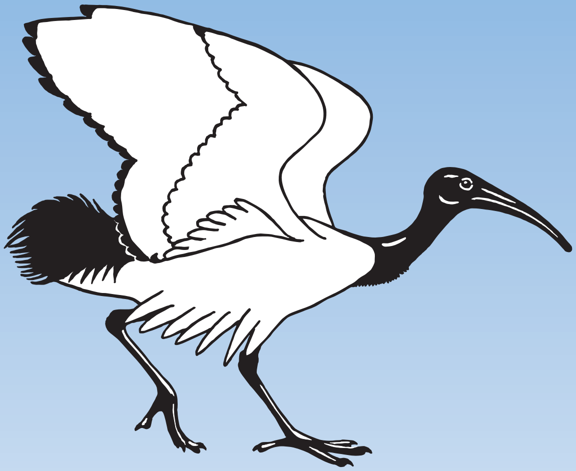
Bulletin of the British Ornithologists' Club



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CONTENTS

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CLUB ANNOUNCEMENTS

The 1007th meeting of the Club was held on Monday 27 March in the upstairs room at the Barley Mow, 104 Horseferry Road, London, SW1P 2EE. The meeting was recorded and a video of the event is available online (https://www.youtube.com/watch?v=OtmwFkt-FZI) and also via the Club website https://boc-online.org/. Nineteen people were present: Ms A. Belman, Mr P. J. Belman, Miss H. Baker, Mr S. Chapman, Ms C. Derrick, Mr M. Howard, Mr A. Jackson, Ms van Keulen, Ms S. Nichols, Dr R. Prŷs-Jones (*Speaker*), Mr N. Redman, Dr A. Richford, Dr D. G. D. Russell, Dr M. Stervander, Mr S. A. H. Statham, Mr C. W. R. Storey (*Chairman*), Ms J. White, Mr G. de Silva Wijeyeratne and Mr J. Woodman.

Dr Robert Prŷs-Jones, Bird Group, Natural History Museum at Tring, spoke on *Wallace's Sarawak bird collections and the development of his ornithological knowledge*. The integration of information from the diaries/notebooks of important 19th-century ornithologists with that from their specimens and accompanying labels can provide intriguing insight into the development of their interest in, and knowledge of, avifaunas. Two key examples, involving major collections now largely held by the Natural History Museum at Tring, comprise Allan Octavian Hume (see Prŷs-Jones 2022, *Arch. Nat. Hist*. 49: 391–407) and Alfred Russel Wallace, the subject of this talk. Although already a highly experienced collector of South American fauna, Wallace had no first-hand knowledge of the South-East Asian fauna when he arrived there for an eight-year visit in 1854. From early November 1854 to January 1856, he was based in Sarawak, and the talk integrated information from his specimen labels with that found in his field notebook listing of 'Birds collected in Borneo', with the aim of unravelling how his skill in identifying the birds he collected there increased over time.

Keep an eye on the BOC website (https://boc-online.org/meetings/upcoming-meeting) and the BOC Twitter account (@online_BOC) for news of upcoming meetings.

BOOK REVIEWS

Louette, M. 2023. *The bird species from the type collection*. Collections of the RMCA. Royal Museum for Central Africa, Tervuren. 179 pp, many colour photos and illustrations. €25.

The Royal Museum for Central Africa (RMCA) was founded in 1897 and currently houses approximately 150,000 bird specimens from throughout Africa but with a special focus on the central portion of the continent. This is the third review of the avian type specimens held in the RMCA, following previous inventories by Louette and co-workers published in 2002 and 2010. However, the latest work is decidedly different to those prior compendia, being considerably more attractive and therefore saleable, with more discursive and general texts aimed to some extent at the interested amateur, rather than solely at museum specialists; however, it is also less complete in its coverage.

The volume under discussion comprises four sections. The first provides background information about the museum, some of the 'personalities' who contributed specimens, notes on terminology, and the like. The bulk of the book is formed by the accounts for each of the taxa (n = 25) accepted as species by the so-called IOC world bird list (www.worldbirdnames.org) for which some or all of the type material is held in RMCA. Each account lists the current name, original combination, and the type material held in Tervuren, together with sections on etymology, remarks on the species' biology and conservation, distribution (including a map) and taxonomic history; an individual set of references is presented for each species. Field photographs, or specially prepared artwork in the case of almost unknown birds such as Itombwe Nightjar *Caprimulgus prigoginei*, illustrate all of the 25 accounts. The same format is employed for the final two, much shorter, sections, which cover (1) six taxa that Louette considers strong candidates for species status in the near future, and in contrast (2) three birds, originally described as species, but which the author treats as 'melanistic morphs'.

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As Louette notes in the prefatory material, RMCA has at least 988 bird type specimens of 227 nominal taxa, and while these were all listed in Louette *et al*. (2010) only a subset is included herein. Nevertheless, a table does list all of the subspecies accepted by the IOC world bird list for which RMCA has type material.

The book can be ordered online by e-mail (publications@africamuseum.be) or via https://www.africamuseum.be/en/research/publications; in the UK it is available from the Natural History Book Service (https://www.nhbs.com/the-bird-species-from-the-type-collection-book).

Guy M. Kirwan

Reference:
Louette, M., Meirte, D., Louage, A. & Reygel, A. 2010. *Type specimens of birds in the Royal Museum for Central Africa, Tervuren*. Royal Museum for Central Africa, Tervuren.

Raffaele, H. A., Wiley, J. W., Garrido, O. H., Keith, A. R. & Raffaele, J. I. 2020. *Birds of the West Indies*. Second edn. Helm, London. 288 pp, 129 colour plates. £22.50.

Raffaele, H. A., Petrovic, C., Colón López, S. A., Yntema, L. D. & Salguero Faria, J. A. 2021. *Birds of Puerto Rico and the Virgin Islands*. Third edn. Princeton University Press, Princeton, NJ. 224 pp, several colour photos and 87 colour plates. £20.

Latta, S., Rimmer, C. & McFarland, K. 2022. *Field guide to the birds of the Dominican Republic & Haiti*. Second edn. Princeton University Press, Princeton, NJ. 228 pp, several colour photos and many colour plates. £20.

Adding to the explosion of recent works on the West Indies, among them two BOC checklists (Kirkconnell *et al*. 2020, Wiley 2021) and a new field guide (Kirwan *et al*. 2019) rooted in HBW/BirdLife taxonomy (del Hoyo 2014, 2016), these three works are all new editions of works first published in 1998, 1983, and 2006, respectively. All possess a similar feel, an impression heightened by the fact that the first two share much of the same artwork, whereas the Hispaniola guide is augmented with a large number of new illustrations painted by Dana Gardner. The Puerto Rico and general West Indies guides further differ in 'prioritising' the regularly occurring species, with vagrants 'demoted' to a section of plates at the end, and the second-named volume even omits some of the exceptionally rare visitors that have been recorded. All three fit easily in a larger jacket pocket or small day-bag, which in the case of the West Indies and Hispaniola volumes represents a marked difference (many would argue improvement) on their first editions, but obviously comes at a price in terms of what is included and what is not. While it will be tempting for many to plump for the one-stop shop of a guide to the entire region, observant users will discover that there are subtle (and sometimes not so subtle) differences in the mapped distributions for Hispaniola between the Latta *et al*. island-specific volume and those in Raffaele *et al*.; for my money, those in the former appear more likely to be accurate. The Puerto Rico volume, however, contains no species distribution maps, which feels like a failing, despite the small size of Puerto Rico, never mind the various Virgin Islands, but both it and the Hispaniola tome do contain useful bird-finding sections (an omission from the whole-region guide). Both visiting and resident birdwatchers in the West Indies have never been better served. Even James Bond might be staggered as to what he started!

Guy M. Kirwan

References:
del Hoyo, J. & Collar, N. 2014. *The HBW and BirdLife International illustrated checklist of the birds of the world*, vol. 1. Lynx Edicions, Barcelona.
del Hoyo, J. & Collar, N. 2016. *The HBW and BirdLife International illustrated checklist of the birds of the world*, vol. 2. Lynx Edicions, Barcelona.
Kirkconnell, A., Kirwan, G. M., Garrido, O. H., Mitchell, A. & Wiley, J. W. 2020. *The birds of Cuba: an annotated checklist*. BOC Checklist no. 26. British Ornithologists' Club, Tring.
Kirwan, G. M., Levesque, A., Oberle, M. & Sharpe, C. J. 2019. *Birds of the West Indies*. Lynx Edicions, Barcelona.
Wiley, J. W. 2021. *The birds of St Vincent, the Grenadines and Grenada: an annotated checklist*. BOC Checklist no. 27. British Ornithologists' Club, Tring.

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

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The *Bulletin* and other BOC publications

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

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

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Taxonomic status of Bay-winged Hawk *Parabuteo* (*unicinctus*) *unicinctus* and Harris's Hawk *P.* (*u.*) *harrisi*, with documentation of delayed plumage maturation in Bay-winged Hawk

by William S. Clark & Sergio H. Seipke

Received 18 June 2022; revised 9 February 2023; published 7 June 2023

http://zoobank.org/urn:lsid:zoobank.org:pupub:1AD464CC-F1CD-4BBC-9F71-E8D3B9720A67

Summary.—The two main populations of *Parabuteo unicinctus* have long been treated as subspecies of the same species: Harris's Hawk *P. u. harrisi* in the southern USA to Costa Rica, and Bay-winged Hawk *P. u. unicinctus* in South America. However, they differ considerably in their morphology, number of plumages, and behavioural ecology. Adult Harris's Hawk differs in multiple plumage characters from adult Bay-winged Hawk, and differences are even more marked in juvenile plumage. Harris's Hawk has two age-related plumages but Bay-winged Hawk shows delayed plumage maturation and has four such plumages. Harris's Hawk breeds and hunts cooperatively, whereas Bay-winged Hawk nests only in pairs, and hunts individually. There are no valid records of Harris's Hawk in South America. We believe that the differences in adult and juvenile plumages, the number of immature plumages, and differences in breeding and hunting mean that Harris's Hawk and Bay-winged Hawk are best treated as separate species.

The two main populations of *Parabuteo unicinctus* have long been treated as subspecies of the same species: Harris's Hawk *P. u. harrisi* (Audubon 1837) of North and Middle America, and Bay-winged Hawk *P. u. unicinctus* (Temminck 1824) of South America. All of the major world bird checklists (e.g., Dickinson & Remsen 2013, del Hoyo & Collar 2014, Clements *et al*. 2022, Gill *et al*. 2023) treat them as conspecific. However, in this paper we document and review evidence that these taxa differ considerably in plumages and behavioural ecology, and, as such, merit consideration as separate species. In particular, the immature plumages of Bay-winged Hawk are not well understood.

Harris's Hawk and Bay-winged Hawk differ diagnostically in adult and juvenile plumages (Clark & Wheeler 2001, Pallinger & Menq 2022). Furthermore, due to delayed plumage maturation, Bay-winged Hawk has four age-related plumages; its Basic II and Basic III have not been well understood but are described fully herein. Basic II and Basic III plumages of Bay-winged Hawk are similar to that of juvenile Harris's Hawk, but are easily distinguished by the presence of flight feather moult, or wave moult fronts. Harris's Hawk regularly hunts and breeds cooperatively (Bednarz 1987, Bednarz & Ligon 1988, Bednarz 1995, Coulson & Coulson 2013, Dwyer & Bednarz 2020), whereas these behaviours have not been reported in Bay-winged Hawk (e.g., Jiménez & Jaksić 1993), although Coulson & Coulson (2012) presented anecdotal accounts to suggest that they may occasionally hunt communally. No published reports of cooperative breeding or hunting in Bay-winged Hawk were found (e.g., Jiménez & Jaksić 1993). The only published comparative DNA studies of these taxa, Riesing *et al*. (2003) and Raposo do Amaral *et al*. (2009), reported a small difference between two samples from Brazil of Bay-winged Hawk and one from the USA of Harris's Hawk. Herein we discuss the many differences between these two taxa, which we believe are sufficient to consider them as species.

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Methods

We have observed, studied and taken more than 100 photographs of both taxa in the field and have examined 119 specimens of *P. unicinctus* from throughout the range in 14 museums: Carnegie Museum of Natural History, Pittsburgh, PA (CM); Cleveland Museum of Natural History, Cleveland, OH (CMNH); Natural History Museum of Los Angeles County, Los Angeles, CA (LACM); Moore Lab of Zoology, Occidental College, Los Angeles, CA (MLZ); Museum of Comparative Zoology, Cambridge, MA (MCZ); Museum of Zoology, University of Michigan, Ann Arbor, MI (UMMZ); National Museum of Natural History, Smithsonian Institution, Washington DC (USNM); Museo de la Plata, La Plata (MLP); Museo de la Estación Biológica de Rancho Grande, Maracay (MEBRG); Museo de las Aves de Patagonia, El Bolsón; Colección Ornitológica Phelps, Caracas (COP); Louisiana Museum of Natural History, Baton Rouge, LA (LSUMNS); Santa Barbara Museum of Natural History, Santa Barbara, CA (SBMNH); and Western Foundation of Vertebrate Zoology, Camarillo, CA (WFVZ) (Table 1). We compared juvenile and adult plumages between both taxa, using primarily the 119 specimens, augmented by >100 photographs of in-hand Harris's Hawks and >10 photographs of Bay-winged Hawks. We also compared photographs of both taxa online at the websites: WikiAves (www.wikiaves.com.br), Macaulay Library (https://www.macaulaylibrary.org) and iNaturalist (https://uk.inaturalist.org/). We compared Basic II and Basic III plumages of Bay-winged Hawk vs. juvenile Harris's Hawk. We searched the literature for reports of cooperative hunting and cooperative breeding, and discuss the DNA evidence to date. We use the moult and plumage terminology proposed by Clark & Pyle (2015).

