo/AL	NM	NM	NM	NM	NM	0.2
Quebrangulo/AL	NM	NM	NM	NM	NM	0.3
Quebrangulo/AL	NM	NM	NM	NM	NM	1.5
Quebrangulo/AL	NM	NM	NM	NM	NM	3.4
Quebrangulo/AL	NM	NM	NM	NM	NM	2.6
Quebrangulo/AL	NM	NM	NM	NM	NM	2.9
Quebrangulo/AL	NM	NM	NM	NM	NM	2.4
Quebrangulo/AL	NM	NM	NM	NM	NM	3.5
Quebrangulo/AL	17	8.0	24	NM	NM	0.9
Quebrangulo/AL	NM	NM	NM	NM	NM	0.8
Quebrangulo/AL	NM	NM	NM	NM	NM	1.6
Quebrangulo/AL	NM	NM	NM	NM	NM	1.1
Quebrangulo/AL	NM	NM	NM	NM	NM	1.9
Quebrangulo/AL	NM	NM	NM	NM	NM	1.8
Quebrangulo/AL	NM	NM	NM	NM	NM	1.2
Quebrangulo/AL	NM	NM	NM	NM	NM	1.4
Quebrangulo/AL	NM	NM	NM	NM	NM	1.2
Quebrangulo/AL	NM	NM	NM	NM	NM	1.8
Quebrangulo/AL	NM	NM	NM	NM	NM	1.4
Poconé/MT	NM	NM	NM	NM	NM	1.2
Quebrangulo/AL	12	3.0	22	10	NM	1.6
Poconé/MT	13	8.0	29	18	250	3.5
Poconé/MT	10	5.0	22	11	80	0.55
Poconé/MT	8	5.0	18	15	153	1.8
Quebrangulo/AL	20	6.0	28	15	NM	0.65

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Locality	External height (cm)	Internal height (cm)	External diameter (cm)	Internal diameter (cm)	Mass (g)	Height above ground (m)
Quebrangulo/AL	13	6.0	26	14	100	1.8
Quebrangulo/AL	NM	NM	NM	NM	NM	1.3
Quebrangulo/AL	NM	NM	NM	NM	NM	8.5
Quebrangulo/AL	NM	NM	NM	NM	NM	1.4
Quebrangulo/AL	NM	NM	NM	NM	NM	0.65
Quebrangulo/AL	NM	NM	NM	NM	NM	0.9
Quebrangulo/AL	NM	NM	NM	NM	NM	1.3
Quebrangulo/AL	NM	NM	NM	NM	NM	0.6
Quebrangulo/AL	NM	NM	NM	NM	NM	0.55
Quebrangulo/AL	NM	NM	NM	NM	NM	1.6
Quebrangulo/AL	NM	NM	NM	NM	NM	1.6
Quebrangulo/AL	14	7.0	28	10	NM	1.1
Quebrangulo/AL	NM	NM	NM	NM	NM	1.8
Quebrangulo/AL	NM	NM	NM	NM	NM	2.8
Quebrangulo/AL	NM	NM	NM	NM	NM	0.8
Quebrangulo/AL	NM	NM	NM	NM	NM	0.85
Quebrangulo/AL	13	5.0	NM	10	NM	1.7
Arcos/MG	NM	NM	NM	NM	NM	1.8
Arcos/MG	NM	NM	NM	NM	NM	1.6
Quebrangulo/AL	14	7.0	28	10	NM	1.8
Quebrangulo/AL	NM	NM	NM	NM	NM	1.3
Arcos/MG	NM	NM	NM	NM	NM	1.2
Quebrangulo/AL	NM	NM	NM	NM	NM	0.3
Arcos/MG	17	9.0	39	18	NM	1.8
Quebrangulo/AL	NM	NM	NM	NM	NM	3.4
Quebrangulo/AL	NM	NM	NM	NM	NM	0.55
Quebrangulo/AL	NM	NM	NM	NM	NM	3.1
Quebrangulo/AL	NM	NM	NM	NM	NM	1.6
Quebrangulo/AL	15	8.0	23	12	NM	1.6
Mean ± SD	**13.3 ± 3**	**6.4 ± 1.6**	**25.5 ± 5.1**	**12.9 ± 2.8**	**152.6 ± 67.5**	**1.8 ± 1.2**
Min.–max.	**8–20**	**3–9**	**18–39**	**10–18**	**80–250**	**0.2–8.5**

TABLE 25

Measurements of Smooth-billed Ani *Crotophaga ani* eggs found in the wild in Brazil. NM = not measured.

Locality	Date found	Clutch	Mass (g)	Length (mm)	Width (mm)
Quebrangulo/AL	26 Nov 1981	14	11.75	35.0	26.0
			10.25	34.0	24.5
			9.75	34.5	26.0
			9.0	30.4	23.5
			11.0	33.5	24.7
			13.5	35.0	28.0
			9.5	33.0	23.5
			10.0	32.7	24.2
			11.5	36.2	25.7
			11.5	33.5	26.6
			13.5	34.7	27.6
			8.25	31.2	22.5
			11.0	34.7	25.0

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Locality	Date found	Clutch	Mass (g)	Length (mm)	Width (mm)
			11.5	33.0	25.6
Quebrangulo/AL	5 May 1986	16	13.8	37.7	25.6
			14.0	34.2	27.2
			12.5	35.6	25.5
			14.3	37.5	26.6
			16.2	39.2	27.6
			15.3	38.5	27.0
			15.3	37.0	27.5
			12.3	35.0	25.4
			15.4	35.0	28.0
			10.9	32.0	25.0
			10.5	31.2	25.9
			12.8	33.3	26.6
			10.3	34.9	27.7
			14.4	36.2	27.2
			15.0	36.6	28.0
			14.5	36.6	27.3
Quebrangulo/AL	9 May 1986	20	11.0	38.4	22.7
			12.5	38.0	24.7
			13.3	37.7	25.0
			13.5	37.5	26.6
			13.3	36.7	25.6
			12.9	36.0	25.4
			11.6	36.3	23.7
			12.0	35.4	25.2
			11.8	35.0	24.6
			10.3	34.4	23.3
			9.5	32.0	22.0
			11.2	34.4	24.4
			12.5	35.0	25.5
			14.2	37.3	26.6
			12.2	35.0	25.5
			12.5	34.4	25.7
			13.8	35.6	26.4
			11.5	34.0	24.7
			10.3	32.3	23.8
			11.8	33.0	25.3
Altamira	4 Feb 1981	2	NM	32.0	26.0
Quebrangulo/AL	28 Apr 1986	11	14.0	37.7	25.4
			13.5	38.5	25.8
			13.1	35.5	25.7
			13.2	35.8	25.7
			13.9	35.7	26.6
			14.3	36.6	26.9
			12.0	35.8	24.7
			11.1	32.9	24.4
			10.6	31.9	24.3
			11.9	33.3	25.4
			11.7	31.9	25.8
Quebrangulo/AL	13 Apr 1986	12	11.0	35.4	24.4

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Locality	Date found	Clutch	Mass (g)	Length (mm)	Width (mm)
			13.5	38.0	26.0
			11.5	35.1	25.0
			11.0	34.7	24.5
			10.8	34.4	24.8
			13.4	35.0	25.0
			11.0	33.3	25.3
			11.0	33.3	25.4
			11.7	34.8	25.4
			11.1	34.5	25.0
			11.3	34.0	24.6
			13.3	36.0	26.0
Quebrangulo/AL	22 Apr 1986	6	15.0	38.0	27.3
			11.8	35.2	27.0
			15.3	36.4	28.7
			15.9	37.0	28.2
			15.0	36.4	28.6
			15.0	37.2	27.8
Quebrangulo/AL	18 Feb 1985	6	NM	37.0	26.5
			NM	37.8	28.4
			NM	37.4	30.7
			NM	31.5	25.7
			NM	36.4	30.8
			NM	35.7	24.7
Quebrangulo/AL	6 Apr 1985	4	15.0	38.2	26.2
			14.0	36.1	25.9
			14.0	36.4	26.2
			13.0	35.0	25.4
Quebrangulo/AL	23 Mar 1985	13	NM	NM	NM
Quebrangulo/AL	2 Apr 1985	4	11.5	32.7	25.0
			12.0	33.5	25.5
			11.5	33.0	25.0
			11.0	32.0	25.1
Quebrangulo/AL	20 Sep 1989	4	16.0	37.2	27.7
			15.0	37.2	27.7
			14.0	37.6	27.2
			13.0	35.2	26.3
Quebrangulo/AL	13 Apr 1985	7	13.9	35.2	27.4
			14.6	37.3	27.2
			11.8	34.2	26.1
			14.3	35.3	27.4
			13.4	35.5	26.2
			12.2	34.5	26.0
			12.8	35.3	25.9
Quebrangulo/AL	19 Jun 2008	6	14.8	34.5	26.9
			13.3	33.7	25.6
			16.3	35.1	26.9
			14.3	34.3	25.1
			15.8	35.9	26.8
			14.3	34.5	25.8
Quebrangulo/AL	17 May 1991	8	13.0	35.1	26.5

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Locality	Date found	Clutch	Mass (g)	Length (mm)	Width (mm)
			12.0	32.4	26.4
			13.5	35.1	21.6
			13.0	35.2	21.9
			13.5	34.8	25.1
			11.5	39.6	25.4
			12.0	33.3	25.5
			13.5	35.6	26.6
Quebrangulo/AL	18 Oct 1989	5	11.0	36.7	27.9
			12.0	39.9	26.4
			10.0	36.5	26.2
			11.5	36.1	26.4
			11.0	36.9	26.5
Quebrangulo/AL	17 May 1991	8	13.0	35.1	26.5
			12.0	32.4	26.9
			13.5	35.1	21.6
			13.0	35.2	21.9
			13.5	34.8	22.1
			11.5	32.6	25.4
			12.0	33.3	25.5
			13.5	35.6	26.6
Quebrangulo/AL	11 Nov 1992	4	NM	NM	NM
Arcos/MG	7 Nov 1995	5	14.0	35.5	26.1
			15.0	38.2	27.7
			16.0	40.5	27.7
			9.0	31.7	27.7
			10.0	33.3	24.8
Arcos/MG	19 Feb 1996	6	11.0	35.0	21.1
			9.0	34.7	26.1
			11.0	34.3	25.6
			11.5	35.9	26.7
			11.0	35.3	26.9
			9.0	33.9	25.7
Quebrangulo/AL	28 Jul 1993	5	14.0	36.1	28.3
			14.0	36.1	27.7
			15.0	34.4	28.3
			14.0	37.2	24.4
			16.0	37.2	27.2
Quebrangulo/AL	23 Dec 1991	3	11.0	33.3	24.9
			11.8	33.3	24.4
			11.0	33.9	24.4
Quebrangulo/AL	28 Jul 1993	7	12.0	33.3	26.1
			11.0	35.9	24.4
			11.0	34.4	24.4
			11.0	35.9	24.4
			9.0	35.9	22.4
			10.0	33.9	24.8
			11.0	35.9	23.3
Quebrangulo/AL	23 Jul 1996	10	12.1	33.9	25.4
			12.0	33.8	25.1
			12.1	36.1	24.7

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Locality	Date found	Clutch	Mass (g)	Length (mm)	Width (mm)
			12.0	35.9	24.7
			12.0	34.9	24.6
			11.0	35.9	23.9
			11.1	33.9	25.0
			10.0	31.7	23.7
			11.1	33.6	24.4
			11.0	34.4	24.5
Mean ± SD		**7.8 ± 4.5**	**12.4 ± 1.8**	**35.1 ± 1.9**	**25.7 ± 1.6**
Min.–max.		**2–20**	**8.2–16.3**	**30.4–40.5**	**21.1–30.8**

recorded 17 days. When there are many eggs and the bottom of the nest is narrow, only the topmost are incubated and hatch. Furthermore, some females start laying before the nest is complete, causing these eggs to be covered with a new layer of material and to eventually rot, as reported by several previous authors (Euler 1900, ffrench 1980, Sick 1997). Incubation starts before all the eggs are laid, and the last eggs may not be fully incubated, because as soon as the first nestlings hatch incubation becomes irregular or absent. For example, on 6 November 1988 at Arcos, there were eight eggs in the bottom of the nest covered with a layer of leaves, above which 14 eggs were laid, and only ten hatched. At Poconé, on 1 February 2006, there were eight eggs in a nest; on 11 February, there were 17 eggs, and on 14 February the first nestling hatched. Over the next three days one chick hatched per day, with four hatchlings on 18 February. The remaining 13 eggs disappeared gradually, leaving only two, which remained until the chicks fledged. On 24 February, the nestlings, aged between six and ten days, weighed between 24 and 40 g. Despite this variation, they all successfully abandoned the nest and hid in the nearby foliage. On hatching, nestlings have smooth and shiny, purplish-black skin devoid of down. The bill and legs are black, commissures pale yellow, and the palate and gape are red, with prominent white markings on the palate, the sides, and the anterior part of the tongue. Black spots frequently appear on the palate and tip of the tongue (Fig. 41). Like the preceding species, chicks leave the nest when still young to explore the environs (e.g., Euler 1900). In one case, they were only six days old. Nestlings are tended by the entire group (Fig. 42).

On 9 March 1985, at Quebrangulo, an old nest containing seven rotten eggs was being reformed by four adults, which placed small branches over them. On 21 March, the nest held two new eggs, and on 3 April a total of seven, but next day the nest was empty and a *Didelphis* sp. was sleeping there. We identified a few cases of predation, all at Quebrangulo. On 21 June 2003, a nest with nine young was predated by a Roadside Hawk *Rupornis magnirostris*. On 27 and 28 May 2006, four young in a nest were taken by a snake (*Philodryas* sp.). On 13 June 2006, 11 eggs in a nest were taken by humans. Finally, on 29 May 2016, a nest *c*.1 m above ground with five nestlings *c*.3 days old was destroyed by cattle.

STRIPED CUCKOO *Tapera naevia*

This species' breeding biology is arguably one of the most interesting among Neotropical birds and it is also one of eight obligate brood parasites in the region (Fiorini *et al*. 2019). Much more frequently heard than seen, *T. naevia* occurs from Mexico to Argentina and throughout Brazil, mainly in partially open areas and therefore benefits from some level of deforestation (Sick 1997, Erritzøe et *al*. 2012, Lowther 2020).

Hartert & Venturi (1909) were first to describe its parasitic behaviour. Since then, several papers have been published describing the species' biology, both in and outside Brazil (Ihering 1924, Snethlage 1928, Dickey & van Rossem 1938, Santos 1938, Pinto 1953,

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TABLE 26

List of bird species documented as parasitised by Striped Cuckoo *Tapera naevia*.

Family/Species	English name	Country	Source
Furnariidae			
Leptasthenura platensis[5]	Tufted Tit-Spinetail	Argentina	de la Peña (2006, 2013)
Phacellodomus rufifrons	Rufous-fronted Thornbird	Argentina, Brazil, Venezuela	Mogensen (1927), Friedmann (1933), Skutch (1969), Thomas (1983), Sick (1997), Ballarini *et al.* (2022), WA 4109421[1], this study
Phacellodomus sibilatrix	Little Thornbird	Argentina	Salvador (2013)
Phacellodomus striaticollis	Freckle-breasted Thornbird	Argentina	de la Peña (1987, apud. Salvador 2013), Pautasso (2002), de la Peña (2013)
Phacellodomus ruber	Greater Thornbird	Argentina, Brazil	Mogensen (1927), Sick (1997), Bodrati & Salvador (2015), WA 5271247[1]
Phacellodomus erythrophthalmus	Orange-eyed Thornbird	Brazil	Sick (1997)
Phacellodomus ferrugineigula	Orange-breasted Thornbird	Brazil	WA 2044657[1]
Anumbius annumbi	Firewood-gatherer	Brazil	This study
Asthenes baeri	Short-billed Canastero	Argentina	de la Peña (2006, 2013)
Cranioleuca vulpina	Rusty-backed Spinetail	Brazil	WA 3769208[1] (see also: WA 3771880[1], WA 3773129[2]), this study
Cranioleuca pyrrhophia	Stripe-crowned Spinetail	Argentina	Bodrati & Salvador (2015)
Certhiaxis cinnamomeus	Yellow-chinned Spinetail	Argentina, Brazil, Suriname, Trinidad & Tobago, Venezuela	Hartert & Venturi (1909), Penard & Penard (1910), Fiebig (1921)[3], Friedmann (1933), Belcher & Smooker (1936), Sick (1953a,b), Haverschmidt (1955b, 1961), Haverschmidt & Mees (1994), Barbaskas *et al.* (2003, *apud* de la Peña 2019), Di Giacomo (2005), de la Peña (2013), Bodrati & Salvador (2015), Murcia *et al.* (2020), WA 1556029[1], WA 3296636[1], WA 3262325[1], WA 3282444[1], WA 3023786[1], WA 1626023[2], WA 1200873[2], WA 793034[2], WA0274[2], WA 30650[2], WA 31148[2], WA 3232730[2], WA4775701[2], WA4202091[2], WA 4175185[2], ML 300508871, ML 37069501[1], ML 84697631[1], ML 204920511[2], this study
Schoeniophylax phryganophilus	Chotoy Spinetail	Argentina, Brazil	Naumburg (1930), Davis (1940c), Giai (1950), Salvador (1982, 2011), de la Peña (1983, 2006, 2013)
Synallaxis erythrothorax	Rufous-breasted Spinetail	Panama	Wetmore (1968)
Synallaxis gujanensis	Plain-crowned Spinetail	Brazil, Suriname	Penard & Penard (1910), Friedmann (1933), Snethlage (1935a, 1935b), Haverschmidt (1955b, 1961), Haverschmidt & Mees (1994)
Synallaxis ruficapilla	Rufous-capped Spinetail	Argentina	Bodrati & Salvador (2015)
Synallaxis cinnamomea	Stripe-breasted Spinetail	Trinidad & Tobago	Belcher & Smooker (1936)

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TABLE 26 *continued*

Family/Species	**English name**	**Country**	**Source**
Synallaxis hypospodia	Cinereous-breasted Spinetail	Brazil	this study
Synallaxis spixi	Spix's Spinetail	Argentina, Brazil	Ihering (1914), Fonseca (1922), Friedmann (1927), de la Peña (1983, 2013)
Synallaxis albescens	Pale-breasted Spinetail	Argentina, Brazil, Panama, Suriname, Trinidad & Tobago	Friedmann (1933), Belcher & Smooker (1936), Hellebrekers (1942), Haverschmidt (1955b), Kiff & Williams (1978), Salvador (1982, 2011), de la Peña (1983, 2013), Haverschmidt & Mees (1994), Sick (1997), Pautasso (2002)
Synallaxis frontalis	Sooty-fronted Spinetail	Argentina, Brazil, Uruguay	Smyth (1928), Friedmann (1933), Pereyra (1938 *apud* de la Peña 2019), Hoy (1968), Salvador (1982, 2011), de la Peña (1983, 2006, 2013), Sick (1997), Di Giacomo (2005), ML 413742151[1], this study
Synallaxis azarae	Azara's Spinetail	Argentina, Colombia	Hartert & Venturi (1909), Friedmann (1933), Pulgarín-R. *et al*. (2007)
Rhynchocyclidae			
Tolmomyias sulphurescens	Yellow-olive Flycatcher	Argentina	Bodrati & Salvador (2015)
Todirostrum spp.[4]		Brazil	Sick (1997)
Poecilotriccus sylvia[4]	Slate-headed Tody-Flycatcher	Brazil	Snethlage (1935a)
Tyrannidae			
Myiozetetes cayanensis[4]	Rusty-margined Flycatcher	Brazil	Snethlage (1935a)
Arundinicola leucocephala[4]	White-headed Marsh Tyrant	Suriname	Penard & Penard (1910)
Troglodytidae			
Thryophilus rufalbus	Rufous-and-white Wren	Nicaragua, Panama	Loetscher (1952), Morton & Farabaugh (1979), Mark (2013), Mark & Rubenstein (2013), Mark & Gamez-Rugama (2015), Dainson *et al*. (2018)
Cantorchilus modestus[4]	Cabanis's Wren	Costa Rica	Kiff & Williams (1978)

---

[1] Host appears on photo.

[2] Host not shown in photo, but author's comment evidences the parasite.

[3] Fiebig (1921) described '*Philydor rufus*', = Buff-fronted Foliage-gleaner *Dendroma rufa*, as a host of *T. naevia*. However, the nest characteristics indicate that the species concerned was almost certainly *Certhiaxis cinnamomeus* (see Erritzøe *et al*. 2012) hence treatment here.

[4] No convincing evidence that these species are hosts of *T. naevia*.

[5] The only species here that does not build a globular nest, but rather a cup placed in a hole or in an old nest of another furnariid (Remsen 2020).

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Figure 43. An aggressive Striped Cuckoo *Tapera naevia* fledgling, Arcos, Minas Gerais, Brazil October 1985 (NORDESTA collection)

Antoniazzi *et al*. 2011, Dainson *et al*. 2018, Nacinovic 2018; for more sources see Table 26). However, many aspects of its breeding biology are still unknown, including the method used to insert its egg into the closed, often narrow, tunnel nests of the species' hosts (Murcia *et al*. 2020).

Twelve brood parasitism events between 1986 and 2020, at Quebrangulo, Alagoas (*n* = 4), Arcos, Minas Gerais (*n* = 6) and Caseara, Tocantins (*n* = 2), were recorded. As an obligate brood parasite, the species does not build a nest. It lays its eggs in various 'closed' type nests, especially those of Furnariidae. Because lists of hosts of *T. naevia* in the literature (Erritzøe *et al*. 2012, de la Peña 2019, Lowther 2020) are incomplete we checked other literature, all 5,589 photos on WikiAves (https://www.wikiaves.com.br/wiki/saci) on 8 April 2023, and all 3,086 photos and 55 videos on Macaulay Library (https://search.macaulaylibrary.org/catalog?taxonCode=strcuc1) on 14 January 2023. All duplicate photos were discarded, and only those where the host appears in the image or the author indicated a host in comments were considered further.

Twenty-seven bird species were identified as hosts of *T. naevia* via this review, including two new hosts via WikiAves: Orange-breasted Thornbird *Phacellodomus ferrugineigula* and Rusty-backed Spinetail *Cranioleuca vulpina*. We also observed a case involving *C. vulpina*, prior to the WikiAves record, as well as two other new species which, until now, do not appear to have been mentioned as hosts: Firewood-gatherer *Anumbius annumbi* and Cinereous-breasted Spinetail *Synallaxis hypospodia*, the first being a new genus, bringing to 29 the number of known hosts, of which 78.6% are Furnariidae (Table 26), including all four of the species reported here for the first time. Only two of the seven species belonging to other families are well documented: Yellow-olive Flycatcher *Tolmomyias sulphurescens* and Rufous-and-white Wren *Thryophilus rufalbus*. The other species involved eggs collected in nests but were not confirmed via direct observation. Haverschmidt (1955b) already drew attention to the need for care with respect to hosts other than furnariids. Two cases illustrate

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the problem; the first described by Fiebig (1921) as being a nest of '*Philydor rufus*', now Buff-fronted Foliage-gleaner *Dendroma rufa*. However, the description and image of the nest seem to be that of Yellow-chinned Spinetail *Certhiaxis cinnamomeus* (see also Erritzøe *et al*. 2012, Bodrati & Salvador 2015), one of the species most parasitised by *T. naevia*. The second is Cabanis's Wren *Cantorchilus modestus*, which was cited as a possible host in Panama (Wetmore 1968). Kiff & William (1978) collected a nest of the species with two eggs in Costa Rica, and reported that one belonged to *T. naevia*. Studies in Nicaragua, including more than 50 nests of *C. modestus*, never found any eggs of the present species (Mark 2013). Thus, the egg from Costa Rica possibly represented a rare event or it is misidentified; the egg is held at the Western Foundation of Vertebrate Zoology, Camarillo, CA (WFVZ 58440). Discarding the five taxa without solid proof of parasitism, the list of hosts numbers 24 species, 22 (91.7%) of them Furnariidae and just two (8.3%) in other families (Table 26).

Below are our field observations of brood parasitism by *T. naevia*.

Phacellodomus rufifrons, Arcos, 10 September 1991: seven eggs in the nest, one of them belonging to *T. naevia*, but it had disappeared on 14 September.

P. rufifrons, Arcos, 15 October 1995: on our arrival at 09.00 h, a young *T. naevia* was observed emerging from the nest. It took a short flight to the trunk below and adopted an aggressive posture (Fig. 43).

P. rufifrons, Quebrangulo, 2 May 2006: at 08.00 h, the nest held seven eggs, six belonging to the host and one from *T. naevia*. The eggs were all predated on 8 May.

Anumbius annumbi, Arcos, 10 August 1991: the nest was constructed on 10 August. On 10 September the nest held one *T. naevia* egg and none of the host. On 14 September 1991, the egg was predated.

Cranioleuca vulpina, Caseara, 23 September 2010: on the banks of a tributary of the Tocantins River, containing a *T. naevia* egg (22.5 × 17.5 mm) and a *C. vulpina* egg (23.0 × 16.5 mm; mass 3.2 g). That of *C. vulpina* disappeared on 2 October. The *T. naevia* egg hatched on 1 October and the nestling first emerged from the nest on 15 October. The nest was observed on 7 October 2010 between 07.30 and 10.30 h. The adults arrived separately at *c*.10-minute intervals, with spiders, Lepidoptera (caterpillars and adults) and Coleoptera prey. During each feeding session, the nestling begged loudly. The nestling finally fledged on 18 October, when well grown, but remained in the upper part of the nest until 20 October, when it started to follow the *C. vulpina* pair.

C. vulpina, Caseara, 20 October 2020: held two eggs, neither of them *C. vulpina*. One was of *T. naevia* and the other of Shiny Cowbird *Molothrus bonariensis* (Fig. 44). The *T. naevia* egg was white and a long oval shape, 22.8 × 16.5 mm, mass 2.9 g, and the *M. bonariensis* egg was 19.5 × 15.8 mm, mass 2.2 g. On 6 November, both eggs were predated.

Figure 44. Rusty-backed Spinetail *Cranioleuca vulpina* nest parasitised by Striped Cuckoo *Tapera naevia* (white egg) and Shiny Cowbird *Molothrus bonariensis*, Caseara, Tocantins, Brazil, October 2020 (NORDESTA collection)

Certhiaxis cinnamomeus, Quebrangulo, 15 April 1986: a nest with five eggs, four of the host and one of *T. naevia.* The four host eggs measured: 18.8 × 14.9 mm, 2.0 g; 19.1 × 15.1 mm, 2.2 g; 18.8 × 15.3 mm, 2.1 g; 17.9 × 14.3 mm. The *T. naevia* egg was 22.5 × 16.9 mm. On 20 April, all five eggs hatched. On 23 April 1986,

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the four nestling spinetails disappeared, and only the *T. naevia* remained. On 7 May the *T. naevia* fledged but stayed near the nest.

C. cinnamomeus, Quebrangulo, 24 May 1989: nest with four eggs, three from the host and one from *T. naevia*. All were predated on 28 May.

Synallaxis hypospodia, Quebrangulo, 11 February 1992: nest with three eggs, two of the host and one of *T. naevia.* The two *S. hypospodia* eggs were white, ovaloid and measured 20.5 × 15.5 mm, 2.5 g, and 20.1 × 15.3 mm, 2.3 g. The *T. naevia* egg was 21.6 × 16.1 mm, mass 2.9 g. The *T. naevia* egg hatched on 20 February, and the host's eggs on 21 February. On 24 February, the nest was predated.

Synallaxis frontalis, Arcos, 17 February 1991: nest with four eggs, three from the host and one *T. naevia.* The host's eggs measured: 17.8 × 14.4 mm, 1.9 g; 17.6 × 14.5 mm, 1.9 g; 17.7 × 14.6 mm, 2.0 g; the *T. naevia* egg 21.6 × 17.0 mm. The *T. naevia* egg hatched on 20 February but the nest was predated on 21 February.

S. frontalis, Arcos, 8 October 1993: five eggs, four from the host and one *T. naevia*. The host's eggs measured: 18.8 × 15.5 mm, 2.1 g; 18.0 × 14.4 mm, 1.9 g; 17.7 × 14.4 mm, 1.8 g; 18.5 × 14.9 mm; the *T. naevia* egg 22.7 × 16.3 mm. The *T. naevia* egg hatched on 10 October and the host's eggs on 11 October. On 14 October the host's four nestlings disappeared, but the *T. naevia* remained. On 26 October the *T. naevia* fledged.

S. frontalis, Arcos, 8 October 2000: a third nest at Arcos contained a *T. naevia* nestling that was a few days old. On 14 October it fledged.

As an obligate parasite, the breeding season of *T. naevia* depends entirely on that of its hosts (Ballarini *et al*. 2022), which thus covers almost the entire year, considering all host species, as already observed by Haverschmidt & Mees (1994). However, regionally the reproductive period is usually more restricted (Friedmann 1933, Salvador 1982, 2011, Di Giacomo 2005).

Nest types of hosts are almost all globular and closed, many having entrance tunnels. Some, such as *Phacellodomus rufifrons* and *Certhiaxis cinnamomeus*, may have 43.7% and up to 75% of their nests parasitised in some regions (Murcia *et al*. 2020, Ballarini *et al*. 2022). It is still unclear how *T. naevia* manages to insert its egg into the oological chamber of these nests, as direct observations are lacking. Some authors have suggested that the adult makes an opening in the side (Fonseca 1922, Sick 1953a,b) or upper part (Giai 1949, Salvador 1982) of the host nest, while others have hypothesised that the adult uses the entrance opening itself (Hoy 1968, Wetmore 1968). It is impossible, however, for *T. naevia* to enter the nest of many of its hosts, mainly because the access tunnels are too narrow (Murcia *et al*. 2020). It seems likely that the cuckoo lays the egg in the tunnel opening, and the egg rolls or is carried into the chamber by the host (Sick 1953b, Murcia *et al*. 2020). *T. naevia* lays eggs with a solid shell (Salvador 1982, Sick 1997, de la Peña 2006), which might facilitate this.