TABLE 1
Number of specimens of Bay-winged Hawk *Parabuteo unicinctus* by age class examined at 14 museums listed in Methods (which see for acronyms) and collected in all parts of South America.

Museum/Age	**Juvenile**	**Basic II**	**Basic III**	**Adult**	**Total**
CM	2	2		2	6
CMNH				1	1
COP	1			1	2
El Bolsón	3				3
LACM	15	1		2	18
LSUMNS	2	3		1	6
MCZ	7	1		2	10
MLP	10	8			18
MLZ	1	1			2
MEBRG	1	1		1	3
SBMNH	1				1
UMMZ	12	5		3	20
USNM	10	5		3	18
WFVZ	8	2	1		11
Totals	73	29	1	16	119

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Results

Adult plumage.—Definitive Basic (adult) plumages of these taxa are similar, but all adults differ in several traits, namely throat markings, colour and markings on the undersides of the remiges, markings on the belly and breast, markings on the leg feathers, and extent of white at the base and tips of the rectrices (Figs. 1–2). *Throat markings*. All adult *harrisi* have an unmarked dark throat, whereas adult *unicinctus* almost always shows a variable amount of white streaking on the dark throat (Fig. 1). *Underside of remiges*. All adult *harrisi* have unmarked dark undersides to the remiges (Fig. 2b), whereas all adult *unicinctus* have whitish primaries with narrow dark bands and black tips on the outer ones, but many adult *unicinctus* have whitish secondaries with narrow dark bands (Fig. 2a), though some have darker secondaries with some narrow white bands (e.g., https://www.wikiaves.com/4185104). All adult *unicinctus* have a broad darker subterminal band on the secondaries

Figure 1a. Adult Bay-winged Hawk *Parabuteo u. unicinctus* at Carnegie Museum, Pittsburgh (CM P94603, Bolivia, August 1922; top in both images) vs. adult Harris's Hawk *P. u. harrisi* (CM P165789, Texas, December 1913; below); note differences in throat, underparts and tarsal markings (W. S. Clark)

Figure 2a. Adult Bay-winged Hawk *Parabuteo u. unicinctus* (left, Venezuela, June 2006); vs. 2b. adult Harris's Hawk *P. u. harrisi* (right, Texas, April 2014); note differences in the colour and markings on the undersides of the remiges, and width of the white base and terminal tail-band (W. S. Clark)

ISSN-2513-9894
(Online)

Figure 3a–b. Juvenile Bay-winged Hawk *Parabuteo u. unicinctus* specimen at the Carnegie Museum (CM P119975; Bolivia, June 1927); vs. 3c–d. juvenile Harris's Hawk *P. u. harrisi* specimen at Museum of Comparative Zoology (MCZ 314440; Texas, December 1909); note differences in the throat, extent of dark on the underparts and upperparts, tarsal markings, and width of the tail-bands (W. S. Clark)

(Fig. 2a). *Underwing-coverts*. Uniformly rufous lesser and median underwing-coverts, and plain black greater underwing-coverts are characters of all *harrisi*. Uniformly rufous lesser and median underwing-coverts and barred greater underwing-coverts are shown by most *unicinctus,* but some are all rufous. *Pattern on underparts*. All adult *harrisi* have unmarked dark underparts, whereas almost all adult *unicinctus* show a variable number of white markings on otherwise dark underparts, especially the belly (Fig. 1). *Markings on leg feathers*. All adult *harrisi* have unmarked rufous tarsal feathers, whereas in adult *unicinctus* they can be rufous or rufous with some pale barring (Fig. 1). *Rectrices*. All adult *harrisi* show a broad white base and tips to the uppertail. All adult *unicinctus* show less white on the base and narrower white tips to the same feathers (Fig. 2). More photographs of adult Bay-winged Hawk can be seen at https://www.wikiaves.com.br/4777890 and https://www.wikiaves.com.br/785274; for adult Harris's Hawk see https://macaulaylibrary.org/asset/477195211 and https://macaulaylibrary.org/asset/475940421.

ISSN-2513-9894
(Online)

Figure 4a. Juvenile Harris's Hawk *Parabuteo unicinctus harrisi* (left, Texas, December 2005) (W. S. Clark); vs. 4b. juvenile Bay-winged Hawk *P. u. unicinctus* in flight (right, Argentina, June 2019 (© Gustavo Sebastian Cabanne); note difference in markings on underparts and underwing-coverts.

Figure 5a. Juvenile Bay-winged Hawk *Parabuteo u. unicinctus* (left, Ecuador, August 2010) (© Roger Ahlman); 5b. juvenile Harris's Hawk *P. u. harrisi* (right, Texas, December 2010) (W. S. Clark); note differences in markings on underparts, head and tarsal feathers.

Juvenile plumage.—Juvenile plumages of the two taxa are consistently and markedly different in multiple characters. *Underparts*. All juvenile *unicinctus* have buffy underparts with narrow dark streaking (Fig. 3a), whereas juvenile *harrisi* have dark underparts with white to buffy markings (Fig. 3c). *Undertail*. Juvenile *unicinctus* has the undertail whitish with narrow dark bands (Fig. 3a), whereas juvenile *harrisi* has a medium grey undertail with fewer and broader dark bands (Fig. 3c). *Upperparts*. Juvenile *unicinctus* has buffy markings on the upper back (Figs. 3b, 5a), not shown by any juvenile *harrisi* (Figs. 3d, 5b). Rufous markings on the upperwing-coverts are visible in juvenile *harrisi* (Figs. 3d, 5b), but the rufous area is smaller and less visible in *unicinctus* (Figs. 3b, 5a). *Underwings*. Underwing-coverts are mostly rufous on *harrisi* but mottled buffy and dark brown in *unicinctus*

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(Online)

Figure 6. Basic II Bay-winged Hawks *Parabuteo u. unicinctus* in flight feather moult (National Museum of Natural History, Smithsonian Institution) (left: ventral; right: dorsal; four from Paraguay and one from Chile); note similarity to juvenile Harris's Hawks *P. u. harrisi* in Fig. 3c–d (W. S. Clark)

TABLE 2
Plumage characters of Basic II and Basic III Bay-winged Hawks *Parabuteo u. unicinctus*. Based on 29 Basic II specimens and two Basic II specimens.

Character/Age	**Basic II**	**Basic III**
Head	Pale cheeks and supercilium	Like adult, or with pale cheeks or eyeline
Throat	Buffy, narrow dark streaks	Whitish streaks
Underparts	Blotched dark brown, buffy areas	Dark brown, some whitish on belly; no buffy
Tarsus feathers	Buffy and rufous barring	Rufous or barred buffy and rufous
Underwing-coverts	Buffy and rufous mix, rufous barring	Mostly rufous, but buffy barring on 'wrists'
Underside to remiges	Primaries like juveniles; single moult wave, and secondaries longer forming ragged rear edge to wing	Like adult; two waves of primary moult
Undertail	Like juveniles, but broader subterminal band; can also be adult-like	Like adult, some whitish on outer feathers
Upperwings	Buffy wing-coverts	Rufous wing-coverts

(Fig. 4). More photographs of juvenile Bay-winged Hawk can be seen at https://www.wikiaves.com.br/3524655, https://www.wikiaves.com.br/807065, https://www.wikiaves.com.br/2664694, and https://www.wikiaves.com.br/1211468; for juvenile Harris's Hawk see: https://macaulaylibrary.org/asset/477177731, https://macaulaylibrary.org/asset/473920961, and https://macaulaylibrary.org/asset/478452121.

Basic II and Basic III plumages.—Only *unicinctus* has intermediate annual plumages between juvenile and adult plumages, taking three years to attain adult plumage. Basic II and III specimens of *unicinctus* are all quite different from juvenile specimens of the same taxon, appearing more like juvenile *harrisi* (Fig. 6). The characters associated with these intermediate plumages are shown in Table 2, determined from 29 specimens of Basic II *unicinctus* from all parts of South America and >100 photographs. They differ from *harrisi*

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(Online)

Figure 7. Basic III Bay-winged Hawk *Parabuteo u. unicinctus* at Western Foundation of Vertebrate Zoology, which showed two waves of primary moult (WFVZ 46385; Chile, August 1937) (top: ventral; below: dorsal); note similarity to Harris's Hawks *P. u. harrisi* in Fig. 3c–d (W. S. Clark)

mainly by showing moult in the inner primaries. Photographs of Basic II *unicinctus* in flight showing primary and body moult can be seen at: https://www.wikiaves.com.br/692648 (p1 and r1 new and underparts show extensive molt); https://www.wikiaves.com.br/4784500 (p7 growing and pp1–6 new, as are many rectrices, with extensive body moult in the underparts); https://www.wikiaves.com.br/1090880 (pp1–6 and many tail feathers new; underparts in extensive moult); and https://www.wikiaves.com.br/3878012 (p7 growing and pp1–6 plus some secondaries and rectrices are new; underparts in extensive moult). We found one specimen of *unicinctus* in Basic III plumage (WFVZ 46385, from Chile); it showed two waves of primary moult and an adult-like undertail (e.g., Fig. 7). Photographs of Basic III *unicinctus* in flight showing two waves of primary moult can be seen at: https://www.wikiaves.com.br/2906986 (new p9 and p1, thus two waves of primary moult; tail almost adult-like); https://www.wikiaves.com.br/1984344 (new p9 and p1; tail almost adult-like); https://www.wikiaves.com.br/3492276 (new p10 and p1; tail almost adult-like); https://macaulaylibrary.org/asset/471713411 (new p10 and p6; tail almost adult-like); and https://www.ecoregistros.org/site/imagen.php?id=130229 (new p8 and p1; tail has many new feathers). A photograph of a Basic III male that was mated with a breeding adult female was taken by M. Juhant near Buenos Aires, Argentina, and showed the characters of this age as listed in Table 2. Harris's Hawk undergoing the second pre-basic moult show flight feather replacement similar to Basic II and III Bay-winged Hawks, but can be distinguished by their new dark (vs. whitish in Bay-winged Hawk) remiges and new adult rectrices. A photograph showing a Harris's Hawk in second pre-basic moult with new dark remiges and rectrices can be seen at https://macaulaylibrary.org/asset/475156091. The only references to mention Basic II and Basic III *unicinctus* plumages we found were Coulson & Coulson (2012), which has a brief description, and the recently published Pallinger & Menq (2022), which described only Basic II plumage.

We found no specimens or photographs exhibiting characters of both taxa. There are mentions of presumed juvenile Harris's Hawks in northern South America (Blake 1977, Coulson & Coulson 2012), but these probably involved Basic II and Basic III Bay-winged Hawks, which as described above possess a similar appearance.

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Behavioural ecology.—Harris's Hawk is a cooperative breeder, with nest helpers and polygamy, as well as cooperative hunting, reported regularly (Bednarz 1987, Bednarz & Ligon 1988, Coulson & Coulson 2013, Clark 2017, Dwyer & Bednarz 2020). We found only one record of a helper at a Bay-winged Hawk nest. M. Juhant (pers. comm.) saw two Basic III breeding Bay-winged Hawks with a juvenile-plumaged helper and chicks in a nest around Buenos Aires. Likewise, we found no reports of Bay-winged Hawk hunting cooperatively (e.g., Jiménez & Jaksić 1993). The two cases of trios reported by Salvador (2012) at 13 nests monitored were most likely cases of polygyny. The female of one trio that laid and incubated the eggs was in Basic II plumage, and the helper female was in adult plumage. Some references report Harris's Hawk as occurring in western South America (e.g., Blake 1977, Ortiz-Crespo 1986), but these are most likely due to sightings and specimens of the previously undescribed Basic II and Basic III plumages of Bay-winged Hawk. All specimens from this region are Bay-winged Hawks. Researchers in Ecuador have seen only Bay-winged Hawk in the field (J. Bednarz pers. comm., P. Bloom pers. comm.).

Coulson & Coulson (2013) found reports of cooperative hunting only in Harris's Hawk and only in North America; they found no records of such behaviour in Harris's Hawk in Middle America and in Bay-winged Hawk in South America. The lack of records of this behaviour from Middle America could be an artefact of fewer observers there. We believe that the lack of records from South America suggests that Bay-winged Hawk does not hunt, or rarely hunts, cooperatively.

DNA studies.—Only two molecular studies have included these taxa, Riesing *et al*. (2003) and Raposo do Amaral *et al*. (2009). The former screened two mitochondrial markers and stated 'Interestingly, intraspecific variability of *Parabuteo unicinctus* is not detected in the five specimens of our study, although the samples investigated cover much of the species' distribution in North and South America. This finding indicates a rapid and recent expansion from South America.' However, their figs. 2–4 show only three specimens. Raposo do Amaral *et al*. (2009) used sequences of mitochondrial DNA and one nuclear intron; they reported a small difference between two samples of *unicinctus* and one of *harrisi*. Lerner *et al*. (2008) sampled only *P. u. harrisi* in their molecular phylogeny of the buteonines.

Discussion

Main findings.—This study documents multiple differences between Harris's and Bay-winged Hawks in both adult plumage (six differences, including two fully diagnosable) and juvenile plumage (five diagnosable differences). In addition, we document a difference between them in plumage maturation: Bay-winged Hawk has four different plumages whereas Harris's has only two. Furthermore, our review of the behavioural and ecological evidence reveals that Harris's Hawk regularly hunts and breeds cooperatively, behaviours not reported for Bay-winged Hawk.