The *T. naevia* eggs we observed were white, like those in Argentina and Brazil (Friedmann 1927, Salvador 1982, de la Peña 1983, 2006, Sick 1997, Di Giacomo 2005, Ballarini *et al*. 2022). However, eggs in northern South America and Central America are polymorphic and may be white, bluish or bluish green (Haverschmidt & Mees 1994, Dainson *et al*. 2018). Although not always easy to distinguish from host eggs, the clutch of *T. naevia* is, as we observed, just one egg per nest (Giai 1949, Salvador 1982, Di Giacomo 2005, de la Peña 2006), very rarely two (de la Peña 1983, Haverschmidt & Mees 1994). The eggs are also proportionately much smaller than the adult, as also noted previously (Penard & Penard 1910, Salvador 1982, Sick 1997, de la Peña 2006). The mean size of six eggs we measured was 22.3 ± 0.5 × 16.7 ± 0.5 mm, mass 2.9 g ($n = 2$) (Table 27). Given that mean adult female mass is 51 g (Lowther 2020), these eggs represent only 5.7% of female weight, very similar to the 5.6% reported by Ballarini *et al*. (2022). Our measurements are within the species'

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TABLE 27
Measurements of Striped Cuckoo *Tapera naevia* eggs found in the wild in Brazil. NM = not measured.

Locality	Date found	Mass (g)	Length (mm)	Width (mm)
Caseara/TO	23 Sep 2010	NM	22.5	17.5
Caseara/TO	20 Oct 2020	2.9	22.8	16.5
Quebrangulo/AL	15 Apr 1986	NM	22.5	16.9
Quebrangulo/AL	11 Feb 1992	2.9	21.6	16.1
Arcos/MG	17 Feb 1991	NM	21.6	17.0
Arcos/MG	8 Oct 1993	NM	22.7	16.3
Mean ± SD		**2.9 ± 0.0**	**22.3 ± 0.5**	**16.7 ± 0.5**
Min.–max.		**2.9**	**21.6–22.8**	**16.1–17.5**

known variation (Mogensen 1927, Smyth 1928, Velho 1932, Salvador 1982, de la Peña 1983, Haverschmidt & Mees 1994, Di Giacomo 2005).

We could not determine the incubation period of eggs, which has been indicated to be shorter than their hosts (Haverschmidt & Mees 1994, Sick 1997, Ballarini *et al*. 2022). However, our observations evidence that *T. naevia* nestlings kill their ‘siblings’ within hours of hatching (Salvador 1982, Haverschmidt & Mees 1994, Bodrati & Salvador 2015, Ballarini *et al*. 2022) using their modified, sharp bill (Morton & Farabaugh 1979). It is therefore unlikely that in parasitised nests with two *T. naevia* eggs more than one nestling survives.

Nestlings remained in the nest 14, 16 and 17 days, leaving it when still unable to fly. This period largely coincides with previous observations of between 16 and 18 days (Salvador 1982, Haverschmidt & Mees 1994, Sick 1997). Ballarini *et al*. (2022) indicated a longer period, mean 20.8 days ($n = 8$). Some authors have indicated that *T. naevia* chicks may destroy part of the host nest or enlarge the tunnel to exit (Salvador 1982, Sick 1953b, Murcia *et al*. 2020), but we did not witness such behaviour. As the tunnel of *Certhiaxis cinnamomeus* does not seem to prevent *T. naevia* parasitism (Murcia *et al*. 2020), a resistant nest with a narrow tunnel may prevent the chick from leaving, thus acting as an essential weapon against parasitism, particularly the super-resistant nests of *C. cinnamomeus* constructed almost 100% of metallic materials (Schirch 1929, Roda & Carlos 2003, Pereira 2011, Chaves *et al*. 2013). We believe it is very difficult for a nestling of *T. naevia* to enlarge or destroy parts of these nests to exit.

Two other observations of note came to light as a result of our review, involving behaviour previously unreported in the literature. In several species of Cuculidae, males present females with food during courtship and copulation (Tubelis & Sazima 2021). An image on WikiAves (WA 4692496) shows one bird, possibly the male, with an insect in its bill, while another nearby is submissive, possibly presaging copulation. If proven, this would be the first case of such behaviour in the subfamily Taperinae (Tubelis & Sazima 2021). The second is a video from São Paulo by A. Gomes of a newly emerged nestling of *T. naevia* being fed by *Certhiaxis cinnamomeus*, which was vocalising very differently from adult *Tapera*, but instead much like its hosts (ML 300508871). This appears to be a typical case of vocal mimicry (*sensu* Dalziell *et al*. 2015) by young *T. naevia*. Mimicry of eggs, whereby they are difficult to differentiate from eggs of their hosts, in size, shape or colour (Dainson *et al*. 2018, Ballarini *et al*. 2022), is thus perhaps not the only strategy used by *T. naevia* to ‘deceive’ its hosts (see review in Dalziell *et al*. 2015). As this is unknown behaviour for the species, it would be interesting to study whether young learn their vocalisations and therefore adapt to the host, or are intrinsic to specific populations. In Pavonine Cuckoo *Dromococcyx pavoninus*, possible mimicry of a host’s nestling plumage (Sepia-capped

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Figure 45. Adult Squirrel Cuckoo *Piaya cayana* bringing a *Pithecopus nordestinus* to feed its nestling, Quebrangulo, Alagoas, Brazil, January 2023 (NORDESTA collection)

Flycatcher *Leptopogon amaurocephalus*) has been observed (Sánchez-Martínez *et al*. 2017). There is still much to be discovered about parasitism by *Tapera* and *Dromococcyx*, the only Cuculidae obligate brood parasites in the Americas.

SQUIRREL CUCKOO *Piaya cayana*

Our observations of this species, describing 16 nests found during 1987–2017 in the states of Minas Gerais and Alagoas, including data on eggs, nestlings, nest, incubation, feeding, seasonality and nest success, have already been published (Studer & Barcena-Goyena 2018); novel information on the white markings inside the nestling's mouth and their unusual behaviour before they can fly were also discussed. Here, we report new observations on a further nest found on 28 December 2022 at Quebrangulo, Alagoas.

This nest was 3.5 m above ground in an old *Vochysia dardanoi* (Vochysiaceae), an endangered tree commonly known as uruçuca, entirely covered by vines, within which the nest was concealed. The external nest materials were smooth, dry sticks and *Usnea angulata* (Parmeliaceae), and the lining comprised narrower, smooth, dry sticks, dry and green leaves of various trees, and some *Usnea angulata* and leaf ribs. The nest was the 'low cup/base' type with external diameter 18 cm, internal diameter 15 cm, external height 13 cm and internal height 5 cm.

Two eggs were laid and measured: 34.2 × 23.6 mm, mass 9.2 g, and 33.8 × 24.4 mm, 9.0 g. We could not determine the incubation period. At ten days old, one nestling emerged and concealed itself in a cypress tree adjacent to the nest; the second left the nest for the same place next day. Thirteen days after hatching, the nestlings could no longer be found near the nest.

On 13 January 2023, we observed the two ten-day-old chicks between 07.00 and 10.00 h. At 07.25 h, an adult arrived with a whole tree-frog *Pithecopus nordestinus* (Fig. 45), which is

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a quite common species. It was presented to one of the nestlings which failed to swallow it. The adult then offered the frog to the other chick, which did swallow it. At 07.35 h, a second adult gave a short call before arriving at the nest with a headless green tree-frog, probably *Boana albomarginata*. The first adult departed and the new arrival presented the tree-frog to one of the nestlings, which swallowed it in *c*.20 seconds. The adult then squatted down beside the young, perhaps because it was raining slightly. After 30 minutes, at 08.05 h, the adult left, and at 08.15 h one adult returned with a very hairy green caterpillar with brown/white spots on the body-sides, which could not be identified. One of the chicks swallowed it whole. At 08.25 h, the other adult reappeared with a large unidentified moth, then brooded the chicks still in light rain. At 09.00 h, both adults arrived with the same species of tree frog, *Scinax* cf. *eurydice*, which were fed alternately to the chicks. One adult then left, while the other remained in the nest until we left at 10.00 h.

Acknowledgements

We thank Luis Batista de Freitas, Felino Pedro Celestino, Flávio dos Santos Pereira, José Maria Andrade, Sergio Ferreira Freitas and Ronaldo Raimundo for their support in the field. We are grateful to NORDESTA Reforestation & Education for research grants and subsistence allowances. Carlos Gussoni, Dárius Tubelis, Yara Ballarini, and Wanieulli Pascoal assisted with some references, and Vítor Piacentini shared his observations of *Uropelia*. Anibal Melgarejo (in memoriam), Robson Figueiredo and André Luiz G. de Carvalho helped identify the *Tropidurus* and *Chironius*, and Larry Noblick, Fred Stauffer and Louis Nusbaumer assisted with plant identifications. We are grateful to Gwyneth Stoudmann for translating the manuscript into English and to Guy Kirwan and the anonymous reviewers for the many suggestions that greatly improved the quality of this manuscript.

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Kenyan records of an unnamed *Riparia* martin first discovered in the highlands of Ethiopia

by James E. Bradley & Victor J. Ikawa

Received 10 May 2023; revised 24 July 2023; published 4 December 2023

http://zoobank.org/urn:lsid:zoobank.org:pub:C3A42BD1-A157-45C9-AFD7-817A1F3B081A

Summary.—We provide field notes, photographic and audio documentation of an unidentified *Riparia* martin from high elevation on Mount Elgon, in western Kenya. We show that the birds differ in appearance and vocalisations from the otherwise similar, sympatric Plain Martin *R. paludicola ducis*, and that it appears to represent the same taxon as the unidentified martin recently documented in the highlands of Ethiopia.

Between 2013 and 2019, Gedeon & Töpfer (2021) observed a small *Riparia* martin nesting at high elevations in Ethiopia which they were unable to identify. The birds most closely resembled Plain Martin *R. paludicola* but differed in several ways, including the more extensively white underparts and distinctly grey-washed upperparts, as well as in their vocalisations. Documenting their observations, the authors noted sympatry with Plain Martin while maintaining reproductive isolation, and proposed that the birds comprised a distinct but unnamed taxon.

On 18 March 2023, with no prior knowledge of the observations in Ethiopia, we observed a colony of martins (hereafter 'Elgon martin') at 3,100 m on the east slopes of Mount Elgon, west Kenya (01°4′11″N, 34°40′16″E), which resembled Plain Martin but with several key characters at odds with that species, including different vocalisations. Additional observations and photographs, including of a small flock foraging over moorlands at 3,400 m, were obtained on 1 April 2023 by VJI, confirming the field marks distinguishing them from Plain Martin.

Collectively, our field notes and media suggest strongly that the Elgon martin is conspecific with the unidentified *Riparia* documented by Gedeon & Töpfer (2021) in highland Ethiopia. Here we detail our observations of this apparently unnamed taxon in Kenya. Our audio recordings were made using a Roland R-05 digital recorder and ME-66 Sennheiser microphone in calm conditions. They were reviewed using Syrinx software (Burt 2006) and archived in the Macaulay Library under catalogue numbers with the prefix 'ML', while comparative audio material (see Fig. 3) was also sourced there. Additional recordings of the Elgon martins not shown in Fig. 3 are archived under the catalogue numbers ML 550233001, ML 551881281, ML 551881311 and ML 551881321.

Colony characteristics

The Elgon martins were found prospecting / nesting in the exposed earth of a vertical roadside bank in subalpine habitat typical of the region, with vegetation in the environs comprising a mosaic of grass (*Festuca*, *Agrostis*, *Themeda* and *Cymbopogon* spp.) and shrub (*Erica*, *Protea* and *Calluna* spp.) cover, with pockets of stunted trees. We estimated there to be no more than a dozen martins present among a small group of Black Saw-wings *Psalidoprocne pristoptera*, which may also have been nesting in the bank. The bank supporting the colony extended *c.*120 m along a straight section of road and was nowhere more than 2 m in height (Fig. 1). The colony was confined to an area spanning no more than 8–10 m in

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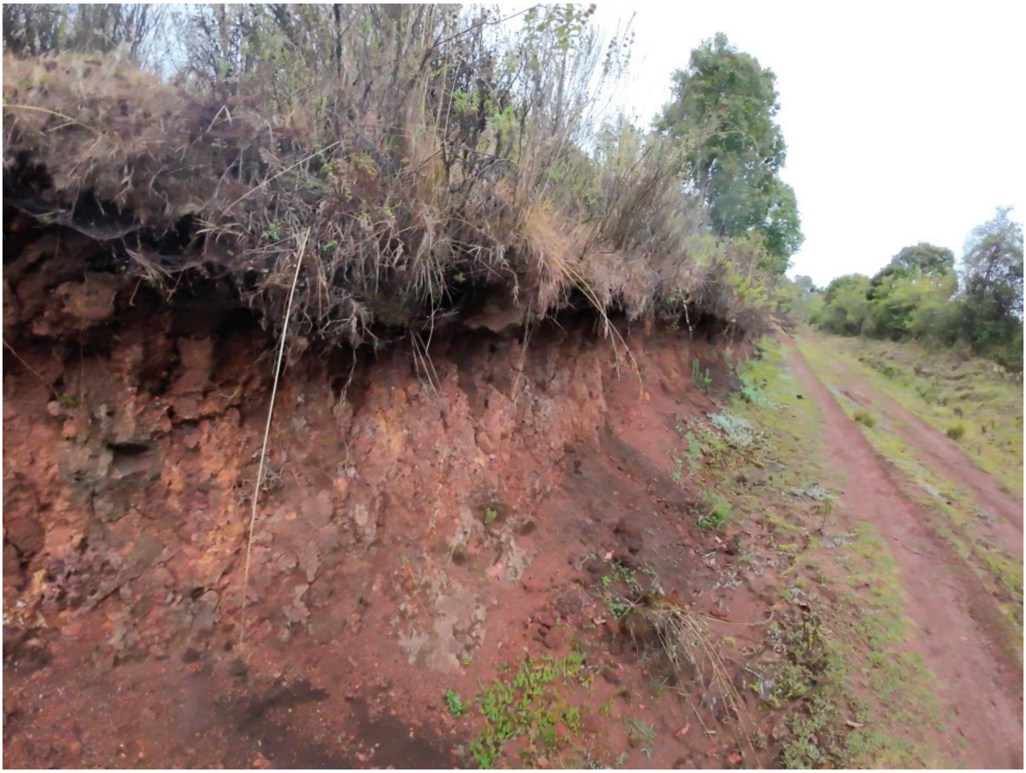

Figure 1. Roadside bank supporting a nesting colony of the unknown martin *Riparia* sp. (and possibly Black Saw-wings *Psalidoprocne pristoptera*) at 3,100 m on Mount Elgon, western Kenya, 1 April 2021 (Victor J. Ikawa)

the central section of the exposed bank, and the burrows were partly concealed beneath an overhanging cover of grasses and forbs.

Field characters

We mostly observed the martins in flight around the colony, although they visited the burrows occasionally, or perched briefly in the dead tops of small trees on the opposite side of the road. They were always in company of Black Saw-wings and were intermittently present around the colony for short periods (up to *c*.15 minutes), sometimes disappearing for as long as 40 minutes.

Our initial views were of a small martin lacking white tail spots and which most closely resembled Plain Martin. The lower underparts, however, appeared particularly bright white, becoming pale, dirty greyish white on the flanks, breast and throat, which parts are warm brown in Plain Martin (Zimmerman *et al*. 1996). The upperparts were grey-brown, palest on the uppertail-coverts (Fig. 2) and much colder-toned than the warm brown upperparts of Plain Martin. More prolonged views revealed what appeared to be rather blackish underwing-coverts contrasting strongly with paler flight feathers, and, in bright light, a faint buff tone and faint dark streaks on the throat and breast.

An additional feature evident in the images included an extension of the pale tones on the throat and breast to the ear-coverts, making the bird appear pale-cheeked. This accentuated the dark lores and crown, giving the birds a contrastingly masked and capped appearance at some angles. In Plain Martins we have observed previously, the ear-coverts

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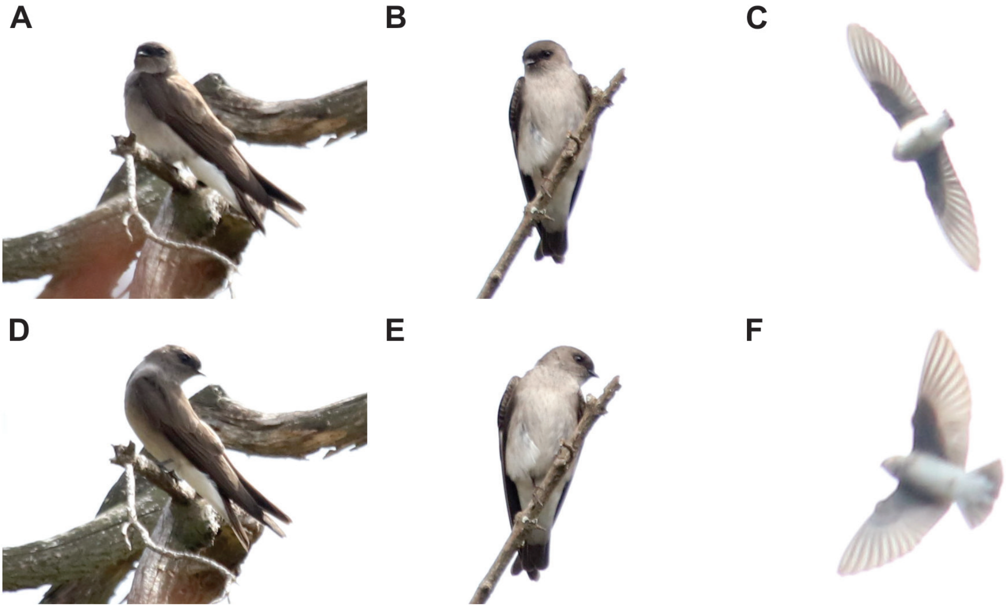

Figure 2. Elgon martins *Riparia* sp. in lateral (A, D), frontal (B, E) and in-flight views (C, F), showing extensively white underparts, pale grey cheeks and cold-toned grey-brown upperparts; Mount Elgon, western Kenya, 18 March and 1 April 2023 (Victor J. Ikawa)

are a warm brown like the throat and breast, and do not contrast markedly with the lores and crown.

Audio recordings

The main call of the Elgon martins, heard while we stood near the colony, was unfamiliar to us: a short, chittering trill with a swift-like (*Apus* sp.) quality, which we interpreted as an alarm call (Fig. 3A). It was wholly unlike the sharp, single-note alarm call of Plain Martin when disturbed at a colony (Fig. 3B). Other calls made by the Elgon martins included short whistled one- and three-part strophes given in flight (Fig. 3D–E), which too were unlike the typical 'purring / churring' flight calls of Plain Martin with which we were familiar. Lastly, a short nasal song phrase terminated by a soft click (or double-click; Fig. 3F) was made by the Elgon martins while perched, and has no known analogous vocalisation in the repertoire of Plain Martin.

Discussion

On reviewing the images and sonograms of the unidentified martins from Ethiopia in Gedeon & Töpfer (2021), it immediately was clear that the Elgon martins are likely to be conspecific with that taxon. They differ from the sympatric Plain Martin subspecies *R. p. ducis*, but are consistent with the Ethiopian birds in appearance and voice. Plumage features shared with the latter include the extensively white underparts (the lower underparts being especially bright) and pale dirty buff throat and breast without brown tones, combined with pale ear-coverts and absence of warm brown coloration on the upperparts. The pale cheeks provide a clear and distinctive field mark distinguishing the Elgon martins from Plain Martin, which has brown cheeks, lacking strong contrast with the crown and lores (Zimmerman *et al*. 1996, Stevenson & Fanshawe 2020). It should be noted that the martins

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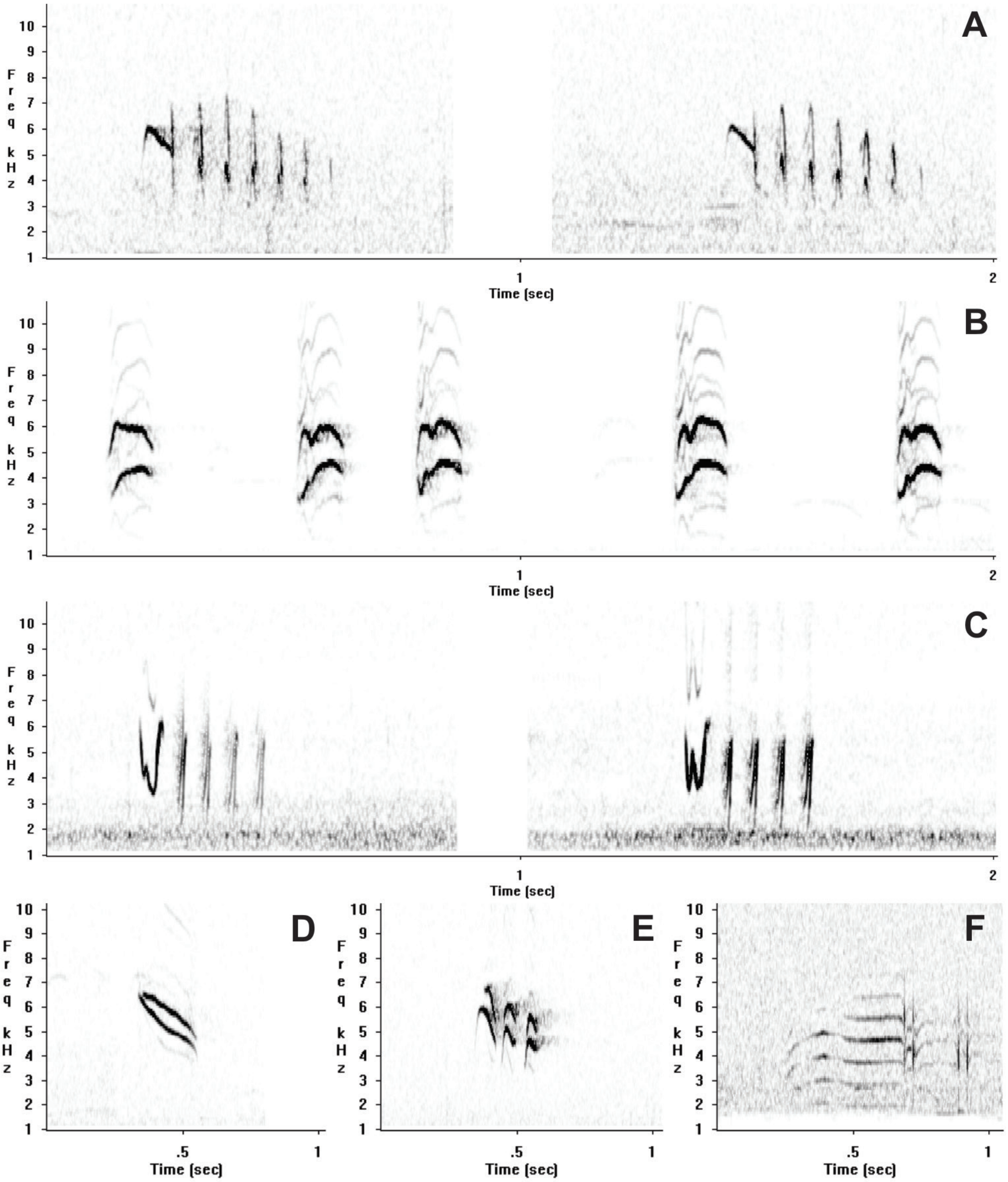

Figure 3. Alarm (trill) calls of the Elgon martins *Riparia* sp. (A: ML 549606191; James E. Bradley) compared to alarm calls of Plain Martin *Riparia paludicola ducis* (B: ML 549607811; James E. Bradley) and Grey-throated Martin *R. chinensis* (C: ML 224442131 and ML 224442041; © S. Toner; see Discussion), with additional flight calls and nasal song phrase of the Elgon martins (D: ML 551881311, E: ML 551881331 and F: ML 551881291; James E. Bradley).

observed in Ethiopia by Gedeon & Töpfer (2021) were compared with *R. p. schoensis*, the local subspecies of Plain Martin in the Ethiopian highlands (Ash & Atkins 2009). While it differs from *R. p. ducis* in Kenya by averaging paler overall (Keith *et al*. 1992), this is trivial compared to the differences between the unidentified Elgon (and Ethiopian) martins and either *R. p. schoensis* or *ducis*.

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In addition, the trill alarm call of the Elgon martins is unlike that of Plain Martin, but is indistinguishable from the 'trill call' documented for the unidentified martins in Ethiopia (Gedeon & Töpfer 2021). The same is true for both the three-part strophe given in flight (Fig. 3E) and the nasal song of the Elgon martins (Fig. 3F), which are consistent with vocalisations made by the birds in Ethiopia referred to as the 'call' and 'squeak call', respectively (Gedeon & Töpfer 2021).

Our observations are fully consistent with those of Gedeon & Töpfer (2021) and we concur that these *Riparia* cannot be referred to Plain Martin. Furthermore, they are sufficiently different from that species to likely involve an undescribed taxon. To our knowledge, there are no known *Riparia* taxa in East Africa, or indeed sub-Saharan Africa, that show the same combination of phenotypic and vocal characters.

Outside the African region, however, there are some similarities between Grey-throated Martin *R. chinensis* of South-East Asia and the Elgon (and Ethiopian) martins. First, a close structural similarity in alarm calls (Fig. 2A, 2C) suggests some affinity, specifically a sharp introductory note blending into a short chittering trill. Second, Grey-throated Martin is described as having an off-white to buff chin / throat (del Hoyo *et al*. 2020) as well as a lack of contrast between the throat and ear-coverts (Brazil 2009), both features that align well with the Elgon (and Ethiopian) martins. While the similarity in alarm calls suggests the undescribed *Riparia* may be more closely related to *R. chinensis* than *R. paludicola*, the main vocalisation of Grey-throated Martin (e.g., ML 531856161) differs noticeably from any vocalisation of the Elgon / Ethiopian martins, ruling out the possibility of conspecificity.

Acknowledgements

Don Turner drew our attention to Gedeon & Töpfer (2021). The Macaulay Library and Sarah Toner made available audio recordings of Grey-throated Martin. We are also grateful for very helpful comments provided by two referees.

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ISSN-2513-9894 (Online)

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What is John Latham's Rose-fronted Parrot?

by John-James Wilson, Clemency Fisher, Tereza Senfeld & J. Martin Collinson

Received 10 May 2023; revised 14 August 2023; published 4 December 2023

http://zoobank.org/urn:lsid:zoobank.org:pub:D7E36DAE-7029-4A47-8EEB-703D4F7BF233

Summary.—In 1822, John Latham gave the name Rose-fronted Parrot to a single specimen owned by Edward Smith Stanley. This specimen, now at World Museum, Liverpool, has never been given a formal scientific name but had been thought to be an undescribed, possibly extinct species, or an unusual young individual of the genus *Psittacula*. Based on a short mitochondrial DNA sequence obtained from the specimen that has 100% similarity with sequences on NCBI GenBank, we conclude that the most plausible identity of the Rose-fronted Parrot is a juvenile Plum-headed Parakeet *Psittacula cyanocephala*.

John Latham was England's leading recorder of 'new' bird species at the dawn of the 19th century (Jackson *et al*. 2013). Between 1781 and 1802, Latham published *A general synopsis of birds* in three volumes and supplements. This was followed by *A general history of birds* in ten volumes and an index between 1821 and 1828 (Jackson *et al*. 2013).

The Rose-fronted Parrot was included in *A general history of birds* (Latham 1822: 186) based on a single specimen owned by Edward Smith Stanley (the 13th Earl of Derby from 1834), but the putative species was not given a scientific binomial. Stanley annotated his personal copy of *A general history of birds* with: 'Query, if this bird may not in reality be the young of some of the long-tailed species, rather than completely distinct. Yet I do not remember to have seen any of those which had acquired the whitish tips to the two middle feathers of the tail, in the earlier stage of life' (Forbes & Robinson 1898: 18).

In the multi-volume register of the 13th Earl of Derby's collections, compiled by his curators Louis Fraser and Thomas Moore in the late 1840s (now at National Museums Liverpool; Largen 1987, Fisher 2002), Rose-fronted Parrot is entry number '765' with the locality 'East Indies'. Nothing else appears to be known about the specimen's provenance. It was bequeathed to the people of Liverpool on the Earl of Derby's death in 1851, along with most of his substantial natural history collections founding what became the Derby Museum, Liverpool Museums (Morgan 1978) and latterly World Museum, National Museums Liverpool. Salvadori (1891: 606) listed Rose-fronted Parrot under 'doubtful species' in an appendix to his catalogue of parrots in the British Museum noting that it was 'probably a young bird'. Henry Ogg Forbes and Herbert Christopher Robinson, the Director of the Liverpool Museums and his assistant respectively, published a catalogue of parrots in the Derby Museum in 1898, which included 'Rose-fronted Parrot Latham' still scientifically 'unidentified', with notes that the skin was 'much damaged' and 'a portion of the back is wanting'. The specimen was not included by Wagstaffe (1978) in his catalogue of avian type specimens in the Liverpool collection.

The specimen (now NML-VZ D765; Fig. 1) received little further attention until the early 1990s when CF and Michael Walters compared the specimen morphologically with the comprehensive collections of *Psittacula sensu lato* at the Natural History Museum, Tring. They were unable to identify the specimen as any known species, speculating it might be an undescribed, extinct species (see Hume & Walters 2012) closely related to Plum-headed Parakeet *P. cyanocephala*, Slaty-headed Parakeet *P. himalayana*, or Intermediate Parakeet

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Figure 1. Specimen in World Museum, Liverpool, used by John Latham for his description of Rose-fronted Parrot (NML-VZ D765) (John-James Wilson)

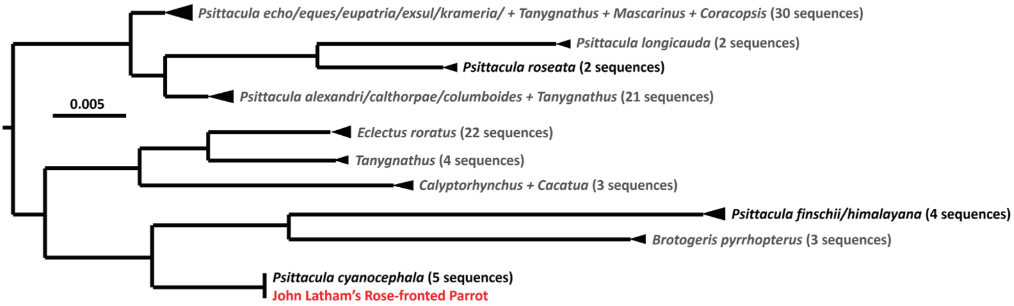

Figure 2. Sub-tree (of a larger tree produced by Neighbor Joining) showing the four putatively closely related *Psittacula* species (Blossom-headed Parakeet *P. roseata*, Grey-headed Parakeet *P. finschii*, Slaty-headed Parakeet *P. himalayana*, Plum-headed Parakeet *P. cyanocephala*) mtDNA cytochrome b sequences in NCBI GenBank aligned by BLAST with the 121 bp sequence obtained from John Latham's Rose-fronted Parrot (NML-VZ D765).