Taxonomic interpretation.—Modern views of species consider them as lineages (segments of population lineages; Mayden 1997, de Queiroz 1999, 2007). This concept is operationalised via integrative taxonomy (Padial *et al*. 2010, Sangster 2018). As described by Sangster (2018) and Wei *et al*. (2022), integrative taxonomy has several main tenets: (i) any type of data is potentially relevant to document differences between species, (ii) different types of evidence are complementary and can highlight different aspects of the speciation process, (iii) taxonomists should try to obtain as many lines of independent data as possible, (iv) data should be integrated to fully understand the evolutionary history of the relevant taxa, and (v) taxonomic evaluations should be revisited when novel data become available.

We used multiple, independent lines of evidence to address the taxonomic status of Harris's and Bay-winged Hawks. The many differences in adult and juvenile plumages

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strongly suggest that Harris's and Bay-winged Hawks each have a unique evolutionary history and are separate lineages. We believe that the differences in number of immature plumages are genetically based and corroborate the evolutionary distinctiveness of these taxa. In any case, we are unaware of any other single species of Accipitridae that has populations with different numbers of annual plumages. Cooperative hunting and breeding by Harris's Hawk and their absence in Bay-winged Hawk may be considered a further indication that the two taxa represent distinct lineages.

The Biological Species Concept (e.g., Mayr 1982, Johnson *et al*. 1999) does not address well how to categorise allopatric taxa as either species or subspecies, as its basis is that populations do not fuse into a single species when they come into contact (Mayr 1982: 285). Morphological differences between adult Harris's and Bay-winged Hawks may help reduce interbreeding if the two taxa were to come into contact. Even if pairing is successful, we suspect eggs would be infertile given differences in plumage maturation, probably reflecting considerable physiological differences between the taxa.

DNA evidence.—Clearly, further molecular comparisons of these taxa are called for, especially whole-genome sampling. The small difference identified between Harris's and Bay-winged Hawks may be interpreted by some as evidence against species rank. However, shallow genetic divergences between species are not unusual in Accipitriformes. For example, several widely accepted allopatric or parapatric species pairs show very low mitochondrial divergence, indicating recent separation or, in some cases, recent gene flow. These include Sanford's Sea Eagle *Haliaeetus sanfordi* / White-bellied Sea Eagle *H. leucogaster* (Wink *et al*. 1996), Himalayan Griffon *Gyps himalayensis* / Eurasian Griffon *G. fulvus* (Johnson *et al*. 2006), Galapagos Hawk *Buteo galapagoensis* / Swainson's Hawk *B. swainsoni* (Bollmer *et al*. 2006, Raposo do Amaral *et al*. 2009), Common Buzzard *B. buteo* / Long-legged Buzzard *B. rufinus* (Raposo do Amaral *et al*. 2009), Eurasian Sparrowhawk *Accipiter nisus* / Rufous-breasted Sparrowhawk *A. rufiventris* (Breman *et al*. 2013) and Eastern Marsh Harrier *Circus spilonotus* / Swamp Harrier *C. approximans* (Oatley *et al*. 2015).

English names.—Many authorities use the name Harris's Hawk for both subspecies of *P. unicinctus* (e.g., Dickinson & Remsen 2013, Gill *et al*. 2023). Clements *et al*. (2022) use Harris's Hawk for the species but Bay-winged Hawk for the subspecies *P. u. unicinctus*. Meyer de Schauensee (1970) used Bay-winged Hawk, with Harris's Hawk in parentheses. Ferguson-Lees & Christie (2001) and del Hoyo & Collar (2014) called the northern taxon (*harrisi*) Harris's Hawk and South American *unicinctus* Bay-winged Hawk, a convention we have followed herein.

Delayed plumage maturation.—Basic II and Basic III plumages of Bay-winged Hawk are not fully described in any raptor handbook, in any South American field guide or handbook, except Coulson & Coulson (2012), who briefly described Basic II and IIII plumages, and a new Brazilian raptor guide (Pallinger & Menq 2022), which described only Basic II plumage, under the vague term 'subadulto.' Delayed plumage maturation in Bay-winged Hawk is shared with three other buteonines in their South American ranges: White-tailed Hawk *Geranoaetus albicaudatus*, Variable Hawk *G. polyosoma* and Black-chested Buzzard *G. melanoleucus*. On the other hand, other buteonines in Harris's Hawk's range in Middle and North America lack delayed maturation, except White-tailed Hawk, which also occurs in South America.

The only accurate field guide illustrations of Bay-winged Hawk plumages we found are in Schulenberg *et al*. (2007), however Basic II and Basic III plumages were neither shown nor described. Ridgely & Greenfield (2001) illustrated adult Bay-winged Hawk with the dark remiges of Harris's Hawk. Brown & Amadon (1989) showed adult Harris's Hawk and juvenile Bay-winged Hawk, but did not indicate the taxon in either case. Del Hoyo *et al*.

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(1994) depicted adults of both taxa, but did not describe differences in juvenile plumages or the Basic II and Basic III plumages of Bay-winged Hawk. Robbins *et al*. (1966) depicted juvenile Harris's Hawk as a typical juvenile Bay-winged Hawk, with whitish underparts narrowly streaked dark and pale undertail with narrow dark bands. All other field guides to North and Middle America have illustrated Harris's Hawk plumages correctly (e.g., Howell & Webb 1995, Angehr & Dean 2010, Clark & Schmitt 2017).

It is not clear that the differences in presence or absence of cooperative hunting or breeding possess any taxonomic value. These could just be an adaptation to prey and habitat differences. As none of the other 320+ diurnal raptors has subspecies with different numbers of immature plumages, this character in itself very strongly hints at their speciation. If they were to hybridise, how many plumages would the offspring have, one, two, or three? Ferguson-Lees & Christie (2001) concluded their account of these taxa with 'the two might be better treated as allospecies', despite being unaware of the Basic II and Basic III plumages of Bay-winged Hawk. We agree that they should be considered as separate species for the reasons presented herein.

Distribution.—Some authorities (e.g., Dickinson & Remsen 2013, Clements *et al*. 2022) have mistakenly listed Harris's Hawk for north-west South America. These records probably involved Basic II or Basic III Bay-winged Hawks, as all authorities were unaware of these plumages and field observers would be unable to separate them from juvenile Harris's Hawk.

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The Founding Feathers: the true ancestry of the domestic Barbary Dove

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Summary.—In 2008 the International Commission for Zoological Nomenclature (ICZN) ruled that the name *Streptopelia risoria* (Linnaeus, 1758) should have priority for both African Collared Dove and its domestic form, Barbary Dove, as it is senior to *S. roseogrisea* (Sundevall, 1857). Many ignored the ruling in the belief that the ancestry of Barbary Dove is still unproven. Given the lack of a name-bearing specimen and in anticipation of the ICZN decision, in 2008 a neotype was designated for *S. risoria*. To clarify the taxonomic status of *roseogrisea*, as its original type series was mixed, in 2018 a neotype was also designated for this junior synonym of African Collared Dove. As the species was assumed to be polytypic, synonymisation of *roseogrisea* with *risoria* at species level was questioned thereafter. The results of a whole genome-resequencing study now show that African Collared Dove is the principal ancestor of Barbary Dove, and that the species is monotypic.

‘*risoria: C*[olumba] *supra lutescens, lunula cervicali nigraon.…Nobis communis Turtur*’
[dove with yellowish upperparts and black neck-ring.…Our common Turtle Dove]
(Linnaeus 1758)

The Barbary Dove, Ringed Dove or Ringneck Dove is the domestic form of African Collared Dove *Streptopelia risoria* (Linnaeus, 1758) and was already known in the 16th century, but details concerning its domestication are unclear. At the time Barbary Dove occurred in two varieties: a pale fawn-coloured form, and a near-white one. The original dark colour of the ancestral species was not then known to exist in captivity.

Long before the wild form was known to science, the pale fawn Barbary Dove had been described by Linnaeus (1758) as *Columba risoria* (Latin *risoris*: a laugher), presumably for its ‘giggling’ call. In his description, Linnaeus also listed *Turtur Indicus* of Aldrovandi (1600), Willughby (1678), Ray (1713) and Albin (1738) in its synonymy. He further stated that the bird was ‘our common Turtle Dove’ (nobis communis Turtur), which may suggest that it was commonly kept in Europe. It was later transferred, via the genus *Turtur* Selby, 1835, to *Streptopelia* Bonaparte, 1855. Its wild counterpart, African Collared Dove, was subsequently named *Streptopelia roseogrisea* (Sundevall, 1857) but, although the scientific name *S. risoria* is senior to *S. roseogrisea*, the latter was commonly accepted in ornithology and used as the valid name for both African Collared Dove and its domestic form until 2008.

Donegan (2007) applied to the International Commission for Zoological Nomenclature (ICZN) to conserve the junior name *roseogrisea* for the wild species but allow continued use of *risoria* for the domestic form, based on their previous approach to domestic mammals and their wild forms (ICZN 2003). However, the ICZN (2008) ruled that the valid name for both the wild and domestic forms is *Streptopelia risoria* (Linnaeus 1758). This change was not

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generally accepted, and many authorities, e.g. Dickinson & Remsen (2013), ignored the ruling in the belief that the ancestry of Barbary Dove is still unproven.

Donegan (2007, 2008) also argued that the nomenclature of *S. risoria* and *S. roseogrisea* is complicated by apparent reference to individuals of other species in the description of *Columba risoria*. This, however, is unlikely as was demonstrated by van Grouw (2018). As Donegan (2008) considered Linnaeus' name to be based on a mixed type series and, in connection with his application but prior to the ICZN's final decision, he established a neotype for *risoria*, based on a pale fawn-coloured specimen from captivity whose label indicated India as the specimen's origin (Fig. 1). The neotype designation for *S. risoria* (Linnaeus 1758) was justified, as no name-bearing specimen for *risoria* is believed to exist (and a type was necessary to define the taxon *risoria* objectively). Although Donegan (2008) argued that both Linnaeus and all other authors referred to in the latter's description, considered *risoria* to occur in India, Donegan ignored that the accounts on which Linnaeus was based include more details on the species as a captive bird in Europe. Captive birds were also the basis of the different illustrations (Fig. 2). A better choice therefore might have been a captive bird from Britain or elsewhere in Europe.

Figure 1. Neotype of *Streptopelia risoria*, NHMUK 2008.3.1 (Harry Taylor, © Natural History Museum, London)

The type series used by Sundevall (1857) to name African Collared Dove, however, certainly *was* mixed as the information concerning *risoria* [African Collared Dove] in Rüppell (1845), where he listed Le Vaillant's La Tourterelle blonde [= *Streptopelia capicola damarensis*] in synonymy, formed the basis for Sundevall's *roseogrisea* (van Grouw 2018). Given the conflict with *capicola*, van Grouw (2018) provided a neotype for *roseogrisea* to clarify its taxonomic status (Fig. 3). As two wild subspecies of African Collared Dove are currently recognised by most authorities, Donegan (2019) argued correctly that objective synonymisation of *roseogrisea* with *risoria* at species level might not be possible for several reasons. Firstly, Donegan (2019) questioned which subspecies is ancestor to the domestic form: the western population, nominate *roseogrisea* Sundevall, 1857, or eastern birds, *arabica* von Neumann, 1904. Further, as the neotype was collected in 'Abyssinia', which could refer to either modern-day Ethiopia or Eritrea, and both subspecies occur in parts of Ethiopia, it is unclear which subspecies the specimen represents. Lastly, if both subspecies have contributed to the domesticated form, and if domestic *risoria* has a mixed origin but is the senior name for the wild species then, according to Donegan (2019), subspecies taxonomy for wild populations would be impossible to unravel, and a further case to reverse the earlier decision (ICZN 2008) would prove necessary. Another possibility was not mentioned by Donegan; the species may be, in fact, monotypic. A molecular study of the history of African Collared Dove, its subspecies and

Figure 2. 'The Turtle Dove from the East Indies' [Barbary Dove], pl. 45 in Albin (1738). Albin wrote that they are 'kept in cages by the curious' and that all plates were based on live birds. Based on its colour and because Eurasian Collared Dove *Streptopelia decaocto* did not occur in Europe at the time, the dove used for this plate must have been a caged Barbary Dove in England. Linnaeus' description of *Columba risoria* was in part based on Albin's plate (Harry Taylor, © Natural History Museum, London)

Figure 3. Adult male African Collared Dove *Streptopelia risoria* collected by Rüppell in Eritrea and the designated neotype for the junior synonym *roseogrisea* of Sundevall, SMF 22887 (Sven Tränkner, © Senckenberg Museum, Frankfurt am Main). The species name *albiventris* on the label is a mistake by Finsch & Hartlaub (1870), who thought the dove collected by Rüppell was the same species as *Turtur albiventris* G. R. Gray, 1844. The latter, however, is a synonym of Vinaceous Dove *Streptopelia vinacea* (J. F. Gmelin, 1789). In their account of '*Turtur albiventris*' Finsch & Hartlaub used this specimen to describe the plumage.

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(Online)

the domestic form was necessary to unravel its internal taxonomy. The decision to do so was made shortly after van Grouw (2018) was published, and the results are presented herein.

Clarifying the status of African Collared Dove

Barbary Dove is widely considered to be the long-domesticated form of African Collared Dove. Shelley (1883) was probably first to recognise it as such, but thereafter many authors confirmed its ancestry based on evidence such as voice, behaviour and colour (Hartert 1916, Goodwin 1952, 1970, van Grouw 2018). Until now, there was no molecular confirmation of this, but based on more than ten years of personal observations on behaviour, voice and inheritance in Barbary, African Collared and Eurasian Collared Doves *S. decaocto* (van Grouw 1999), there appeared no doubt as to Barbary Dove's ancestry. Eurasian Collared and Barbary Doves readily hybridise, their offspring are fertile (van Grouw 1999) and, in places where both species occur, e.g. the Canary Islands, hybrid characters appear in both species (van Grouw 2022). However, for many reasons, e.g. voice, behaviour, range and colour, Eurasian Collared Dove is unlikely to have contributed to the domestic Barbary Dove. Also, Eurasian Collared Dove does not become tame in captivity, even after several generations, whereas wild-caught African Collared Doves quickly settle down in confinement (HvG pers. obs.).

Apart from its ancestry, nothing appears to be known of the early history of the domestic Barbary Dove. Aldrovandi (1600) received his live birds—a fawn male and white female—from Egypt and despite old common names like Indian Turtledove and, for the 'white' form, Java Dove (Swinhoe 1866; see Fig. 4), it is probable that the first domestication indeed occurred in Egypt (Sonnini de Manoncourt 1799).

Supposed differences between the two subspecies of African Collared Dove are marginal. Eastern *arabica*, in north-east Sudan, Eritrea, north-east Ethiopia, northern Somalia, and southern Arabia (Dickinson & Remsen 2013), is described as being slightly darker with more greyish underwings than nominate *risoria* (former *roseogrisea*) (Goodwin 1983, Gibbs *et al*. 2001), which ranges from Senegambia and Mauritania to central and southern Sudan and north-west Ethiopia (Dickinson & Remsen 2013). However, these characters occur throughout the species' range. Moreover, many 'nominate-like' features—paler coloured with whitish underwings—are also found in supposed *arabica* (HvG pers. obs.), making the hypothesis of two subspecies questionable. A third subspecies—*bornuensis*

Figure 4. Colombe Blanche *Columba alba* (= white form of Barbary Dove), pl. 46 in Temminck (1808) (Harry Taylor, © Natural History Museum, London)

Figure 5. Holotype of *Streptopelia roseogrisea bornuensis* Bannerman, 1931, adult male, Maidugari, Bornu, northern Nigeria, 20 December 1922, NHMUK 1923.10.26.8 (Jonathan Jackson, © Natural History Museum, London)

Bannerman, 1931—from northern Nigeria (for the province of Bornu), was described also as darker than the nominate (Bannerman 1931, Fig. 5) but is no longer recognised due to this character not being consistent.

The following questions need to be addressed using genetic data if the taxonomy of *S. risoria* is to be resolved: (1) is African Collared Dove the sole ancestor of domestic Barbary Dove, or has Eurasian Collared Dove contributed?; (2) are the two currently recognised subspecies of African Collared Dove, *risoria* and *arabica*, genetically distinct or not?; (3) if African Collared Dove possesses two genetically differentiated subspecies, can it be determined which, *risoria* or *arabica*, was involved in the domestication of Barbary Dove?; and (4) is 'modern' Barbary Dove genetically identical to 'early' Barbary Dove prior to European invasion by Eurasian Collared Dove, or are they now 'polluted' with Eurasian Collared Dove genes?

To achieve this, we elected to generate and analyse whole genome-resequencing data from samples of the following (see Table 1): historic museum specimens of Eurasian Collared Dove from 'India' and 'Arabia'; historic museum specimens of both subspecies of African Collared Dove; historic museum specimens of Barbary Doves of different origin; and modern captive Barbary Doves of different origin.

Methods

DNA extraction and quantification.—A total of 26 *Streptopelia* samples were loaned from multiple museums (23 dry toe-pad samples) and one private collection (three dry feather quills). The samples date from between 1871 and 2019 (Table 1). For DNA extraction and preparation for sequencing, we treated not only the historic but also more recently collected quill samples as 'historic' due to the post-collection storage conditions of the latter, thus all

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TABLE 1
Specimens sampled by this study. Museum acronyms: NHMUK = Natural History Museum, Tring; NMW = Naturhistorisches Museum Wien; SNM = Statens Naturhistoriske Museum, Copenhagen; SAM = South Australian Museum, Adelaide.

Species	**Locality**	**Collection date**	**Specimen number**	**Sample**	**Notes**
Streptopelia decaocto	Rajasthan (Rajputana), India	07/05/1871	NHMUK 1889.2.2.1485	D1 (toe-pad)	
Streptopelia decaocto	Rajasthan (Rajputana), India	14/06/1875	NHMUK 1889.2.2.1407	D2 (toe-pad)	
Streptopelia decaocto	Punjab (Mughal Serai), India	12/01/1875	NHMUK 1889.2.2.1505	D3 (toe-pad)	
Streptopelia decaocto	Oman, east Arabia	21/11/1977	NHMUK 1977.25.4	D4 (toe-pad)	
Streptopelia decaocto	Rostaq, Oman, east Arabia	19/04/1975	NHMUK 1975.8.4	D5 (toe-pad)	
Streptopelia decaocto	Imhoff, Saudi Arabia	10/11/1978	NHMUK 1978.7.2	D6 (toe-pad)	
Streptopelia decaocto	Bir Salem, coastal Israel	24/11/1918	NHMUK 1965.M.4694	D22 (toe-pad)	
Streptopelia risoria (*roseogrisea*)	South-west of Maidugari, Bornu, north Nigeria	24/12/1922	NHMUK 1923.10.26.9	D7 (toe-pad)	'*S. r. bornuensis*' collected at same time and place as holotype of *bornuensis* (see Fig. 5)
Streptopelia risoria (*roseogrisea*)	Mali (French Sudan)	15/11/1931	NHMUK 1932.8.6.25	D8 (toe-pad)	'*S. r. bornuensis*'
Streptopelia risoria (*roseogrisea*)	Tibesti, north Chad	01/04/1953	NHMUK 1955.41.12	D9 (toe-pad)	
Streptopelia risoria (*roseogrisea*)	El Fasher, Darfur, Sudan	16/03/1920	NHMUK 1920.12.22.54	D23 (toe-pad)	Specimen appears to have *S. decaocto* features, see Fig.13
Streptopelia risoria (*arabica*)	Western Saudi Arabia	29/02/1948	NHMUK 1965.M.4702	D10 (toe-pad)	
Streptopelia risoria (*arabica*)	Aden, Yemen, Arabia	25/02/1922	NHMUK 1965.M.4705	D11 (toe-pad)	
Streptopelia risoria (*arabica*)	Jeddah, Saudi Arabia	16/04/1934	NHMUK 1934.9.20.89	D12 (toe-pad)	
Streptopelia risoria (domestic form)	Preston Hall Aviary (captive)	before 1881	NHMUK 1881.5.1.2776	D13 (toe-pad)	Fawn
Streptopelia risoria (domestic form)	Staffordshire (captive)	24/03/1891	NHMUK 1891.3.14.2	D14 (toe-pad)	Fawn
Streptopelia risoria (domestic form)	India (captive)	before 1900	NHMUK 2008.3.1	D15 (toe-pad)	Fawn, neotype of *risoria*
Streptopelia risoria (domestic form)	Australia (feral)	1893	NMW 48.483	D16 (toe-pad)	Fawn
Streptopelia risoria (domestic form)	Europe (captive)	before 1900	NMW 37.875	D17 (toe-pad)	White
Streptopelia risoria (domestic form)	Adelaide, Australia (feral)	07/05/1992	SAM B46855	D18 (toe-pad)	Fawn
Streptopelia risoria (domestic form)	Copenhagen (captive)	09/01/1951	SNM 57.011	D19 (toe-pad)	Fawn
Streptopelia risoria (domestic form)	Copenhagen (captive)	04/10/1960	SNM 64.268	D20 (toe-pad)	Fawn
Streptopelia risoria (domestic form)	Europe (captive)	Before 1900	SNM 57.012	D21 (toe-pad)	White
Streptopelia risoria (domestic form)	Kuwait origin (captive)	2018	LDA (collection HvG)	D24 (feather quill)	Fawn and crested
Streptopelia risoria (domestic form)	Dutch origin (captive)	2018	LDB (collection HvG)	D25 (feather quill)	White
Streptopelia risoria (domestic form)	Belgium origin (captive)	2019	LDC (collection HvG)	D26 (feather quill)	White and silkie

samples were processed in a PCR-free laboratory dedicated to handling ancient DNA. During DNA extraction, the toe-pads were digested whole, while for feathers the *c*.5 mm tip of each quill (containing dried blood residues) was used. A 'blank' negative control extraction was included to screen for potential cross-contamination. We followed the Campos & Gilbert (2012) method for extracting DNA from historic keratinous materials, as follows. To remove potential external contaminants, the dry tissue was washed by vortex with 0.5 ml of a 5% dilution of commercial-strength bleach solution, followed immediately by a 0.5 ml ethanol wash and rinsing with two rounds of molecular grade water to remove bleach residue. The cleaned tissue was then immersed in 300µL of digestion buffer and incubated overnight (minimum 20 hours) at 57°C with 350RPM agitation. Subsequently DNA was recovered from the digested material using a silica-based purification that utilises Monarch DNA clean-up columns (New England Biolabs). DNA was eluted in 42µL of EBT constituting a mixture of Buffer EB (Qiagen) and 0.05% TWEEN20 detergent (Sigma Aldrich) and was quantified using the Qubit 4.0 Fluorometer (Thermo Fisher Scientific, Inc) and the 5200 Fragment Analyzer system (Agilent Technologies).

Genomic library building and sequencing.—Extracted DNA plus additional extraction blanks were converted into BGISeq sequencing technology-compatible (see Supplementary Table 1) single-stranded shotgun libraries following the Santa-Cruz Reaction (SCR) method of Kapp *et al*. (2021). DNA input volume and amount were determined via the tier system presented with this method. Libraries were purified using MinElute reaction clean-up columns (Qiagen) and were subsequently eluted in 30µL of EBT. The number of PCR cycles for each sample was determined through a real-time quantitative PCR performed on the purified libraries. Per sample, 10µL DNA library template was used for a single reaction of PCR amplification per 50µL containing 2.5U PFU Turbo CX Polymerase, 1× PFU Turbo buffer, 0.4 mg ml^{-1} bovine serum albumin (BSA), 0.25 µM mixed dNTPs, 0.1 µM BGI forward primer, and 0.1 µM BGI reverse index-primer. Amplified libraries were purified using a 1.4X beads:library ratio of HiPrep PCR clean-up beads (Magbio Genomics), were eluted in 30µL of EBT, quantified using the Qubit 2.0 Fluorometer (Thermo Fisher Scientific, Inc) and 2100 BioAnalyzer (Agilent), and were sequenced across a total of ten DNBseq-G400 lanes using 100bp SE sequencing chemistry via BGI Europe's commercial service. The raw sequence data generated can be accessed at the ENA Project ID PRJEB58897.

Data processing.—Sequence reads were mapped to the *Streptopelia turtur* reference genome (bStrTur1.1, Dunn *et al*. 2021) using PALEOMIX v.1.2.13.4 BAM pipeline (Schubert *et al*. 2014). This pipeline includes the trimming of adapters using AdapterRemoval v.2.2.0 (Schubert *et al*. 2016) according to the default parameters, followed by alignment of sequences against the reference genome using BWA v.0.7.17 backtrack algorithm (Li & Durbin 2009). The next step removes PCR duplicates using Picard MarkDuplicates (http://broadinstitute.github.oi/picard/) and, finally, local realignment around indels was performed using GATK v.3.8.3 IndelRealigner module (McKenna *et al*. 2010).

Multidimensional scaling plot.—We created a pseudo-haploid SNP panel using the function -doHaploCall in ANGSD v.0.931 (Korneliussen *et al*. 2014), which randomly samples one read at each site and retains the base if it fulfills the used filtering parameters. Sampling was restricted to only those scaffolds with a length of >1 Mb. Transitions were removed to avoid aDNA damage that could be found in historic samples. Sites with base quality and mapping quality lower than 30 were discarded. The final SNP dataset consisted of 4,287,405 transversion sites. We then used the SNP dataset to generate a multi-dimensional scaling (MDS) plot by estimating the pairwise distances between samples using Plink 1.90 (Chang *et al*. 2015).

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Nuclear genome phylogeny.—To estimate evolutionary relationships among *Streptopelia* individuals included in the dataset, a nuclear genome phylogeny was inferred. For this analysis, a Common Pheasant *Phasianus colchicus* (Liu *et al*. 2019) was included as the most external outgroup, as well as Band-tailed Pigeon *Patagioenas fasciata* (Murray *et al*. 2017). For each genome, ANGSD v.0.931 was implemented to generate genomic consensus sequences using *Streptopelia turtur* as reference genome ('-dofasta2' option). Then, 1,000 independent phylogenetic trees were estimated in RAxML-ng v.0.9.0 (Kozlov *et al*. 2019) under the GTR+G evolutionary model, using 1,000 random regions of 5,000 bp taken from the genomic consensus sequences previously created. Prior to the phylogenetic analysis, a quality check was implemented on the multiple sequence alignments using the function 'check' in RAxML-ng to search for format issues, including duplicate sequences. Later, all gene trees were concatenated to generate a species tree using ASTRAL-III (Zhang *et al*. 2018) which was visualised using the Interactive Tree Of Life (iTOL) v4 online tool (Letunic & Bork 2019).

Finally, a relative frequency analysis was implemented in DiscoVista (Sayyari *et al*. 2018) to measure discordance between the 1,000 individual gene tree topologies and the species tree generated with ASTRAL-III. This analysis evaluates the frequency of all gene tree topologies around internal branches of the inferred species tree.