P. intermedia, which is now known to be a hybrid of the other two (Rasmussen & Collar 1999). This theory was retained by Hume (2017) who thought the specimen more likely to be an adult female than a young bird. Other species in this group are Grey-headed Parakeet *P. finschii* (often considered part of a superspecies with *P. himalayana*) and Blossom-headed Parakeet *P. roseata* (often treated as a superspecies with *P. cyanocephala*) (Rasmussen & Collar 1999).

Several full and partial mitochondrial DNA sequences for *Psittacula sensu lato* are now available on NCBI GenBank (Sayers *et al*. 2021), including *P. cyanocephala*, *P. himalayana* and *P. roseata* (e.g., from Groombridge *et al*. 2004, Braun *et al*. 2019, Dey *et al*. 2021). To establish the identity of the Rose-fronted Parrot we designed and trialled new pairs of primers (registered in the BOLD Systems Primer Database, www.boldsystems.org; Ratnasingham & Hebert 2007) specifically for the *Psittacula* mtDNA cytochrome b gene. By using a mtDNA gene, which are more abundant in cells, we maximised the chance of PCR amplification success from the >200-year-old specimen, but due to the uniparental inheritance of mtDNA could not preclude the possibility of hybridisation and introgression obscuring analyses.

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Figure 3. Ventral and dorsal views of juvenile specimens (from bottom) of Slaty-headed Parakeet *Psittacula himalayana* (NML-VZ D662b), Latham's Rose-fronted Parrot (NML-VZ D765) and Plum-headed Parakeet *Psittacula cyanocephala* (NML-VZ T2889 and NML-VZ T2890bis) (John-James Wilson)

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The primers were designed manually against sequences of *Psittacula* obtained from NCBI GenBank. A first PCR of 35 cycles was performed at annealing temperature 55°C using primers *Psit F2* and *Psit R2* producing a product of 170 bp. Two microlitres of the PCR product was used as a template for a second PCR of 35 cycles at annealing temperature 55°C with primers *Psit F1* and *Psit R2*. A 121 bp fragment was sequenced. Our molecular methods otherwise followed those of Senfeld *et al*. (2019). Sequences <200 bp are not accessioned by NCBI GenBank, but the sequence is publicly available on BOLD Systems under Process ID NMLVZ002-23.

The Rose-fronted Parrot sequence was compared to archived sequences of birds of known identity using NCBI BLAST (https://blast.ncbi.nlm.nih.gov/Blast.cgi) and possessed 100% similarity with five sequences of *P. cyanocephala* (KJ456434.1, NC_054153.1, GQ996508.1, GQ996501.1, AY220109.1). The next two most similar sequences (97.52%) were from Eclectus Parrot *Eclectus roratus* (KM372510.1, MG429727.1) (Fig. 2).

Using Juniper & Parr (1998) we compared the plumage features of the Rose-fronted Parrot with two juvenile *P. cyanocephala* (NML-VZ T2889, NML-VZ T2890bis) collected by George Frederick Leycester Marshall, and a single juvenile *P. himalayana* (NML-VZ D662b), held at World Museum, Liverpool (Fig. 3). The features are consistent with the specimen being a juvenile *P. cyanocephala*. The head is green tinged grey (Juniper & Parr 1998) although there is considerable variation in the brightness of the green in other specimens. The tail matches the length and plumage of the *P. cyanocephala* specimens, but not the larger *P. himalayana*, with the uppertail being bright blue and the tip white (see Rasmussen & Collar 1999).

We conclude that the most plausible identity of the Rose-fronted Parrot is a juvenile *P. cyanocephala*, which species has recently been moved to the genus *Himalayapsitta* (Braun *et al*. 2019) although this proposal has yet to receive widespread support.

Acknowledgements

We are grateful to two reviewers whose comments substantially improved the submitted manuscript.

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A nesting aggregation of Blue-fronted Lancebill *Doryfera johannae*, with additional remarks on a cave nest of the species

by Guy M. Kirwan & Douglas G. D. Russell

Received 6 June 2023; revised 2 September 2023; published 4 December 2023

http://zoobank.org/urn:lsid:zoobank.org:pub:71B3E6D0-7EAE-4D44-957D-745EE63135EF

Summary.—We report an unusual nesting aggregation of the poorly known Blue-fronted Lancebill *Doryfera johannae*, a trochilid that is thinly and disjunctly distributed in the Andes and Pantepui. The nests were clustered on wooden, man-made structures and were at different stages of the breeding cycle. Photos on publicly accessible databases provided evidence that the species' habit of nesting on buildings is geographically widespread. One nest of *D. johannae* described in the literature was sited at the base of deep shaft into an underground cave system; we report additional details associated with this nest. Nesting aggregations are apparently rare in the family Trochilidae and cave-nesting is evidently limited to a comparatively small number of species, despite essentially obligate colonial breeding in permanently dark sites, especially caves, by members of the closely related family Apodidae.

The hummingbird genus *Doryfera* Gould, 1847, comprises two species (Dickinson & Remsen 2013). Green-fronted Lancebill *D. ludovicae* is distributed from northern Costa Rica through Panama, and in the Andes from western Venezuela to north-west Bolivia. Blue-fronted Lancebill *D. johannae* is also primarily Andean, occurring from central Colombia to central Peru, with a separate population in the Pantepui of southern Venezuela, northernmost Brazil and western Guyana. Of the two species, the breeding biology of Green-fronted Lancebill is far better known, especially following the detailed study by Greeney *et al*. (2006). Both species are essentially solitary, although pairs are occasionally observed (Snow & Gochfeld 1977, Hilty & Brown 1986; GMK pers. obs.).

For *D. johannae*, the few published nesting data (Stiles & Kirwan 2018) are as follows. In south-eastern Ecuador, a nest in a cave shaft with a single egg (size 15 × 10 mm) was found in mid-July 1976 (Snow & Gochfeld 1977); this nest was suspended from a rock overhang in a cave and was a cylindrical structure of moss and cobwebs, with the cup in the top. It measured 110 mm top to bottom, with an internal diameter of 30 mm and internal depth of 29 mm. The egg was described as unincubated but was subsequently broken and not preserved, unlike the nest, which is in the Natural History Museum, Tring (NHMUK N/1978.1.2). Grantsau (1988: 22) reported additional egg data, mass 0.5 g, size 9.2 × 15.0 mm, but their provenance is unknown (perhaps his own, otherwise unpublished, data); he repeated Ruschi (1974) as the source for nest measurements of 60 mm top to bottom, with external diameter of 70 mm and internal diameter of 30 mm. A short video (Macaulay Library; www.macaulaylibrary.org, ML 201629101) of another nest that held two nestlings in early December 2014 at Río Bigal Biological Reserve in north-east Ecuador, discovered by H. Jacob, was referenced by Stiles & Kirwan (2018). Elsewhere, in central Colombia, a female with enlarged follicles was collected in September (Stiles 1999). Here, we report some additional breeding data for the species including an apparently unusual aggregation of

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active nests, which provides evidence also that *Doryfera* can accept man-made situations in which to breed, together with additional information concerning the remarkable 1976 nest.

Observations of Río Bigal nests

The following observations were made by GMK during 3–9 November 2017, at Río Bigal Biological Reserve (00°32′13.1″S, 77°25′28.5″W) on the south-east edge of Sumaco Napo Galeras National Park, Orellana province, eastern Ecuador, at *c*.950 m. All of the nests reported below were within the confines of, or in very close proximity to, the reserve 'headquarters', an open-sided, two-storeyed, principally wooded construction that is in virtually continual human use throughout the day (and night). One nest (nest 1) was attached to the underside of a wooden chalet on struts, *c*.2 m above ground, less than 10 m from the part of the main building in which the other nests were sited. Two of the other nests (2 and 3) were attached to the ceiling of the ground storey of this building, and within *c*.3 m and clear sight of each other; a fourth nest (nest 4) was sited under the ceiling of the upper storey and again within approximately 3 m of those on the ground storey, but obviously not in sight of the others. The remains of three older nests in various states of decay were also discovered on the upper storey of the main building, one of them sited on the underside of a wooden table, at one of its corners, less than 100 cm above floor level. Each active nest was constructed entirely of dry mosses, liverworts and spider webs, with no apparent lining. Their overall colour was generally brown but variable quantities of fresh green material was incorporated into all four of the nests, as described below. They were attached to the wooden substrate with a strong lip consisting of an obvious mat of spider webs. Nests were measured using dial callipers and are listed in order of discovery. There is some evidence from these measurements of the phenomenon reported by Greeney *et al*. (2006): 'dimensions show that nest cups were round early in incubation or before the onset of incubation, but that cups and nest cylinders stretched as incubation continued, and especially during the nestling period'. The length of the 'tail' below the nest, at 25.1–153.0 mm (mean 87.9 mm), was somewhat longer than that, 40–80 mm, observed in nests of *D. ludovicae* examined by Greeney *et al*. (2006). To minimise disturbance, GMK did not attempt a very close examination of the contents of any of the nests.

Nest 1.—outside breadth 127.5 mm, outside depth 89.0 mm, inside diameter 42.9 × 55.0 mm, entrance lip diameter 25.5 mm and height 14.9 mm, extraneous material below nest 86.7 mm, distance between roof and top of nest 24.0 mm, and length of attachment of spiders' web 37.5 mm. This nest contained two nestlings (Fig. 1A) which, based on comparison with the data presented by Greeney *et al*. (2006) for *D. ludovicae*, were probably *c*.10 days old; they were largely dark with well-developed charcoal blackish-looking pin feathers over the entire body including the wings and tail, although some pinkish skin was still visible in places on the dorsal surface, and the bill was somewhat pinkish black on the maxilla, still yellow-orange over most of the mandible, with paler yellow gape flanges.

Nest 2.—outside breadth 85.7 mm, outside depth 93.8 mm, inside diameter 50.6 × 47.4 mm, entrance lip diameter 25.4 mm and height 18.3 mm, extraneous material below nest 86.9 mm, distance between roof and top of nest 20.4 mm, and length of attachment of spiders' web 34.9 mm. Sited *c*.2.5 m above ground level, this nest contained two all-white and well-incubated eggs (Fig. 1B).

Nest 3.—outside breadth 122.6 mm, outside depth 111.3 mm, inside diameter 29.5 × 51.0 mm, entrance lip diameter 24.5 mm and height 30.2 mm, extraneous material below nest 25.1 mm, distance between roof and top of nest 10.5 mm, and length of attachment of spiders' web 34.9 mm. Sited *c*.2.5 m above ground level, empty (Fig. 1C) but apparently ready for eggs, as it (like all of the nests) was being regularly visited by a female.

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Figure 1. Four active nests of Blue-fronted Lancebill *Doryfera johannae* found at Río Bigal Biological Reserve, Orellana province, eastern Ecuador, November 2017: A (nest 1, with two nestlings); B (nest 2, with two well-incubated eggs); C (nest 3, empty but apparently ready for eggs; see text); and D (nest 4, with one very recently hatched chick) (Guy M. Kirwan)

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Nest 4.—outside breadth 82.4 mm, outside depth 60.7 mm, inside diameter 42.9 × 37.5 mm, entrance lip diameter 22.2 mm and height 17.8 mm, extraneous material below nest 153.0 mm, distance between roof and top of nest 23.6 mm, and length of attachment of spiders' web 52.0 mm. Contents: one very recently hatched chick, presumably less than 24 hours old, with the eggshell remnants still beside it (Fig. 1D). The chick's appearance was very similar to that of <3-day-old young of *D. ludovicae* depicted by Greeney *et al*. (2006: fig. 3): entirely naked with largely pink skin, but dark grey at the front of the head, over the forecrown and face, and on the upper back, with a blunt-tipped pale to medium yellow bill. For *D. ludovicae*, Greeney *et al*. (2006) noted that the dorsal surface of nestlings darkened considerably within 48 hours after hatching.

In addition to the video by H. Jacob mentioned above, the following previously unpublished data are now available based on material archived at Macaulay Library: two nests constructed in close proximity of which only one appeared active (with an adult perched on the rim, perhaps feeding young) under a rock overhang at Cascada Hollín, Loreto road, Napo province, Ecuador, in late December 2010 (P. Smith, ML 255461721); adult female feeding a fledged juvenile, from a nest sited 'underneath the house' at Reserva La Isla Escondida, Putumayo, Colombia, February 2017 (J. Beckers, ML 265577041 and ML 265577081); female on a nest (stage unknown, but constructed 1 m above ground on an abandoned house) at Cerro Chiviaza, Morona-Santiago province, Ecuador, early September 2019 (J. Brito, ML 175870381); nest (stage unknown) at Puente Quita Calzones, Cuzco, Peru, in late September 2021 (D. Thomas, ML 384867521); female on a nest (stage unknown) at WildSumaco Lodge, Napo province, Ecuador, late July 2022 (N. Hayward, ML 471598241 and ML 471591051); and female nestbuilding (nest appears largely complete) at Restaurante La Cumbre, Pasco, Peru, early September 2022 (T. Aronson, ML 481601191 and ML 481601201). No detailed notes are available on any of these nests, but the structure, materials, attachment, and substrate of those in September 2019 and 2021, July 2022, and September 2022 appear very similar to the nests found at Río Bigal. Only the nests in December 2010 and September 2021 were sited in natural localities, whereas the others were all on wooden buildings.

The Cueva de los Tayos nest

The 1976 British Cave Research Association Expedition was organised by the Scottish explorer Stan Hall (1936–2008) to investigate the Cueva de los Tayos (Cave of the Oilbirds [*Steatornis caripensis*]) on the east slope of the Andes, in Morona-Santiago province, south-east Ecuador. Until the Tham Luang cave rescue of Thailand in 2018 it was the most remarkable and expensive caving expedition in history. Motivated by the extraordinary claims in Erich von Däniken's *The gold of the gods* (1973), the 1976 expedition aimed principally to archaeologically investigate the cave system and research the gold sculptures, metal plaques, stone carvings and gold supposedly found by Däniken (b. 1935) and his colleague János Juan Móricz (1923–91) during their 1969 exploration of the caves. Whilst no evidence of treasure was found, the 70+ strong expedition personnel, notably including the astronaut Neil Armstrong, made several significant scientific discoveries, including the first known nest and egg of *Doryfera johannae* by James K. Campbell on 15 July 1977, evidently in close proximity to an active colony of *Steatornis caripensis* studied by Snow (1979). Snow & Gochfeld (1977) gave a detailed description and account of the hummingbird nest but, 46 years after it was collected, we obtained further information from surviving expedition members and their families.