Whole mitochondrial genome phylogeny.—A whole mitochondrial genome phylogeny was also estimated from the data. Sequence reads were mapped to the *Streptopelia decaocto* mitogenome (NC_037513.1) using PALEOMIX v.1.2.13.4 with the same parameters as described above. Consensus sequences were then generated using the '-dofasta2' function in ANGSD v.0.931. A mitochondrial genome sequence alignment was performed using the global pair iterative method as implemented in MAFFT v7.490 (Katoh & Standley 2013). A maximum likelihood phylogenetic tree was then estimated using RAxML-ng v.0.9.0 under the GTR+G evolutionary model.

D-statistics.—We used D-statistics, as implemented in ADMIXTOOLS (Patterson *et al*. 2012), to test the obtained topology in the species tree, as well as to explore the possibility of admixture among Eurasian Collared Dove (ECD), African Collared Dove (ACD) and domestic Barbary Dove (DBD). The previously generated dataset of SNPs was used for this analysis, and *Patagioenas fasciata* was used as outgroup in all of the tests described below. First, to understand the position of sample *S. risoria* D09 from Chad in the obtained tree, which appears in an intermediate position between the two *S. risoria* subspecies clades, a test was done in the form D(Outgroup, ACD-D09; ACD-*risoria*, ACD-*arabica*). A second set of tests was implemented to explore the possibility of admixture between ECD and DBD, using each DBD to be compared in the form D(Outgroup, ECD; DBD, ACD). A third set of tests aimed to clarify possible gene flow between ECD and ACD (*arabica* subspecies), comparing ECD against ACD samples of the *risoria* and *arabica* subspecies. Then, to explore in more detail the admixture patterns obtained in the last two tests, we implemented another D statistics analysis in form D(Outgroup, ACD/DBD; ECD, ECD) expecting to find the populations involved in the admixture process. Finally, with the intension to describe the different levels of ECD admixture in our DBD samples a set of tests was implemented in form D(Outgroup, ECD; DBD, DBD).

For any D-statistics analyses in the form D(Outgroup, A; B, C), any deviation of the result from 0 suggests possible shared ancestry or gene flow between the tested populations. If D <0, A and B share a higher level of genetic drift than expected, indicating possible gene flow; If D >0, it indicates possible gene flow between A and C. Deviation from 0 was considered statistically significant when the Z-score was below –3 or above +3. The significance of the test was estimated using a weighted block jack-knife procedure over 1 Mb blocks.

Results

We generated between *c*.86 and 278 million sequencing reads for each of the 26 sequenced specimens. Average read length ranged from 44 to 81 bp, and 22–59% of these reads could be mapped to the *Streptopelia turtur* reference nuclear genome, yielding final depths of coverages spanning *c*.1.23–8.48×. For full details see Supplementary Table 2. Both the MDS and whole-genome phylogeny show clear structure (Figs. 6–7), in particular separating the samples into three general groups. At a broad level, the MDS identifies the three groups as consisting of *S. decaocto*; domesticated Barbary Doves (*S. r. domestica*); and both putative subspecies of African Collared Dove (*S. r. risoria* and *S. r. arabica*) (Fig. 6). While this general separation into three groups is confirmed in the phylogeny based on 1,000 concatenated trees, it provides additional insights relevant to the initial questions raised. Firstly, rather than being reciprocally monophyletic, at face value our data reveal that *arabica* may be derived from *risoria*, given the relative placement of *risoria* sample D09 from Chad as more closely related to *arabica* samples than the other *risoria*. Secondly, domestic Barbary Dove derives principally from *arabica* African Collared Dove. We undertook several steps to explore these findings further. Firstly, we performed a relative-frequency analysis using DiscoVista to query the robustness of the species tree structure (Fig. 7B). These results confirm both high support for the separation of *S. decaocto* from other *Streptopelia* samples analysed (branch 6, Fig. 7B), and that *S. r. arabica* is more closely related to domestic Barbary Doves than to *S. r. risoria* (branch 8, Fig. 7B). However these results also revealed that the observed frequencies obtained for branches 7 and 9 (relating to the placement of *risoria* sample D09 and *arabica* D12, respectively) show high levels of discordance. This could potentially be caused by lack of resolution, hybridisation, or gene-tree estimation errors (Sayyari *et al*. 2018). The whole mitochondrial genome phylogeny estimated was also found to be generally consistent with the structure recovered for the whole-genome phylogeny, although small differences were observed (Fig. S1). Specifically, most of the domestic Barbary Doves were placed in the African Collared Dove clade, with the

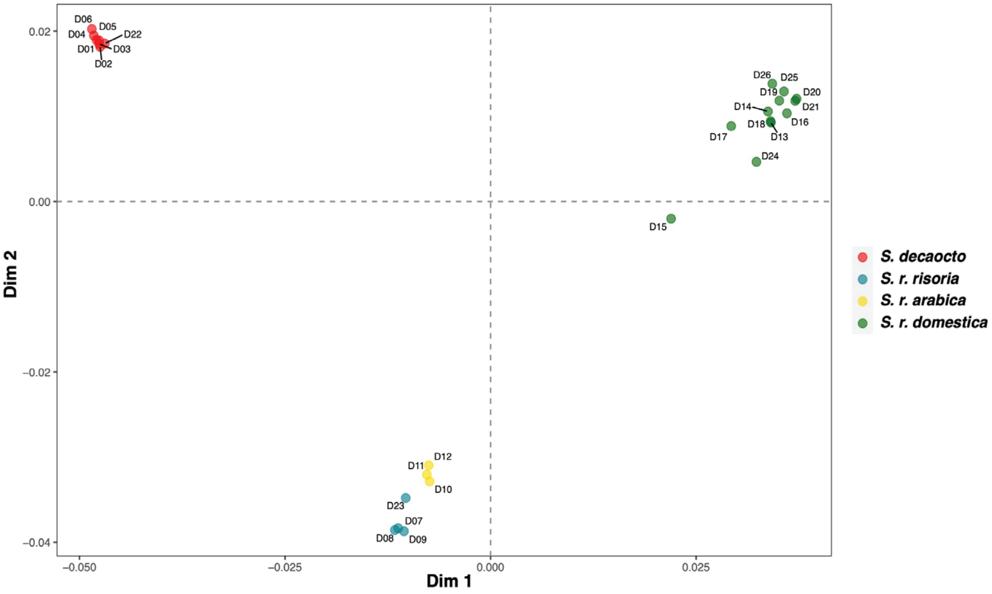

Figure 6. Multi-dimensional scaling (MDS) plot of all *Streptopelia* samples included in this study, using 4,287,405 random SNP variants from genomic data.

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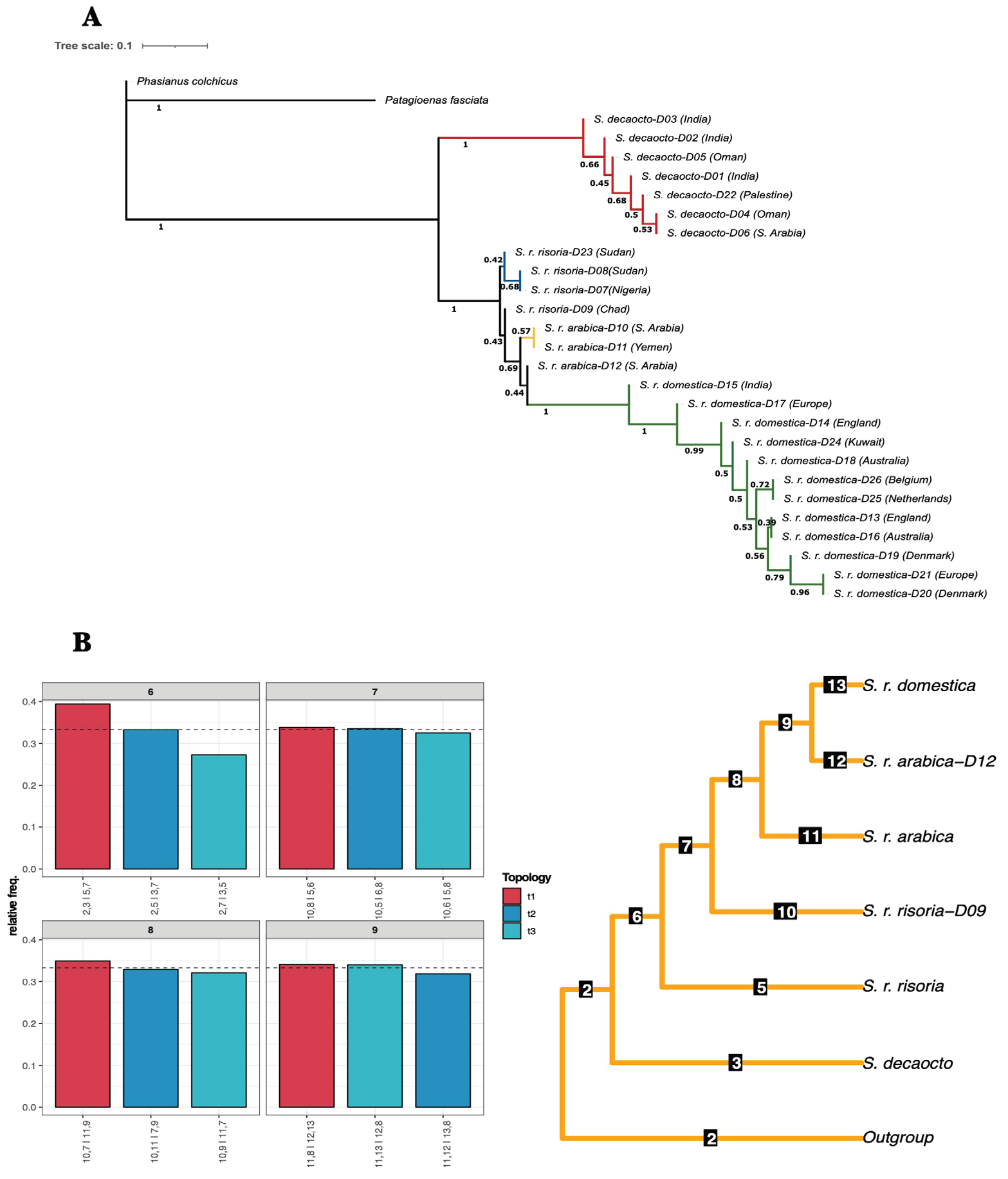

Figure 7. Concatenated nuclear genome phylogeny and relative frequency analysis of the concatenated species tree. (A) Maximum likelihood phylogenetic tree generated with ASTRAL-III using 1,000 genomic regions. The tree was rooted on Common Pheasant *Phasianus colchicus*. Bootstrap values are shown at the base of each internal node. Branch clade colour patterns match the colours used in the MDS plot in Fig. 6. (B) DiscoVista relative-frequency analysis. The tree at the left represents the species tree estimated by ASTRAL-III with monophyletic clades collapsed, where numbers are used to label the different branches of the tree. At the right, the frequencies of three possible configurations around focal internal branches are presented. Each box title refers to an internal branch on the left-hand tree. The first topology in red is the main topology followed by the other two alternatives in blue. On the Y-axes the relative frequency is indicated and the dashed lines represent the 1⁄3 threshold. On the X-axis each quartet topology is shown using neighbouring branch labels.

exception of four that were placed among Eurasian Collared Dove (samples D15, D16, D24 and D25). This could suggest possible admixture for those samples. Furthermore, we observed

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that *risoria* D09 from Chad was placed among the *arabica* samples, adding to the possibility that this sample or its lineage contains admixture with populations of the latter.

With respect to the question as to whether *arabica* and *risoria* are reciprocally monophyletic, we used D-statistics to explore the intermediate position of the *S. r. risoria* sample from Chad, D09, that places it as ancestor to the *arabica* clade (Fig. 8). Specifically, we compared this sample with all other *risoria* and *arabica* samples, finding that while in general D09 seems more closely related to other *risoria* than to *arabica* samples, one exception is its relationship to *arabica* D10, from Saudi Arabia, which may suggest a history of gene flow between the ancestors of D09 and *S. r. arabica* populations. Thus could explain the high discordance observed in branch 7 of the relative-frequency analysis (Fig. 7A).

D-statistics (Fig. 9) reveal a clear signal of admixture between Eurasian Collared and domestic Barbary Doves. When subspecies *arabica* was used in these tests, the signal is less strong and in some cases non-statistically significative (see Figs. S2–S3), which could be explained by a close relationship between *S. r. arabica* and domestic Barbary Doves, or be due to some degree of gene flow between Eurasian Collared and African Collared Doves in Arabia. To explore further for gene flow between Eurasian Collared and *arabica* African Collared Doves, we implemented another D-statistics analysis comparing each Eurasian Collared Dove against African Collared Dove samples of both subspecies (Fig. 10). The results showed that *S. decaocto* samples share a higher number of alleles than expected with the samples of *S. r. arabica*, suggesting possible gene flow between them. All tests showed a similar pattern (Fig. S4) except sample D09 from Chad which had less negative or even non-statistically significant D-values in line with our other results (Figs. 7–8) indicating that it is an admixed individual of the two *S. risoria* subspecies.

To identify which Eurasian Collared Dove populations were involved in the admixture processes, we performed additional D-statistics analyses that compared each domestic Barbary Dove, and each *arabica* African Collared Dove, against all Eurasian Collared Doves (Fig. 11). All tests revealed a similar pattern, in which all historic domestic Barbary Doves or *arabica* African Collared Doves share significantly more alleles with European Collared Doves

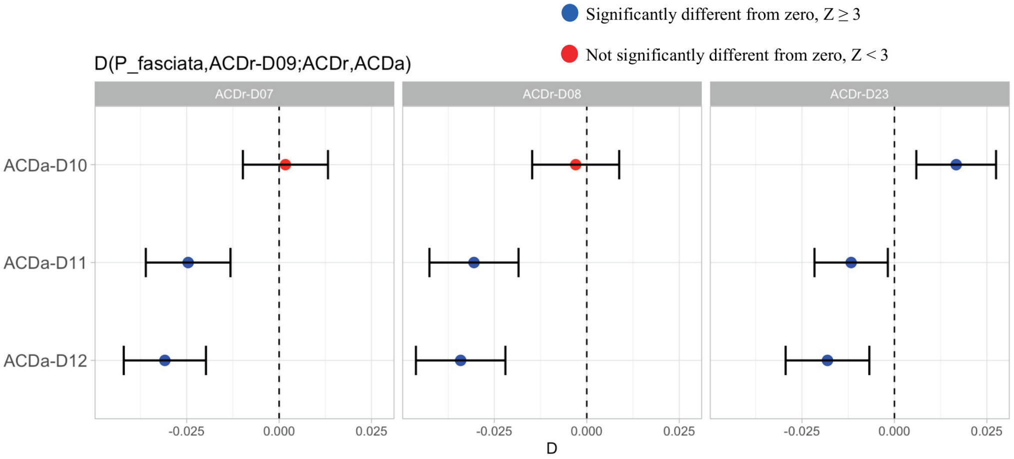

Figure 8. D-statistics analysis testing the species tree topology in Fig. 7 to confirm the intermediate position of *S. r. risoria* sample D09 between the *S. r. risoria* and *S. r. arabica* clades. The sample was compared with those of *risoria* (ACDr) and *arabica* (ACDa). D09 seems closer related to other *S. r. risoria* than to *S. r. arabica*, except sample D10, confirming its placement in the species tree and suggesting possible gene flow between *S. r. risoria* sample D09 and *S. r. arabica*. Band-tailed Pigeon *Patagioenas fasciata* was used as outgroup.

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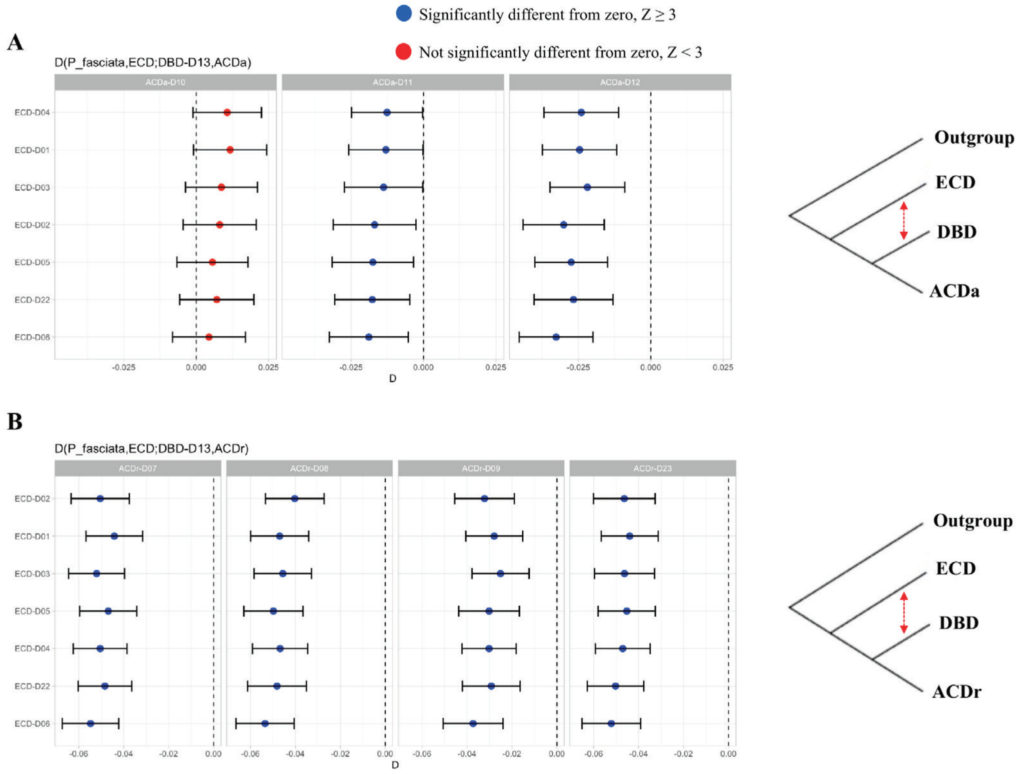

Figure 9. D-statistics analyses testing possible admixture between Eurasian Collared Dove *Streptopelia decaocto* (ECD) and domestic Barbary Dove (DBD). Results indicate gene flow between them. Band-tailed Pigeon *Patagioenas fasciata* was used as outgroup in all analyses. For this analysis each DBD was tested, obtaining a similar pattern. The plots shown were chosen as examples of the results: (A) when samples labelled *S. r. arabica* (ACDa) were used; and (B) samples labelled *S. r. risoria* (ACDr). ACDr samples show higher admixture signals than ACDa samples. The trees at the right represent the structure for each D-statistics test and the red arrows the gene-flow patterns obtained.

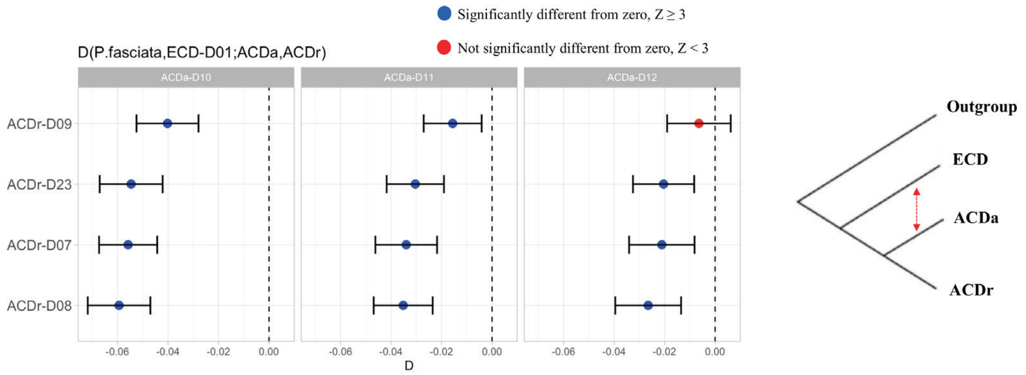

Figure 10. D-statistics analyses to test the possibility of admixture between Eurasian Collared Dove *Streptopelia decaocto* (ECD) and samples of *S. r. arabica* (ACDa). ACDr represents samples of *S. r. risoria*. Band-tailed Pigeon *Patagioenas fasciata* was used as outgroup in all analyses. An independent test was performed using each ECD sample in our dataset. The plot shown is used as an example of the results, which suggest admixture between ECD and ACDa. The tree at the right represents the structure for the D-statistics test and the red arrows the gene-flow pattern obtained.

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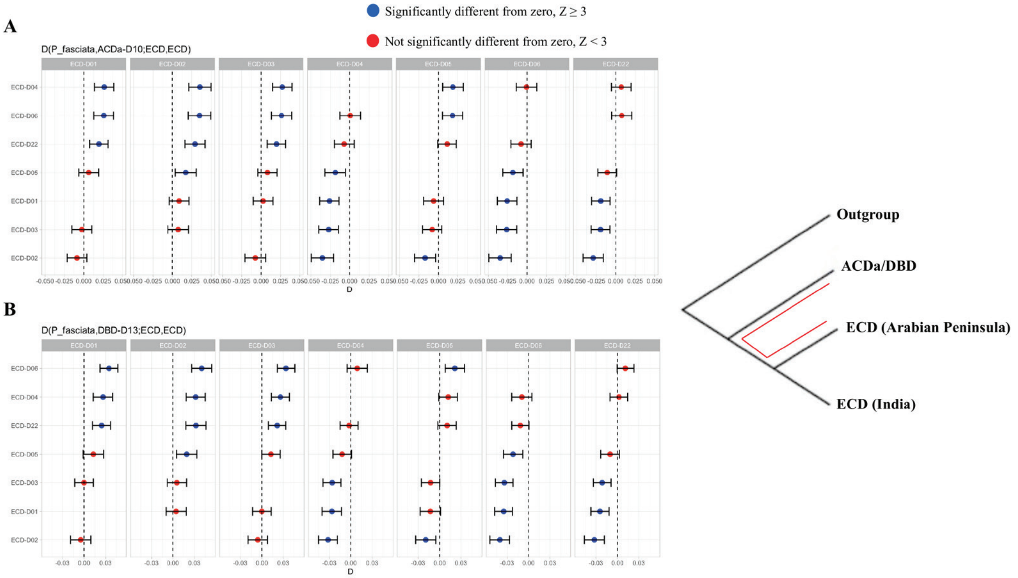

Figure 11. D-statistics analyses to identify Eurasian Collared Dove *Streptopelia decaocto* (ECD) populations involved in admixture with domestic Barbary Dove (DBD) and African Collared Dove *S. r. arabica* (ACDa). Band-tailed Pigeon *Patagioenas fasciata* was used as outgroup in all analyses. ECD samples on the Y-axes represent the second ECD population tested in the D-statistics structure at the top of each plot. All DBD and ACDa samples were tested. The plots shown are used as example of the results. All tests show a similar pattern in which DBD or ACDa significantly share more alleles with ECD from Arabia (mainly D06, D04 and D22) than to ECD from India (D01, D02 and D03), independent of age or geographical origin. The tree at the right represents the structure of the D-statistics analyses implemented and the red line shows the shorter branch in the analyses between ACDa/DBD and ECD. (A) Plot showing the results for ACD samples. (B) Plot showing the results for DBD samples.

from Arabia (mainly D06, D04 and D22) than to birds from India (D01, D02 and D03). This was consistent irrespective of the age or geographical origin of the DBD sample (Figs. S5–S6). These results therefore imply that admixture has occurred between the two species in the Arabian Peninsula.

Lastly, we used D-statistics to explore the different levels of Eurasian Collared Dove admixture in our domestic Barbary Dove samples (Fig. 12). The results revealed a consistent pattern, in which the most modern samples (D25 and D26 from 2018 and 2019) show the strongest signals of admixture with Eurasian Collared Doves (Fig. S7). In contrast, the pre-1900 samples (in particular D15 and D17) show much lower signals of admixture. This result appears to be in accordance with prior results for samples D15 and D17 (Fig. 7A, Fig. S2–S3).

Conclusions and Discussion

Considering these results, how can we answer the four questions we originally posed?

(1) *Is African Collared Dove the sole ancestor of domestic Barbary Dove, or has Eurasian Collared Dove also contributed?* Although our genomic data provide strong evidence that African Collared Dove is the principal ancestor of Barbary Dove, there is evidence of some admixture with Eurasian Collared Dove. Naturally, we caveat that given our limited sample size, we cannot fully describe the geographic extent over which admixture has occurred. However, in light of the facts that (i) our evidence suggests that *S. r. arabica* is the ancestor of the domestic form, and (ii) the admixture signal is similar in all historic domestic Barbary

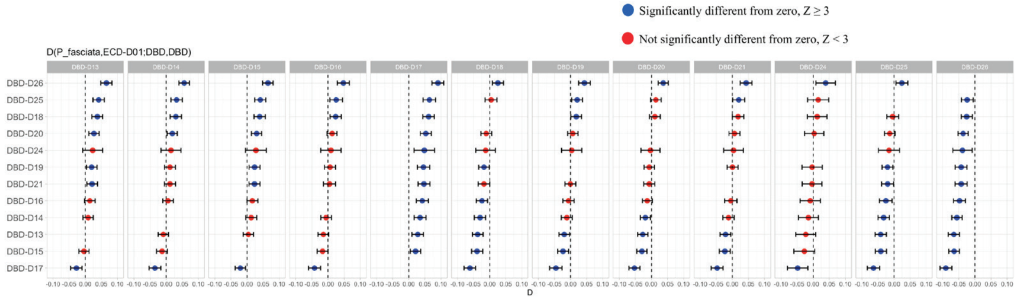

Figure 12. D-statistics analyses exploring the level of admixture between Eurasian Collared Dove *Streptopelia decaocto* (ECD) and domestic Barbary Dove (DBD). Band-tailed Pigeon *Patagioenas fasciata* was used as outgroup. DBD samples on the Y-axes represent the second DBD population tested in the D-statistics structure at the top of the plot. The same analysis was implemented for each ECD sample in our dataset. All results showed a similar admixture. The plot shown was chosen as an example of the results. The most modern samples (DBD-D25 and DBD-D26) show stronger signals of admixture with ECD, whereas DBD-D15 and DBD-D17 had the lowest levels of admixture.

Doves analysed irrespective of geographic origin, this provides strong evidence that admixture occurred early in the domestication process, hence allowing Eurasian Collared Dove genetic material from Arabia to spread across the domestic Barbary Dove range.

Theoretically only a single cross can release ‘foreign’ genes into a population which, we stress, is categorically *not* the same as having multiple ancestors. Red Junglefowl *Gallus gallus*, for example, is still recognised as the major ancestor of the domestic chicken, but this does not preclude participation by other species (Lawal *et al*. 2020). The admixture with Eurasian Collared Dove happened very early in the domestication, and most likely even before, as the admixture is also seen in African Collared Doves from Arabia (see Results above). Further, Barbary Dove has all the morphological and behavioural characters of African Collared Dove, therefore we consider the latter to be the principal ancestral species.