Snow & Gochfeld (1977) described that the nest was 'collected by J. K. Campbell at the bottom of the 75 m shaft' and 'attached by a thick tab of cobweb to a slight rocky overhang

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Figure 2. The 'Paz de Luz Divina' entrance shaft to Cueva de los Tayos, Morona-Santiago province, south-east Ecuador, where the first nest of Blue-fronted Lancebill *Doryfera johannae* was collected (see Fig. 3) (© Eileen Hall)

1½m up from the bottom of the shaft'. We believe the shaft in question is that noted in Toulkeridis (2015) and christened by the expedition 'Paz de Luz Divina' (Peace of Divine Light). It is one of three shafts (two of them large) into the cave complex and is located *c*.4 km west of the town of Tena and 3 km south-east of San Pedro, at 01°00′3″S, 77°51′26″W; elevation 610 m. Eileen Hall (*in litt*. 2018), who also visited the cave system, estimated the shaft in question to be *c*.6–7 m wide at the entrance (see Fig. 2); Arthur Champion (*in litt*. 2018), another member of the expedition, reported that the shaft is only 50 m deep, with the difference being due to the way the winch and gantry were set up.

J. K. Campbell (*in litt*. 2018) provided the following description. 'The shaft was quite broad and quite a lot of light reached the bottom, which was covered in boulders and had a small amount of vegetation. I was near one of the walls when I noticed a strange-looking object above my head and wondered what it was. I never thought it might be a

Figure 3. Nest of Blue-fronted Lancebill *Doryfera johannae* collected at Cueva de los Tayos, Morona-Santiago province, south-east Ecuador, by J. K. Campbell in July 1976, held in the Natural History Museum, Tring (NHMUK N/1978.1.2) (Jonathon Jackson, © Trustees of the Natural History Museum, London)

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bird's nest—at the bottom of a deep shaft. I reached up and felt it and it just came away in my hand. I was rather distressed to find it *was* a bird's nest with some eggs (*sic*) in it and immediately tried to put it back in the same place, but it wasn't possible'. 'So, I took it out of the cave and showed it to Barbara Snow. I think she then descended the cave with me the next day and I showed her where it had been, and she was able to identify the bird when it returned looking for its nest'. Beginning ten days after the nest was collected, Snow observed a pair of *D. johannae* at the entrance to the same shaft and watched the female descend into it carrying nesting material on multiple occasions over several days (Snow & Gochfeld 1977). She also witnessed a third *Doryfera* (sex unknown) being chased away from the vicinity by the male, and stated that other expedition members reported seeing a dark hummingbird ('probably a lancebill') halfway down another of the cave's principal entrance shafts (60 m away). These additional data are interesting because they suggest a degree of territoriality or defence of the area around the nest in the species (at variance with the observations made at Río Bigal) and that nesting deep in the shaft of caves was not a one-off event.

Photos of the adults were taken at the time and have been supplied by James Campbell (confirming the species identification); the nest deposited at NHMUK is shown in Fig. 3. The distended ('pendent'), somewhat cylindrical appearance, particularly compared to those at Río Bigal, is potentially attributable to the Los Tayos nest having less basal support from the substrate, similar to the variation in shape and its causes that Greeney *et al*. (2006) noted in Green-fronted Lancebill.

Discussion

Our knowledge of the life history of Green-fronted Lancebill is considerably more detailed than the information available for Blue-fronted Lancebill (see summary in Stiles & Kirwan 2018). In Costa Rica, the first-named species breeds in the latter half of the wet season to the start of the dry, between August and January (Stiles & Skutch 1989), while in Colombia nesting has been recorded between July and late January (Hilty & Brown 1986, Ramírez González & Arias García 1994). Further south, a nest with eggs was found in Junín, eastern Peru in mid-September 1972 (Snow & Gochfeld 1977), with others discovered in north-west Ecuador in June–January (Greeney & Nunnery 2006). In eastern Ecuador, 36 nests were found between September 2001 and March 2002, with an obvious peak in (asynchronous) activity between mid-October and mid-December (Greeney *et al*. 2006), which is potentially mirrored by Blue-fronted Lancebill lower on the same slope of the Andes (GMK pers. obs.). The nest of Green-fronted Lancebill is constructed by the female over period of 12–16 days, and is a rather bulky cup of moss, tree-fern scales, fine fibres and cobwebs, placed in a dark, usually humid site, typically being attached to a hanging rootlet or vine under a rock overhang in a dark ravine or gorge (with the lower part often elongated to form a cylindrical structure) but can sometimes be attached to a wire under a bridge or roof, or less often be sited on a small ledge in a gorge or cave (Greeney *et al*. 2006). Green-fronted Lancebill frequently nests alongside streams, typically 0.8–6.0 m above ground; all of those found by Greeney *et al*. (2006) were in such situations. In comparison, the nests of *D. johannae* described herein were tens of metres from the nearest stream. The clutch in *D. ludovicae* is typically two white eggs, size 15.6–15.7 × 11.1 mm, in eastern Peru (Snow & Gochfeld 1977) or 14.1–15.7 × 9.1–10.0 mm, in eastern Ecuador (Greeney *et al*. 2006); incubation takes 19–21 days and the fledging period is 29–30 days (Greeney *et al*. 2006).

The nest found during the Los Tayos expedition appears quite unique among those described for Trochilidae (but not of course in the closely related Apodidae) in being sited very deep (either laterally or, especially, vertically) within a cave. In addition to Green-

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fronted Lancebill, Lopes *et al*. (2020) reported multiple nests of the recently described Dry-forest Sabrewing *Campylopterus calcirupicola* in limestone caves, one of which was up to 15 m inside, albeit the cave in question was described as having a large entrance which made its confines still rather light.

Colonial or pseudo-colonial nesting (with concurrently active nests, even if at different stages) seems rare in hummingbirds: in Peru, Carpenter (1976) found that multiple females of Andean Hillstar *Oreotrochilus estella* will nest semi-colonially in particularly suitable sites; Solano-Ugalde (2008) reported finding 11 nests, of which at least seven were active, of the closely related Ecuadorian Hillstar *O. chimborazo* under a concrete bridge in northern Ecuador, mirroring earlier observations of 'colonial nesting' by this species reported by Smith (1969); and for Cuban Emerald *Chlorostilbon ricordii* Regalado Ruiz (1998) found six nests, all with eggs, in very close proximity (some just 30 cm apart), in north-east Cuba. Clustering of nests has also been reported in Black-chinned Hummingbird *Archilochus alexandri* in south-east Arizona (Greeney & Wetherington 2009). In northern Chile, Estades *et al*. (2018) reported as many as 13–20 simultaneous nests of Chilean Woodstar *Eulidia yarrellii* during different breeding seasons (between 2006 and 2008) sited in a small (1.4-ha) olive grove, with multiple cases of nests in adjacent trees and five instances of two nests in the same tree, but inter-nest distances were not reported. In this case, it is clear that the habitat was unusually suitable for the species and its breeding, but also for the field workers to find nests, compared to the native vegetation surrounding the study site (Estades *et al*. 2018).

The novel data reported here suggest a degree of plasticity in the nesting ecology of *D. johannae*, e.g., willingness to accept man-made nest sites, echoing the detailed observations by Greeney *et al*. (2006) for *D. ludovicae*, but also those by Ramírez González & Arias García (1994). Given the number of nests of *D. johannae* sited on buildings reported via the online platform eBird in recent years, it appears that such acceptance may more easily enable studies of this still poorly known hummingbird in the future.

Acknowledgements

GMK is particularly grateful to Thierry Garcia for making his stay at Río Bigal Biological Reserve so hospitable. Neil Bostock and Andrew Marshall accompanied GMK in the field and enabled some of the observations reported here. We are indebted to surviving members of the 1976 Los Tayos Expedition including notably Philip Ashmole, James K. Campbell, Arthur Champion and John Whalley. Further information and images were also kindly provided by artist Eileen Hall (the daughter of Stan Hall). Fernando Medrano alerted us to the paper on Chilean Woodstar. We are grateful to our referees, Robert Bleiweiss, Harold Greeney and Karl Schuchmann, for their constructive comments on the submitted manuscript, and Chris Sharpe for steering the paper through the editorial process.

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First confirmed record of Arrowhead Piculet *Picumnus minutissimus* in French Guiana

by Paul Lenrumé

Received 15 June 2023; revised 8 August 2023; published 4 December 2023

http://zoobank.org/urn:lsid:zoobank.org:pub:C46EDCB1-755E-4A1C-9090-95F738B58A5D

Summary.—I report the first record of Arrowhead Piculet *Picumnus minutissimus* in French Guiana and the first to be documented away from Suriname of this species, which until now was considered endemic to the latter country. Although it seemed more likely the species would be found in degraded coastal habitats, similar to those in Suriname, the bird was in the interior forest block at a former gold mining site now characterised by shrubby vegetation corresponding to the species' ecological requirements. This is not only the easternmost record of the species but probably also the most southerly. I discuss the issue of the species' status in French Guiana: is it a rare breeder in under-surveyed western French Guiana, or is this piculet capable of dispersing across the forest block and the Maroni River?

On 16 September 2020, during a bird survey I photographed and sound-recorded an Arrowhead Piculet *Picumnus minutissimus*, possibly an adult female, along the Paul Isnard dirt road *c.*80 km south of Saint-Laurent-du-Maroni and 10 km north-west of the Citron gold mining camp in the interior of western French Guiana (*c.*04°46'N, 54°00'W). The area adjacent to the dirt road had been severely degraded by gold mining and is characterised by shrubby vegetation composed mainly of *Mimosa pigra*, *Senna multijuga* (both Fabaceae) and dense herbaceous plants, with areas that are both wet (due to the presence of old gold mining ponds) and dry with bare laterite. The area hosts an avifaunal assemblage characteristic of open and semi-open coastal habitats, comprising mostly generalist and common species, although a few that are rare in French Guiana like Brown Jacamar *Brachygalba lugubris* occur there.

At *c.*09.00 h, I heard a distant song resembling White-barred Piculet *Picumnus cirratus*, Arrowhead Piculet *P. minutissimus* or White-bellied Piculet *P. leucogaster*. All three have very similar songs and are basically inseparable by ear (B. J. O'Shea *in litt.* 2023). However, the latter two are not known to occur in French Guiana (CHG 2022), whilst White-barred Piculet is restricted to sandy woodland on the west coast between Sinnamary and Awala-Yalimapo (GEPOG 2022). In degraded habitats of the country's interior, only Golden-spangled Piculet *P. exilis*, whose song is very different, is frequently recorded. Thus, the probability that it was one of the two species unknown in French Guiana seemed as likely as a White-barred Piculet outside its habitat and known range. I broadcast the song of Arrowhead Piculet and the bird responded almost immediately by singing (https://www.xeno-canto.org/634915) before I saw it approaching the road *c.*2 m above ground. I could see the characteristic scaly breast and belly, and took photographs to document the record (Figs. 1–2). However, I quickly lost sight of the bird and, because the site is remote and difficult to access, no one was able to return to search for the species in the period following the observation.

The record was accepted by the French Guiana rarities committee (CHG 2022). As a result, French Guiana has 18 woodpecker species, three of them *Picumnus*. Arrowhead Piculet is distinguished from the others mainly by its scaly underparts and creamy apical spots dorsally. As mentioned, its song is very similar to those of White-bellied Piculet and

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Figures 1–2. Arrowhead Piculet *Picumnus minutissimus*, Paul Isnard road, 10 km north of Citron, French Guiana, 16 September 2020 (Paul Lenrumé)

Figure 3. Habitat of Arrowhead Piculet *Picumnus minutissimus*, Paul Isnard road, 10 km north of Citron, French Guiana, 16 September 2020 (Paul Lenrumé)

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White-barred Piculet, and there are few recordings of any of the three species on Xeno-canto (www.xeno-canto.org) or in Macaulay Library (www.macaulaylibrary.org).

Discussion

This unexpected record raises questions as to the species' status in French Guiana. Until now, it has been considered the only bird species endemic to Suriname (Remsen *et al*. 2021) as sightings in Guyana (B. J. O'Shea *in litt*. 2023) and French Guiana (Tostain *et al*. 1992) were undocumented and not confirmed. In Suriname, it is common on the coast, especially around Paramaribo where the species is the most abundant woodpecker (O. H. Ottema & B. J. O'Shea *in litt*. 2023). It frequents varied habitats including secondary woodland, mangroves, riparian forest, cultivated and degraded areas, and gardens (Ribot 2021).

My observation is remarkable for being the easternmost, and probably southernmost, record. Moreover, it was made in the interior forest block whereas Suriname records are mainly in the littoral. However, other species typical of open coastal habitats are not uncommon at mines in the interior of French Guiana. Relatively large tracts of interior forest have been cleared, and open to semi-open environments characterised by regrowth harbour many species not usually found in the forest block, such as Black-faced Tanager *Schistochlamys melanopis* (GEPOG 2022). Thus, the habitat in which the bird was observed is not as atypical as its location might suggest.

Two hypotheses could explain this isolated record. One cannot rule out that Arrowhead Piculet is a rare resident in western French Guiana. There are very few birdwatchers in this region, and the possibility of confusion with the scarce White-barred Piculet could mean it has gone unnoticed. Plainly, more records in the country will be needed to confirm this hypothesis. The notion of a bird wandering from Suriname is also credible as the species is common <200 km away (Ribot 2021). Nevertheless, woodpeckers are not generally known for their dispersal abilities and the Maroni River is likely to be a significant barrier for small species. However, many sections of the Maroni River contain numerous islets, reducing the distance of open water for birds to cross.

The possibility of hybridisation between these closely related species should not be overlooked (Winkler *et al*. 2020a,b) as the border region between Suriname and French Guiana is a potential contact zone. The individual I photographed, however, did not show any characters to cast doubt on its identity as a pure Arrowhead Piculet.

Acknowledgements

Thanks to Olivier Claessens for his comments; and to Brian O'Shea, Otte Ottema and Jan Hein Ribot for information they shared on piculets in Suriname and Guyana; the CHG, Biotope and GEPOG shared pertinent information; Emile Fonty commented on the habitat at the observation site; and, finally, comments by a referee and the editor improved the submitted manuscript.

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Speciation in the Karamoja Apalis *Apalis karamojae*

by Peter Boesman & N. J. Collar

Received 3 July 2023; revised 23 August 2023; published 4 December 2023
http://zoobank.org/urn:lsid:zoobank.org:pub:282FFF60-EA8E-43A6-BA67-078576C7198F

Summary.—The Karamoja Apalis *Apalis karamojae*, a threatened species (IUCN Vulnerable), consists of two subspecies, the nominate in Uganda and *stronachi* in Tanzania plus south-west Kenya, the latter distinguished by being slightly darker with more extensive grey on the underparts. Recent evidence, however, indicates that the two taxa are highly divergent in voice. Analysis of recordings of their duets confirms this: the nominate sings very rapid phrases of short simple notes whereas *stronachi* uses musical slurred whistles, very different in note length and strongly different in max. frequency; moreover, in two independent tests nominate birds failed to react to *stronachi* songs, indicating reproductive barriers between them. Re-examination of specimen material and a review of online photographs confirm the greater amount of grey on the underparts of *stronachi*. Taken together these differences indicate that *stronachi* merits species rank. The two taxa are specialists of mature whistling-thorn *Vachellia drepanolobium*, which is cut for fuelwood and to open up pasture, so that their long-term survival is likely to depend on the integrity of protected areas.

The Karamoja Apalis *Apalis karamojae* is a rather rare cisticoline warbler known from relatively few semi-arid localities in north-east Uganda (nominate subspecies), north-central Tanzania and adjacent south-west Kenya (subspecies *stronachi*), with an IUCN Red List status of Vulnerable (Ryan 2006, Shaw & Mungaya 2006, BirdLife International 2023). Research has progressively shown that the species' long-known association with whistling-thorn acacia *Vachellia drepanolobium* (Collar & Stuart 1985, Urban *et al*. 1997, Stevenson & Fanshawe 2002) reflects a strong dependency (Shaw & Mungaya 2006, Shaw *et al*. 2010, Salmah & Onongo 2023), and only its presence in patches of the similar *V. seyal* prevents this dependency from being total (P. Shaw *in litt*. 2023). Indeed, the birds' white wing line and outer rectrices appear to mimic the long white spines of whistling-thorn, whilst their grey upperparts blend well with the colour of the plant's galls (P. Shaw & B. W. Finch *in litt*. 2023), suggesting a highly specific adaptation in plumage. However, whistling-thorn is widespread in eastern Africa, across seven countries, so the question arises over what causes the bird to be so much more restricted in range than the plant (Shaw & Mungaya 2006). At one stage it was speculated that 'the very extensive clearing and cultivation in recent times round the shores of Lake Victoria' might be responsible for producing the 'extraordinary distribution' of the species' Ugandan and Tanzanian populations (Hall & Moreau 1962, Turner 1977), but this suggestion became less plausible once the Tanzanian birds were recognised as taxonomically distinct (Collar & Stuart 1985, Stuart & Collar 1985).

Against this, it has to be said that the characters that distinguish southern *stronachi* from the northern nominate are few in number and weak in strength, so that it could be argued that the differences involved might simply reflect a cline in which the intervening populations have been extirpated (plausibly due to habitat conversion, as suggested above). Stuart & Collar (1985) diagnosed *stronachi* as 'darker brownish-grey on the mantle, back, rump and uppertail-coverts', the male being 'mottled grey against a very pale creamy-

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white background' on the underparts, very pale grey on the throat but 'much darker on the breast and flanks and paler again on the belly', whereas the male nominate has 'creamy-white underparts' but grey flanks. Female *stronachi* has 'creamy-white underparts with a slight but variable suffusion of grey', the female nominate 'a white underside and only a slight creamy suffusion'. Males of both taxa are consistently darker than their counterpart females, such that *stronachi* females are only slightly darker than nominate males. (Somehow from this female *stronachi* emerged as 'paler than nominate' in Urban *et al*. 1997.) These distinctions were made using a tiny sample of specimens (one male, one female from Uganda, one male from Tanzania in the Natural History Museum, Tring, UK [NHMUK], one male from Uganda, three females from Tanzania in the National Museums of Kenya, Nairobi [NMK])—these being all the material available in museums except one from Uganda in the Field Museum of Natural History, Chicago (*fide* VertNet)—and must be subject to caveats about individual variation. Nevertheless, basic mensural data suggested that *stronachi* is a somewhat larger phenotype, which was supported by measurements of 17 live birds from Tanzania (Shaw *et al*. 2005).

For the entirety of the 20th century the voice of Karamoja Apalis remained undocumented (e.g. Urban *et al*. 1997). However, the pioneer of research into the species in Tanzania, Philip Shaw, established that the song there, atypically for an *Apalis*, consists of 'a series of musical, fluid phrases, each comprising 2–5 (commonly four) notes… [in] a rapid, well-synchronised, antiphonal duet… [at] 2.7–3.2 notes per second' (Shaw *et al*. 2005). He further found that 'most pairs (though not individuals) were highly responsive to taped songs, approaching closely from distances of 50 to 100 m, and singing persistently' (Shaw & Mungaya 2006). Indeed, it was by speculatively broadcasting the song in an area dominated by whistling-thorn near the Maasai Mara National Reserve that Shaw obtained the first record of the species for Kenya (Boy 2004, Shaw 2007). Consequently when in 2011 colleagues in Uganda sought to search an area of their country for the species they took a copy of Shaw's recordings to facilitate their work. But it did not: on all three occasions when the opportunity arose to play the song to birds already detected 'there was no response whatsoever' (Opige & Skeen undated, Nalwanga *et al*. 2016). More intriguingly, by chance the survey team managed to hear a snatch of song from a pair, and found it 'quite different to that of the Tanzanian birds, being sharper and faster' (Opige & Skeen undated, Nalwanga *et al*. 2016).

The circumstance in which the song of one population sounds 'quite different' ('quite' taken here to mean 'very', not 'somewhat') from that of another, and in which birds from one population do not respond to the song of birds from the other, intimates a level of taxonomic differentiation greater than is typical of subspecies. We therefore sought to assemble and review what material we could, focusing naturally on the acoustic evidence.

Methods

Acoustic evidence.—During a visit to Pian-Upe Wildlife Reserve, Uganda, in June 2022, PB made several sound recordings of at least three duetting pairs of *A. k. karamojae*, finding it easy to attract singers by playing back their songs initially recorded at a considerable distance (and noting a complete absence of response to the song of *A. k. stronachi*). These were seemingly the first recordings of the nominate to be made publicly available, on both Macaulay Library (ML; https://www.macaulaylibrary.org/) and Xeno-canto (XC; https://www.xeno-canto.org) databases, although more recently D. Muhumuza has posted a recording (ML 509203471) made in the same general area in December 2022. However, a reasonable sample of online recordings of subspecies *stronachi* is available in both ML and

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XC (albeit with considerable overlap), in addition to the information in Shaw *et al*. (2005). Recordings analysed of both taxa are indicated in Appendix 1.

The very different songs of the taxa are immediately obvious to the ear, but to quantify vocal differences we defined and measured the following sound parameters: max. note length, pace of the notes sung by a single individual, highest frequency in a song phrase, and min. and max. frequency of the notes in a song phrase. We made sonograms using CoolEdit Pro (Blackman-Harris window at 1,024 band resolution for the sharpest image), and measured sound parameters manually using visual rulers for time and frequency on screen.

Recordings of call notes proved to be too scarce to attempt to quantify any differences.

Morphological evidence.—In the paper establishing *A. k. stronachi* (Stuart & Collar 1985) Simon Stuart measured and examined all the specimens used in the diagnosis, whereas NJC inspected only the material in NHMUK. For the present study NJC could only re-examine the NHMUK material (male holotype of *stronachi*, male and female *karamojae*), but requested photographs of the four specimens (male *karamojae*, three female *stronachi*) in NMK. However, a search was also conducted online for photographs of the two taxa, using only the first of any taken on the same day by the same photographer, resulting in a sample of seven reasonably sharp digital images of *karamojae* and 15 of *stronachi* (Appendix 2). These were assessed informally and independently by PB & NJC.

Taxonomic criteria.—To help decide taxonomic rank under the Biological Species Concept, we employed the system of scoring in 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, 2.0–4.9 medium, 5.0–9.9 major and 10+ exceptional) and one behavioural or ecological character (allowed 1) may be counted. Effect sizes were obtained via the online calculator at https://lbecker.uccs.edu/.

Results

Acoustic evidence.—Pairs of both *A. k. karamojae* and *A. k. stronachi* typically sing a synchronised antiphonal duet. In nominate *karamojae* each bird sings a phrase that very rapidly repeats 1–3 very short, simple, unslurred notes, usually visible on a sonogram as straight, steeply ascending or descending lines (Fig. 1). Often, one bird would utter only whip-like ascending note types and the other respond with descending note types alone, either perfectly synchronised or at a different pace, resulting in, e.g, a loud urgent rhythmic fast *chip/wip-chip/wip-chip/wip-chip/wip…* or cyclical *WIbidi-WIbidi-WIbidi-WIbidi…* sometimes breaking into a rapid bubbling-piping reminiscent of an excited Eurasian Oystercatcher *Haematopus ostralegus*. By contrast, in *stronachi* each bird typically whistles a relatively relaxed phrase of two musical slurred notes repeated many times, with one individual singing A C A C and the other B D B D, thereby resulting in a typical structure ABCDABCD (Fig. 2). Occasionally, only a single whistle is repeated by each bird. During a song phrase, a bird may change note type, which may induce the mate to change notes as well, e.g., *piiuu-wíid-yuwíid-yuwíid-yuwíid… dyuuwíid-dyuuwíid piiuu… yuwíid-yuwíid*, etc., the result as melodious as in an accomplished singer like Oriole Warbler *Hypergerus atriceps*. In some cases, the simple structure ABCD is less evident on a sonogram, for example

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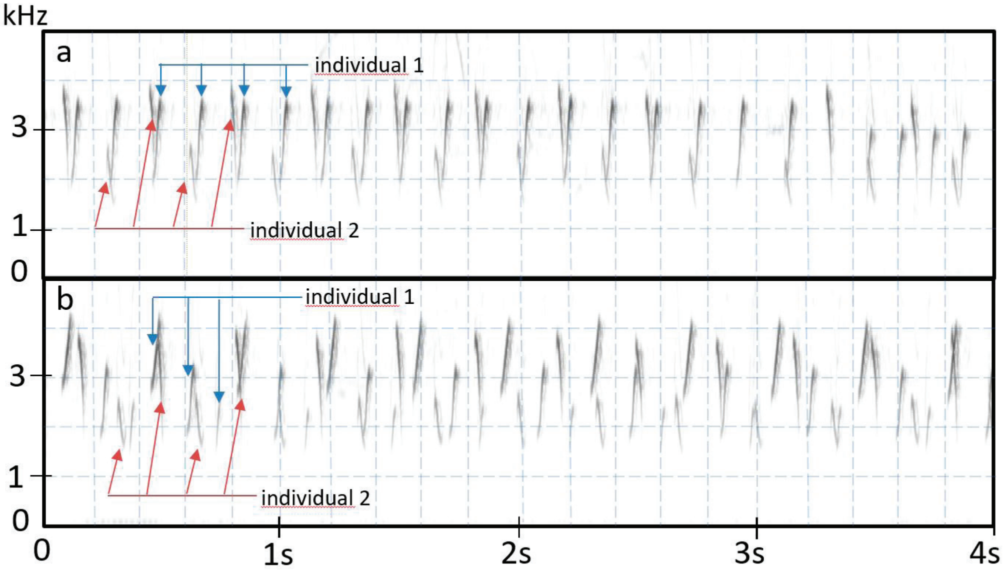

Figure 1. Sonograms of duets of Karamoja Apalis *Apalis k. karamojae*. Two different fragments of XC 739395, Uganda, P. Boesman. **a**: one bird gives a single ascending note and the other gives two different descending notes in perfect synchrony; **b**: one bird repeats three different descending notes while the other gives two ascending notes, with a slight difference in pace.

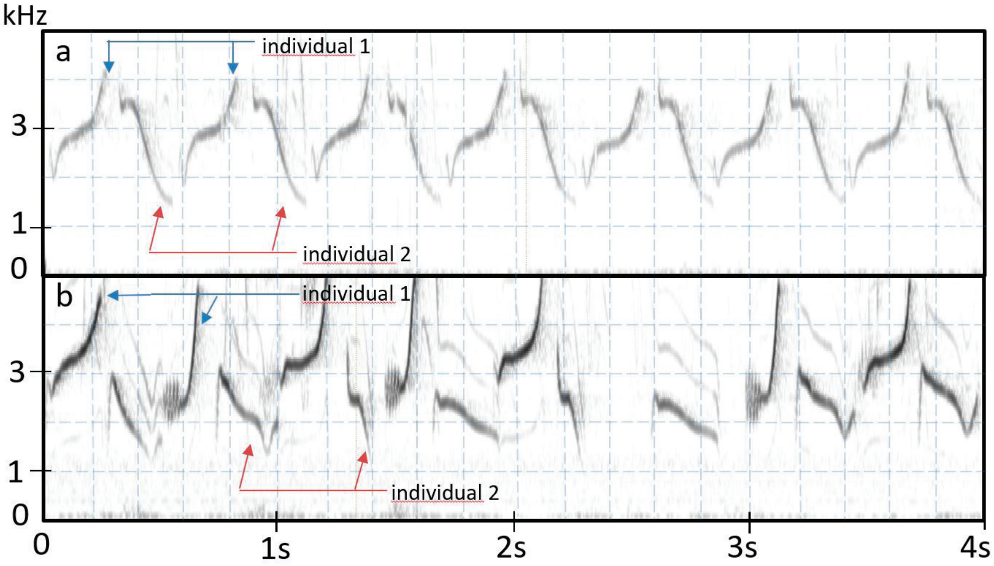

Figure 2. Sonograms of duets of Karamoja Apalis *Apalis karamojae stronachi*. **a**: ML 332837061, Tanzania, C. Leven. One bird gives a single upslurred note and the other a descending note in perfect synchrony; **b**: XC 146332, Tanzania, C. Leven. One bird gives two different ascending notes, the other utters two complex descending ones, with frequent switches in note type.

when a bird loses synchrony for a while, when a change in note type is not immediately picked up by the mate, or when a third bird (possibly an offspring) joins in. Notes can be either underslurred, overslurred, ascending or descending, or may possess a slightly more complex modulation.

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Figure 3. Three Karamoja Apalis *Apalis karamojae* in the Natural History Museum, Tring, left and centre *A. k. karamojae* (female NHMUK 1976.9.33 left, male NHMUK 1933.2.6.18 centre), right *A. k. stronachi* (holotype, male NHMUK 1962.10.8) (N. J. Collar, © Trustees of the Natural History Museum, London)

Figure 4. Four Karamoja Apalis *Apalis karamojae* in National Museums of Kenya, Nairobi, left *A. k. karamojae* (male 12907), other three *A. k. stronachi* (female NMK 12904, female NMK 12906, female NMK 12905) (© Peter Njoroge)

Figure 5. First photograph in Kenya of *Apalis karamojae stronachi*, Naibor-Mara Camp between Narok and Keekorok, Maasai Mara National Reserve, 4 January 2005 (© Brian Finch)

Morphological evidence.—Photographs of the material from which *stronachi* was described show that it is softly mottled grey on the underparts, rather than plain whitish as in the nominate (Figs. 3–5). This is most obvious in the (male) holotype of *stronachi*, NHMUK 1962.10.8, which is strikingly clouded with mid-grey on the underparts, in contrast to the pure white of the male and female nominate (NHMUK 1933.2.6.18 and 1976.9.33, respectively), although its markings are somewhat patchy and smudgy, not regular (Fig. 3). The NMK material does not show the difference so clearly (these are the specimens responsible for the remark in Stuart & Collar 1985 that *stronachi* females 'are only slightly darker than nominate males'), but it is still apparent that the Ugandan (left-hand) bird is plainer and paler below than the three from Tanzania (Fig. 4). The online photographic sample and first photograph taken in Kenya (Fig. 5) confirm that *stronachi* has pale greyish breast-sides and flanks, sometimes also across the breast, suffused and / or mottled, whereas

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TABLE 1
Measurements of four sound parameters in the songs of *Apalis k. karamojae* and *A. k. stronachi*: duration of longest note in a song phrase; max. pace in notes per second of a single individual; highest frequency reached in a song phrase; and total bandwidth (max. minus min. frequency) of a song phrase. Values indicate average ± standard deviation.