(2) *Are the two subspecies of African Collared Dove genetically distinct or the same?* Our results suggest the species can be considered monotypic, given the very limited genomic divergence between proposed subspecies and because *S. r. risoria* appears paraphyletic with the placement of Chad sample D09 as sister to *S. r. arabica*. One possibility is that the subspecies instead represent natural morphological and genetic structure arising across the species’ range, which analysis of a denser sample spanning the full geographical range could address.

Minor morphological differences in a species are often individual rather than taxonomic, and in this case earlier intermixing with Eurasian Collared Dove may also play a role (see Fig. 13). All but one of the described subspecies of Eurasian Collared Dove is now a considered synonym of the nominate because the supposed morphological differences are marginal and not consistent (van Grouw 2022). As the voice and behaviour of Barbary and African Collared Doves are similar (HvG pers. obs.), and differences in colour between African Collared Dove populations are minor and inconsistent, monotypy would be unsurprising.

(3) *If African Collared Dove has two genetically different subspecies, which is involved in the domestic Barbary Dove?* Irrespective of whether African Collared Dove should be considered polytypic, it is clear that domestic Barbary Dove derives from individuals assigned to *arabica*. This, combined with the evidence of early admixture with Arabian Peninsula Eurasian Collared Doves, may provide strong evidence for domestication having occurred in the region around the Red Sea, in line with earlier suggestions that domestication originated in Egypt (Sonnini de Manoncourt 1799).

Figure 13. The outer web of the outer tail feathers of Eurasian Collared Dove *Streptopelia decaocto* (left, NHMUK1889.2.2.1407, sample D2) is coloured and the coloured part extends beyond that on the inner web. The outer web of the outer rectrices of African Collared Dove *S. risoria* is usually not coloured (right, NHMUK1934.9.20.89, sample D12). First-generation hybrids (F1) between the two species have the outer web coloured, extending slightly beyond the coloured part of the inner web. The middle tail (NHMUK1920.12.22.54, sample D23), however, looks like a F1 hybrid based on morphological characteristics, but genetic analyses show it is a pure African Collared Dove; morphological differences within a species are often individual, rather than taxonomic characters (Jonathan Jackson, © Natural History Museum, London)

(4) *Are 'early' and 'modern' Barbary Dove genetically identical, or is the latter now 'polluted' by Eurasian Collared Dove genes?* Comparing the phylogenetic and admixture profiles of our Barbary Dove samples, we find neither evidence for major differences in origin nor admixture with Eurasian Collared Doves in the historic samples. Additionally, Barbary Dove has maintained similar genetic proportions of Eurasian Collared Dove through time, but modern samples D25 and D26 showed a much stronger admixture due to the fact that these samples are from after the invasion of Eurasian Collared Dove into western Europe. Since then, knowingly and unknowingly, breeders have crossed Barbary Doves with the now common Eurasian Collared Dove. Interestingly, the third modern sample, D24, did not show stronger admixture. Although the individual was received by HvG as a live bird in 1997 (died 2020) from Kuwait, according to the breeder the alleged origin of its ancestors was the Philippines. Eurasian Collared Dove does not (yet) occur in the Philippines, which may well explain its genetic make-up. The same applies to other more modern samples D18 (1992), D19 (1951) and D20 (1960), which are from countries where Eurasian Collared Dove does not occur or did not at the time. In sum, it appears that, other than in countries where Eurasian Collared Dove has invaded, over the last 100 years the domestic Barbary Dove has been genetically stable.

As indicated in earlier publications (e.g., Shelley 1883, Hartert 1916, van Grouw 1999, 2018) and now confirmed by genetic analysis, Eurasian Collared Dove has not contributed significantly to the domestic Barbary Dove, and African Collared Dove is the latter's principal ancestor. Despite being usually divided into two subspecies, African Collared Dove can be considered monotypic, and the domestic form (Barbary Dove) probably derived from the Arabian population.

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Figure 14. Possible syntypes at the American Museum of Natural History, New York, of *Peristera ridens* Brehm & Brehm 1855, collected by A. E. Brehm at Khartoum, Sudan in April–June 1851, from left to right, juvenile male, AMNH 613796; male, AMNH 613797; male, AMNH 613798; male, AMNH 613799; female, AMNH 613800. The name *ridens* (Latin *ridere*: to laugh) for the species given by Brehm & Brehm, 1855, is also senior to Sundevall's *roseogrisea*, but was never commonly used (Tom Trombone, © American Museum of Natural History, New York)

Furthermore, given that our data indicate that African Collared Dove is monotypic, the earlier assignment of a neotype for *roseogrisea* Sundevall, 1857, to clarify the status of this junior synonym (van Grouw 2018), is valid. The taxonomy of African Collared Dove is therefore as follows: *Streptopelia risoria* (Linnaeus, 1758), neotype at the Natural History Museum, Tring, NHMUK 2008.3.1 (Fig. 1), based on Donegan (2008). Synonyms: *Columba alba* Temminck, 1808, pl. 46 (see van Grouw 2018; Fig. 4), type specimen whereabouts unknown; *Peristera ridens* Brehm & Brehm, 1855, five possible syntypes at the American Museum of Natural History in New York (AMNH 613796–613800; Fig. 14); *Columba roseogrisea* Sundevall, 1857, neotype at the Senckenberg Museum, Frankfurt am Main, SMF 22887 (Fig. 3), based on van Grouw (2018); *Turtur fallax* Schlegel, 1873, holotype at Naturalis Biodiversity Center, Leiden, RMNH.AVES.87889; *Turtur roseogriseus arabicus* von Neumann, 1904, type specimen whereabouts unknown; *Streptopelia roseogrisea bornuensis* Bannerman, 1931, holotype in Tring, NHMUK 1923.10.26.8 (Fig. 5).

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Supplementary Materials

Figure S1. Maximum likelihood whole-mitochondrial genome phylogeny. Oriental Turtle Dove *Streptopelia orientalis* was used as outgroup. Bootstrap values are shown at the base of each internal node. The four different taxa are labelled as follows: Eurasian Collared Dove *S. decaocto* (red), African Collared Dove *S. r. risoria* (blue), *S. r. arabica* (yellow) and Barbary Dove *S. r. domestica* (green).

Figure S2. D-statistics analyses testing possible admixture between Eurasian Collared Dove *Streptopelia decaocto* (ECD) and domestic Barbary Dove (DBD) or African Collared Dove *S. r. arabica* (ACDa). Above each set of plots the analysis structure is shown. Each set of plots presents the results for each DBD in our dataset, excluding D13 which is shown in Fig. 4A. Band-tailed Pigeon *Patagioenas fasciata* was used as outgroup in all analyses. Deviation from 0 was considered statistically significant when Z-score was more or less than 3. The results for the domestic Barbary Doves D15 and D17 show distinct admixture patterns, suggesting that these samples present lower admixture with ECD, as also indicated by the results of other analyses (Fig. 7A and Fig 12).

Figure S3. D-statistics analyses testing possible admixture between Eurasian Collared Dove *Streptopelia decaocto* (ECD) and domestic Barbary Dove (DBD) or African Collared Dove *S. r. risoria* (ACDr). Above each set of plots the analysis structure is shown. Each set of plots presents the results for each DBD in our dataset, excluding D13 which is shown in Fig. 4B. Band-tailed Pigeon *Patagioenas fasciata* was used as outgroup in all analyses. Deviation from 0 was considered statistically significant when Z-score was more or less than 3. As in Fig. S2, domestic Barbary Dove sample D17 seems to exhibit the lowest admixture signals with ECD.

Figure S4. D-statistics analyses testing the possibility of admixture between Eurasian Collared Dove *Streptopelia decaocto* (ECD) and African Collared Dove *S. r. arabica* (ACDa). Each ECD sample in our dataset was tested. Each set of plots represents the performed analysis. All tests are presented here except the analysis for sample D01 which is shown in Fig. 5. Band-tailed Pigeon *Patagioenas fasciata* was used as outgroup in all analyses. Deviation from 0 was considered statistically significant when Z-score was more or less than 3.

Figure S5. D-statistics analyses were performed to identify the Eurasian Collared Dove *Streptopelia decaocto* (ECD) populations involved in the admixture with African Collared Dove subspecies *arabica* (ACDa). ECD samples at the Y axes represent the second ECD population tested in the D-statistics structure shown at the top of each plot. All ACDa samples were tested. The set of plots corresponding to sample D10 can be found in Fig. 6A. Band-tailed Pigeon *Patagioenas fasciata* was used as outgroup in all analyses. Deviation from 0 was considered statistically significant when Z-score was under or above 3.

Figure S6. D-statistics analyses to identify the Eurasian Collared Dove *Streptopelia decaocto* (ECD) populations involved in admixture with domestic Barbary Dove (DBD). ECD samples on Y-axes represent the second ECD population tested in the D-statistics structure above each plot. All DBD samples were tested. The set of plots corresponding to sample D13 are shown in Fig. 6B. Band-tailed Pigeon *Patagioenas fasciata* was used as outgroup in all analyses. Deviation from 0 was considered statistically significant when Z-score was more or less than 3.

Figure S7. D-statistics analyses to explore different levels of admixture between Eurasian Collared Dove *Streptopelia decaocto* (ECD) and domestic Barbary Dove (DBD). DBD samples on Y-axes represent the second DBD population tested in the D-statistics structure shown above the plot. Each ECD sample in our dataset was tested. All results are shown except those for sample D01 shown in Fig. 7. Band-tailed Pigeon *Patagioenas fasciata* was used as outgroup in all analyses. Deviation from 0 was considered statistically significant when Z-score was more or less than 3.

Table S1. BGI sequencing technology-compatible adapter and splint sequences. BGI_AD1 adapter and splint are homologous to the Illumina P7 adapter and splint and BGI_AD2 adapter and splint are homologous to the Illumina P5 adapter and splint defined in Kapp *et al*. (2021).

Table S2. Sequencing data generated for all the *Streptopelia* samples used in this study. [1] Final reads used in the analyses after removing PCR duplicates and quality filtering.

Results of ornithological inventories in north-west Minas Gerais state, Brazil, with notes on distribution and conservation

by Eduardo França Alteff

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http://zoobank.org/urn:lsid:zoobank.org:pu:pub:6B5428B0-BBD8-46A4-A53F-42C14F7A03A0

Summary.—Based on 30 days of field surveys in the north-west of the state of Minas Gerais, Brazil, in 2014, I report notable records of 40 bird species. In total, 293 species were recorded at three sites, including 15 species at risk of extinction (at state, national or global levels) and another four species whose status is insufficiently known to be placed in any threat of extinction category in Minas Gerais or Brazil. Records of three species are new for the São Francisco basin, and 13 are new for north-west Minas Gerais. Among the rarest species reported are Dwarf Tinamou *Taoniscus nanus*, Jabiru *Jabiru mycteria*, Black Hawk-Eagle *Spizaetus tyrannus*, Ocellated Crake *Micropygia schomburgkii*, Uniform Crake *Amaurolimnas concolor*, Russet-mantled Foliage-gleaner *Syndactyla dimidiata*, Minas Gerais Tyrannulet *Phylloscartes roquettei*, Chapada Flycatcher *Guyramemua affine*, Reiser's Tyrannulet *Phyllomyias reiseri*, Rufous-tailed Attila *Attila phoenicurus*, Black-collared Swallow *Pygochelidon melanoleuca* and Blackish-blue Seedeater *Amaurospiza moesta*.

Brazil has one of the richest avifaunas in the world with 1,971 species (Pacheco *et al*. 2021). The state of Minas Gerais is situated at the intersection of the Cerrado, Atlantic Forest and Caatinga biomes (Olson *et al*. 2001) and, consequently, harbours at least 787 of those species (Mattos *et al*. 1993, Ribon *et al*. 2006). Therein, the municipality of João Pinheiro, in north-west Minas Gerais, was defined as a priority area for bird conservation, regarded as 'very high' in biological importance, whilst the municipality of Vazante was identified as of 'extreme' importance (Drummond *et al*. 2005). The birds of the north-west of the state have been researched since the 19th century, starting with the Danish naturalist Peter Wilhelm Lund, who stayed in the municipality of Paracatu during 3–15 September 1834 (Pinto 1938). In the last three decades, the avifauna of this region has received greater attention (Mattos *et al*. 1991, Lopes *et al*. 2008a, Faria *et al*. 2009, Mazzoni *et al*. 2015).

However, due to the large area of north-west Minas Gerais, the number and coverage of bird surveys is still small. With the loss of native vegetation over time, many areas are cleared without their biodiversity being known. Faunal inventories assume an important role in decision-making for the management and conservation of natural resources. Given this scenario, my aim is to present the results of avifaunal inventories and noteworthy records from two field surveys in north-west Minas Gerais. Furthermore, comments are made on the natural history of some species, geographic distribution and on actions that may contribute to bird conservation in the studied region.