	Max. note duration (seconds)	**Max. pace** (notes/second)	**Max. frequency** (Hz)	**Frequency range** (Hz)
A. k. karamojae (*n* = 5)	0.041 ± 0.004	7.0 ± 1.3	4,340 ± 196	3,020 ± 312
A. k. stronachi (*n* = 8)	0.274 ± 0.016	2.0 ± 0.2	5,062 ± 283	3,662 ± 364
Effect size	21	5.5	3	1.9

nominate *karamojae* lacks this feature or shows much less of it, at the breast-side or flank, tucked along the line of the folded wing.

Taxonomic criteria.—Measurement of sound parameters in song phrases (see Table 1) indicates an exceptional difference in note duration (effect size 21 [!], Tobias score 4) and a major difference in pace (effect size 5.5, score 3), with also a medium difference in max. frequency (effect size 3, score 2). Given that note duration and pace are not wholly independent parameters (short notes can be delivered slowly, but long notes cannot be uttered quickly) we set aside pace here and allow scores of 4 for note duration and 2 for max. frequency. A score for the difference in underpart coloration would be 2 based on Fig. 3 but only 1 based on Fig. 4, and we opt cautiously for the latter; moreover, although the holotype of *stronachi* is very slightly darker above than the two birds from Uganda, this might simply reflect individual variation (and in any case judging subtle differences in shades of plumage in online photographs is not wise). In that same tiny sample re-measured at NHMUK we found that while bill and tarsus of the holotype of *stronachi* show little or no difference in length from the two Ugandan birds, the wing (54 mm vs. 48 [male] and 47 [female]) and tail (48 mm vs. 43 [male] and 42 [female]) certainly do. This conforms with the extra evidence in Stuart & Collar (1985), and the online photographs also tend to suggest a longer tail in *stronachi*, but we offer no score for this apparent distinction.

Discussion

Taxonomic conclusion.—The lack of response in nominate birds to playback of *stronachi* (independently observed twice) strongly suggests that their songs serve as species identifiers and thus also reproductive barriers (naturally a reverse test, exposing *stronachi* to nominate song, is desirable, but the one-way barrier is close to conclusive). Furthermore, species which duet for territory defence and pair bonding, assisted by their offspring (which thereby gradually learn perfect duet synchronisation), possess a fairly complex social behaviour that further promotes reproductive isolation. These insights vindicate the scoring of the distinctiveness of *stronachi* in the paragraph above, which totals 7 and thereby qualifies it for species rank. We suggest that this is a conservative characterisation of the differences between *stronachi* and the nominate, for several reasons. First, given that the threshold for an 'exceptional' difference is an effect size of 10, triggering a score of 4, an effect size of 21 would appear so remarkable—we have never encountered a degree of difference remotely as strong in more than a decade of applying the Tobias criteria to closely related taxa—as to merit a higher score still. Second, the evidence certainly points towards a difference in wing and tail length which, when more birds are sampled, will probably yield a score of 1, possibly 2. There is also the claim of a darker shade on the upperparts (see above) which might hold true, and another concerning a difference in call: Nalwanga *et al*. (2016) believed they had detected such a difference in the nominate, without

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stating their evidence, but they mentioned that a pair gave a '*teeeng-teeeng*' double note, 'higher pitched at the beginning', which does not accord with any call mentioned by Shaw *et al*. (2005) for *stronachi*. Moreover, Phil Shaw (*in litt*. 2023), who spent a total of seven weeks in the Wembere Steppe and Serengeti ecosystem, reports that the call of a nominate bird recorded by PB on Xeno-canto (XC739393)—a curt gruff buzz: *hrr*—is 'not one I recognise'.

Despite the relatively low sample sizes in the comparisons between songs (five for the nominate, eight for *stronachi*), the duets produced by the two taxa were consistent within the sample and with (a) the evidence in Shaw *et al*. (2005), who were using their own extensive, independent set of recordings of *stronachi*, and (b) the testimony of Opige & Skeen (undated) and Nalwanga *et al*. (2016) concerning the nominate. Moreover, although the differences in plumage and morphometrics could be argued to represent no more than the ends of an interrupted cline, the difference in song cannot reasonably be considered clinal or dialectal. Dialects in oscine passerines have been documented for many species (Marler & Slabbekoorn 2004) and are typically reflected by subtle changes in adjacent populations which, over longer distances, may cumulatively result in song phrases that sound quite different at the geographical extremes. In the case of Karamoja Apalis, however, the known min. distance between the two taxa is only *c*.350 km, and the difference in song structure and note properties is very abrupt, entirely unlike the circumstances and conditions involved in dialects (or clines).

For several decades, vocal differences among oscine passerines have been used in a multitude of cases to settle the taxonomy of species complexes (Alström & Ranft 2003), based on the assumption that they represent a strong reproductive barrier between closely related species (Remsen 2005). This assumption has been confirmed by extensive playback experiments that prove a strong correlation between the degree of acoustic divergence and the ability of birds to discriminate taxa by their songs (Freeman & Montgomery 2017). Even in the genus *Apalis* several taxa have been accorded species status based largely on vocal evidence (Morel & Chappuis 1992). In the case of cryptic species, vocal divergence has often been the first or sole indirect indicator of genetic divergence, e.g. many species in the genera *Acrocephalus*, *Cisticola*, *Phylloscopus*, *Anthus*, *Sheppardia*, *Certhia* and, perhaps most notably, the *Vidua* indigobirds (Morel & Chappuis 1992, Payne 1982, Martens 2010, van Els & Norambuena 2018). Even in genera composed of species that are morphologically rather distinctive, many cases are known of a few members that are extremely similar except in voice, e.g. Eastern *Phylloscopus orientalis* and Western Bonelli's Warblers *P. bonelli* (Helb *et al*. 1982), Eastern *Sylvia crassirostris* and Western Orphean Warblers *S. hortensis* (Svensson 2012), Little *Bradypterus baboecala* and Highland Rush Warblers *B. centralis* (Boesman 2016a, Dowsett-Lemaire 2022), Choco *Myiothlypis chlorophrys* and Golden-bellied Warblers *M. chrysogaster* (Boesman 2016b), Ethiopian *Psophocichla simensis* and Groundscraper Thrushes *P. litsitsirupa* (Boesman 2016c). Continued treatment of Karamoja Apalis as a single species, thereby rejecting the taxonomic significance of a very different voice, would be wholly inconsistent with the above and indeed with a multitude of recent cases promoting and accepting taxonomic rearrangements on the basis of far less prominent vocal differentiation. We therefore recommend the treatment of *Apalis karamojae stronachi* as a species.

The vernacular name for *A. stronachi* might be Maasai Apalis; but we do not offer this as more than a suggestion. It is not even certain that the species is an apalis. D. Moyer in Shaw *et al*. (2005) considered *stronachi* to resemble a prinia more than an apalis in behaviour and voice, and Shaw *et al*. (2005) themselves thought that the vocal difference of *stronachi* suggested it might better be placed in a different genus. However, the song of the newly restricted monotypic *A. karamojae* (for which the name Karamoja Apalis should surely be retained) is in fact not that different from, e.g., Brown-headed Apalis *A. alticola* or Grey

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Apalis *A. cinerea*. Consequently the notion that *A. karamojae* and *A. stronachi* belong in a different genus from other apalises is perhaps less plausible than the possibility that *stronachi*, under unknown evolutionary pressures, diverged vocally so much that it lost the typical features of the genus. Such vocal anomalies within a genus are not unusual; even in *Apalis* the long trilling whistle of Chestnut-throated Apalis *A. porphyrolaema* stands out as an example.

Genetic analysis will of course help to resolve these uncertainties, and we strongly encourage such a study. This is an interesting case to investigate how long the taxa have been separated, as there is scant information on the time it takes for bird taxa to reach such levels of vocal divergence, or on the drivers of such changes. While the standard taxonomic case in an integrative assessment would seek complementary differences in morphology, voice and genetics, nonetheless there are some species that have long been separated but evolved only minimal vocal differences, e.g. a multitude of species in the genus *Zosterops* (Pearson & Turner 2017), Rote Leaf Warbler *Phylloscopus rotiensis* (Ng *et al*. 2018) and the *Calliope* rubythroats (Liu *et al*. 2019), while few species are known that separated very recently but diverged significantly in voice, as in the special case of brood-parasitic *Vidua* indigobirds (Sefc *et al*. 2005). In the present case, we have to express the view that, even if *A. karamojae* and *A. stronachi* were to be found to be genetically near-identical, we would be reluctant to accept that they could be considered conspecific under the Biological Species Concept, given the strong reproductive barriers that their songs represent.

Conservation prognosis.—Splitting a species necessarily means that the new 'offspring' species have smaller ranges and populations than their 'parent', requiring reassessments of their conservation status. In cases of species already threatened with extinction the need for such assessments is all the more pressing. Here, while not presuming to trespass into the formal process of re-evaluating their Red List status, we briefly review the circumstances of the two 'offspring' species as we judge them to be.

Historical and recent records of Karamoja Apalis *sensu novo* were mapped by Salmah & Onongo (2023). Recent records indicate the species' persistence in Kipedo National Park in far north-east Uganda and 200 km to the south near 'Mount Kamalinga' (Collar & Stuart 1985), i.e. the Kamalinga Hills, extending into Napak District and Bokora Wildlife Reserve, but there is no confirmation of presence at the two other historical sites, Mount Moroto (north-east of Napak near the Kenya border) and Mount Kadam ('Napiananya' or 'Napianyenya', west and north of Pian-Upe Wildlife Reserve). Most importantly, however, recent records also involve 15 new localities south of Mount Kadam, spanning around 100 km from Soroti in the west to just north-east of Mount Elgon in the east, eight of them inside the southern limits of Pian-Upe Wildlife Reserve. These findings are supported by (but omit mention of) a record of one 25 km north of Mbale in 2015 (D. Pomeroy *per* P. Shaw in BirdLife International 2023), i.e. at *c*.01.30°N, 34.18°E, slightly further south than any of the sites in Salmah & Onongo (2023).

All Tanzanian records of the 'Maasai Apalis' up to May 2016 are mapped in the Tanzania Bird Atlas (http://tanzaniabirdatlas.net/maphtm/0820_nmap.htm), and involve 29 localities ('plots'), all positioned between 02°S and 05.25°S and all but two between 33°E and 35°E (the two outliers being further east but the more distant one, in Tarangire National Park, earmarked for deletion for lack of documentation). A record from square 3303A, first reported as Shinyanga in Shaw *et al*. (2010), is labelled as 'a significant range extension' made 'the only time this area has been visited for birding'. The degree to which this record represents an extension in knowledge rather than an expansion of range may not be easy to gauge. However, the rigorous ecological field work that established the species' strong association with whistling-thorn (Shaw & Mungaya 2006) generated a highly

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plausible hypothesis that the apalis expanded its range in Tanzania from the Wembere Steppe northwards into the Serengeti ecosystem and adjacent Maasai Mara in Kenya as a knock-on effect of rinderpest elimination in the 1960s: this enabled a sixfold increase in wildebeest *Connochaetes taurinus* numbers, which caused grass volume and hence grass fires to diminish, which in turn enabled whistling-thorn acacia to expand within grassland areas (Shaw *et al*. 2010).

This body of research showed that the apalis in Tanzania requires the tallest, densest stands of *Vachellia drepanolobium* and is therefore negatively affected by cutting and clearing of such habitat (Shaw *et al*. 2005, 2010, Shaw & Mungaya 2006). A similar ecological constraint in Uganda seems also to affect the apalis, which was recorded in recent surveys only in taller than average whistling-thorn habitat (Salmah & Onongo 2023). The future of the two species therefore appears to depend on the proactive management of extensive tracts of mature whistling-thorn, which (given the increasing human demands for grazing land and fuelwood) seems unlikely to occur in the long term anywhere outside protected areas. On the other hand, the record from Shinyanga in Tanzania and the multiple records extending the southern boundary of the range in Uganda indicate that undiscovered populations of both species are highly likely to exist. A redoubling of research and survey effort in Uganda, Kenya and Tanzania is needed to help clarify the true range of the two species and the measures—including, conceivably, translocation, e.g., to the relatively well-protected but isolated Laikipia (P. Shaw *in litt*. 2023)—most appropriate to their long-term conservation.

Acknowledgements

We warmly thank the recordists and photographers (see Appendix 1 and 2) who posted their material on Macaulay Library and Xeno-canto, and Peter Njoroge (NMK) for taking the photograph in Fig. 4 and permitting its use here. Brian Finch took the photograph in Fig. 5 and he, Phil Shaw and Simon Stuart provided very helpful comments as referees, with Lincoln Fishpool kindly adding others.

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Appendix 1: Sound recordings analysed in this study

Apalis k. karamojae: XC 739394/ML 466839481, XC 739395/ML 466839491, XC 739396/ML 466839861, XC 739397/ML 466840171, ML 509203471.

Apalis k. stronachi: XC 146332/ML 332837021, XC 648013, XC 718598/ML 440009331, XC 755876, ML 332837061, ML 332837121, ML 550227171, ML 547993521.

ML = Macaulay Library; XC = Xeno-canto. Recordists: Abdul Adam, Peter Boesman, James Bradley, Isaac Kilusu, Paulo Kivuyo, Catriona Leven, Deogratius Muhumuza.

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Appendix 2: Online photographs inspected in this study

Apalis k. karamojae: ML 438235841, ML310449731, ML 496910021, ML 486375761, ML 473365201, ML 405679141, Salmah & Onongo (2023: fig. 5).

Apalis k. stronachi: (Kenya) ML 577089561, ML 555463391, ML 547994721, ML 477479131, ML 472399641, ML 441255561, ML 415114251; (Tanzania) ML352403481, ML 253848101, ML 170629521, ML 119518351, ML 108697311, ML 335533951, ML 302702781, ML 205491021.

ML = Macaulay Library. Photographers: Nik Borrow, James Bradley, Nancy Christensen, Gary Douglas, Bradley Hacker, Neil Hayward, Charley Hesse, Marcel Holyoak, Victor Ikawa, Alain Jacot, Alex Kanzira, Helmut Laussmann, Alexander Lees, Lisa & Li Li, Larry Moss, Jonathan Onongo, Niall D. Perrins, Fanis Theofanopoulos.

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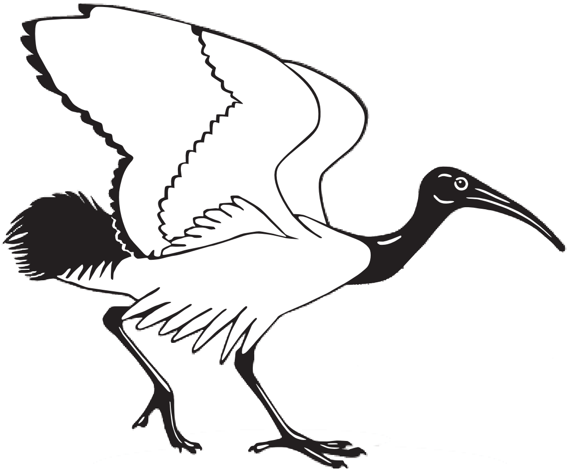

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