Material and Methods

Study area.—The municipalities of João Pinheiro, Vazante and Paracatu are all in north-west Minas Gerais (Fig. 1), in the Cerrado biome (Olson *et al*. 2001). All study sites are in the Paracatu River sub-basin, which covers 4,137,171 ha. The Paracatu itself is 465 km long

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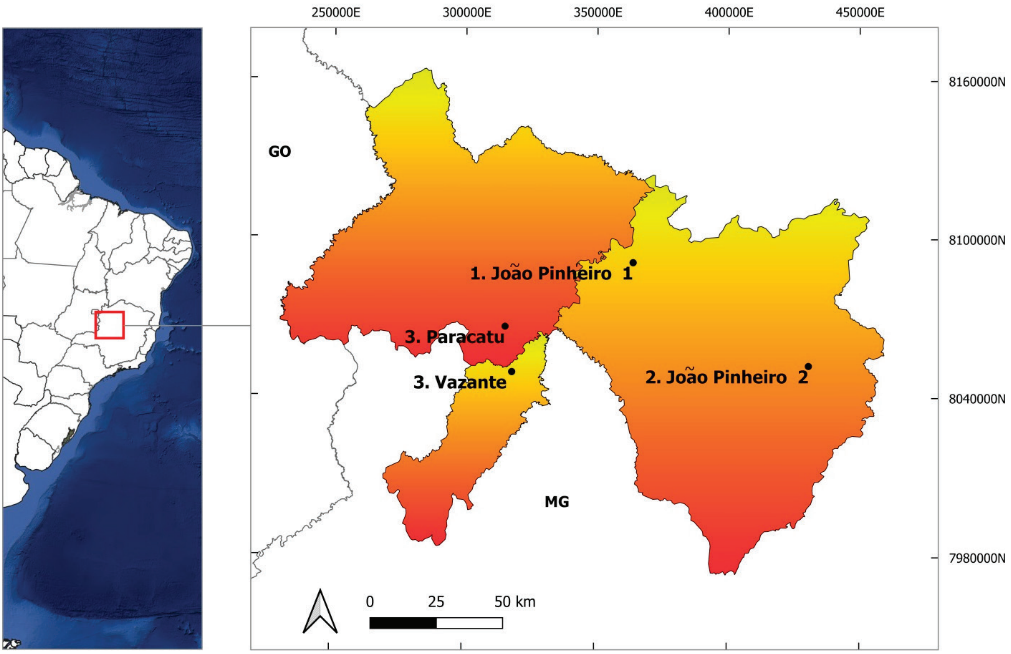

Figure 1. Location of the study sites in the municipalities of João Pinheiro, Vazante and Paracatu, in north-west Minas Gerais state, Brazil. States: MG = Minas Gerais, GO = Goiás.

and is a left-bank tributary of the middle São Francisco River. According to the Köppen classification, the region's climate is Aw with a dry winter (Alvares *et al*. 2013), and in the study region there are two well-defined seasons: dry (May–September) and wet (October–April). Phytophysiognomies cited herein were characterised *sensu* Oliveira-Filho & Ratter (2002). The study localities are described below.

1. *João Pinheiro municipality 1*. In the north-west of the municipality around Mutuca stream (17°15′45″S, 46°17′02″W; 535 m), the Verde River and its tributary, Feio stream (17°17′34″S, 46°10′55″W; 513 m), there are *c*.20,000 ha of diverse habitats including gallery forest, *cerradão*, *cerrado sensu stricto*, *campo cerrado*, *campo sujo*, *campo limpo*, *veredas*, forestry and other anthropogenic areas.

2. *João Pinheiro municipality 2*. In the east of the municipality, the main rivers are the Santo Antônio (17°37′05″S, 45°39′14″W; 626 m) and its tributary, the Contenda (17°38′40″S, 45°35′09″W; 758 m). The site covers *c*.8,000 ha, with gallery forest, *cerradão*, *cerrado sensu stricto*, *campo cerrado*, *campo sujo*, *campo limpo*, *veredas*, silviculture and disturbed areas.

3. *Vazante and Paracatu municipalities*. In Vazante, study sites were on the Paracatu River (17°35′36″S, 46°35′49″W; 534 m), and on the right bank of its tributary, the Escuro River (17°33′41″S, 46°39′57″W; 521 m). Remnants of natural vegetation (nearly 1,500 ha) included gallery forest, *veredas*, *cerradão*, *cerrado sensu stricto*, *campo cerrado* and *campo sujo*. Forestry predominates in the region, with cattle ranching in several places. In Paracatu, sites were on the left bank of the Escuro River, at the border between the municipalities of Paracatu and Vazante, where the largest forest remnant in the region, >1,000 ha (17°35′57″S, 46°42′35″W; 532 m), is found. There is also a tributary of the Escuro, Escurinho stream (17°28′29″S, 46°44′45″W; 534 m). Habitats include gallery forest, *cerradão* and *cerrado sensu stricto*. Silviculture is the principal economic activity, with land earmarked for agriculture and livestock, sometimes integrated (agroforestry).

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Avifaunal surveys.—The first survey occurred on 26 April–12 May 2014 (late wet season), with the second on 22 July–6 August 2014 (dry season). Field work was undertaken at three locations, with a sampling effort of 210 hours over 30 days (ten days at each site, five per season). Observations were made with binoculars, between 05.00 h and 22.00 h, mostly in early morning and late afternoon, using a sound-recorder plus directional microphone and a digital camera to document interesting records. Some sound-recordings and photographs have been deposited in the WikiAves database (www.wikiaves.com.br) and are indicated by the reference number that corresponds to the file on the website (e.g., WA 5218872 = www.wikiaves.com.br/5218872).

Systematics and taxonomy follow Pacheco *et al*. (2021). Conservation status (threatened, Near Threatened or Data Deficient) is based on the most recent listings at state (Fundação Biodiversitas 2007, Copam 2010), national (ICMBio 2014, MMA 2022) and global levels (BirdLife International 2023). Distribution maps were consulted on the BirdLife International website (www.birdlife.org). Distances reported for range extensions were measured using Google Earth.

The list of species in north-west Minas Gerais was compiled from the literature (Lopes *et al*. 2008a, Faria *et al*. 2009, Mazzoni *et al*. 2015). To prepare a list of species recorded in the São Francisco basin, the synthesis of the avifauna of the São Francisco River in Minas Gerais, which lists 614 species (Diniz *et al*. 2012), and an inventory of the lower and middle São Francisco River in Bahia, during which 315 species were recorded (Schunck *et al*. 2012), were compared. These studies totalled 620 species, with six exclusive to the Bahia portion of the river, Indigo Macaw *Anodorhynchus leari*, Common Ground Dove *Columbina passerina*, Straight-billed Woodcreeper *Dendroplex picus*, Lesser Wagtail-Tyrant *Stigmatura napensis*, Rufous-crowned Greenlet *Hylophilus poicilotis* and Yellow-faced Siskin *Sporagra yarrellii* (Diniz *et al*. 2012, Schunck *et al*. 2012), although one (Rufous-crowned Greenlet), is plainly out of range (BirdLife International 2023) and was considered incorrect, thus 619 species in total.

To define records as the first for north-west Minas Gerais and/or the basin, the previous literature was searched (e.g., Lopes *et al*. 2008a, Faria *et al*. 2009, Diniz *et al*. 2012, Schunck *et al*. 2012, Mazzoni *et al*. 2015), as well as the online database WikiAves (2023).

Results and Discussion

A total of 293 bird species was recorded at the three sites over 30 days (Appendix), or 37% of the avifauna of Minas Gerais (Mattos *et al*. 1993, Ribon *et al*. 2006) and 47% of the avifauna of the basin; 252 species were recorded in April/May 2014 and 267 species in July/August 2014. Species richness was considerable, especially as the study did not include the early wet season, when most species breed and activity is greatest (pers. obs.).

After ten days at each study site, 239 species were recorded in Vazante and Paracatu municipalities (194 in the wet season and 212 in the dry season). At 'João Pinheiro 1', 234 species were found (191 in the wet and 211 in the dry), whilst at 'João Pinheiro 2', 182 species were identified (147 in the wet and 156 in the dry). The smallest number of species was at the site where the vegetation was mainly grassland, with little forest and usually small fragments. The number of species recorded was consistently higher in the dry season, which was contrary to expectations (pers. obs.).

Some 140 species were recorded at all sites (47%), 82 at two locations (28%) and 71 were exclusive to one locality (25%). Mention must be made of the 15 species at risk of extinction (Appendix), of which 14 are threatened at state level, three nationally and three globally, including one Critically Endangered at state level. Records of all threatened species are detailed under Noteworthy records. Four species are Data Deficient at state or national

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level (Appendix), a category used for species too poorly known to assign an IUCN Red List category. Three species are so classified at state level—Sungrebe *Heliornis fulica*, Suiriri Flycatcher *Suiriri suiriri suiriri* and Reiser's Tyrannulet *Phyllomyias reiseri*—and one in Brazil, Chapada Flycatcher *Guyramemua affine*.

Despite the São Francisco River being relatively well sampled from an ornithological standpoint, records of three species were new for the basin, Uniform Crake *Amaurolimnas concolor*, Swallow-winged Puffbird *Chelidoptera tenebrosa* and Rufous-tailed Attila *Attila phoenicurus*. Another three were added to the list of species in the basin in Minas Gerais, namely Buff-fronted Owl *Aegolius harrisii*, Black-collared Swallow *Pygochelidon melanoleuca* and Sungrebe *Heliornis fulica* (Ubaid *et al*. 2012, Silva *et al*. 2017, Souza *et al*. 2018), thus 620 species are now known from the São Francisco basin in Minas Gerais and 625 species across the entire basin.

The survey produced records of 13 species new for north-west Minas Gerais: Gilded Hummingbird *Hylocharis chrysura*, Grey-breasted Crake *Laterallus exilis*, *Amaurolimnas concolor*, Pavonine Cuckoo *Dromococcyx pavoninus*, Buff-fronted Owl *Aegolius harrisii*, *Chelidoptera tenebrosa*, Barred Forest Falcon *Micrastur ruficollis*, Cinereous-breasted Spinetail *Synallaxis hypospodia*, Eared Pygmy Tyrant *Myiornis auricularis*, Chilean Elaenia *Elaenia chilensis*, Reiser's Tyrannulet *Phyllomyias reiseri*, *Attila phoenicurus* and Orange-fronted Yellow Finch *Sicalis columbiana*.

In the municipalities of Unaí and Cabeceira Grande, 316 species were recorded by Lopes *et al*. (2008a), with 24 subsequently added to the list, increasing it to 340 species (Mazzoni *et al*. 2015). Elsewhere, in north-west Minas Gerais, at Fazenda Brejão, Brasilândia de Minas municipality, 273 species were found, including 14 not recorded by other studies (Faria *et al*. 2009): Tataupa Tinamou *Crypturelus tataupa*, Giant Wood Rail *Aramides ypecaha*, Limpkin *Aramus guarauna*, Pied Lapwing *Vanellus cayanus*, Large-billed Tern *Phaetusa simplex*, Blue Ground Dove *Claravis pretiosa*, Stripe-breasted Starthroat *Heliomaster squamosus*, Black-and-white Hawk-Eagle *Spizastur melanoleucus*, Blond-crested Woodpecker *Celeus flavescens*, White-throated Woodcreeper *Xiphocolaptes albicollis*, Rusty-backed Spinetail *Cranioleuca vulpina*, Greenish Elaenia *Myiopagis viridicata*, Small-billed Elaenia *Elaenia parvirostris* and Yellowish Pipit *Anthus chii*. The sum of previous avifaunal studies in north-west Minas Gerais (354 species) and the data presented here (an additional 13 species), is 367.

Interesting records made during the surveys, including range extensions and natural history observations, together with remarks on conservation, are reported below.

Noteworthy records

DWARF TINAMOU *Taoniscus nanus*

Endangered at state, national and global levels. On 5 May 2014, one was sound-recorded at João Pinheiro in *campo sujo* with nearby *vereda*, in the headwaters of the Santo Antônio River. Endemic to the Cerrado (Silva & Bates 2002), typical of grasslands, rare and difficult to detect due to its secretive behaviour (Silveira & Silveira 1998, BirdLife International 2023). In north-west Minas Gerais, there are records in the municipalities of Bonfinópolis de Minas (Silveira & Silveira 1998), as well as at Patrocínio, in the Triângulo Mineiro (Machado *et al*. 1998), and Serra da Canastra National Park and environs (São Francisco basin), in the west of the state (Silveira 1998, Silveira & Silveira 1998, WikiAves 2023). Silveira & Silveira (1998) listed records at six localities, which subsequent work has approximately doubled (Kirwan *et al*. 2015, WikiAves 2023). During 16 years of sporadic field work in the Cerrado biome, principally in Minas Gerais, Goiás and Distrito Federal, with knowledge of its principal vocalisation since 2007, this is my only record of the species, providing some measure of its rarity.

ISSN-2513-9894
(Online)

BARE-FACED CURASSOW *Crax fasciolata*
Endangered in Minas Gerais and Vulnerable globally. In João Pinheiro, one on 29 July 2014 along Feio stream, and a male on 3 August 2014 at the Santo Antônio River. In Paracatu, a male was seen on 8 May 2014 at the Escuro River. Occurs mainly in riparian and gallery forests, but will use *cerrado sensu stricto* and even approach houses in rural landscapes, searching for food (pers. obs.). Most records are in forests on banks of rivers and streams (Bagno & Marinho-Filho 2001). Hunting, together with habitat loss, are responsible for its reduced numbers (BirdLife International 2023).

LONG-TAILED GROUND DOVE *Uropelia campestris*
Seen on both surveys, at all sites, with *c.*12 in total. One was sound-recorded in *campo sujo* on 29 April 2014, and another was seen beside highway BR-040, feeding on grain spilt from passing trucks (corn and soybeans). Uncommon, generally in grassland (Stotz *et al*. 1996). In Minas Gerais, its range encompasses the north, north-west, a small part of the Triângulo Mineiro, and the centre of the state (BirdLife International 2023, WikiAves 2023).

SCALED PIGEON *Patagioenas speciosa*
Three heard on 25 July 2014 in Vazante, in *cerradão*, of which one was sound-recorded. Uncommon (Stotz *et al*. 1996), often in forest, but also in nearby open areas (pers. obs.). Has probably declined due to habitat loss (BirdLife International 2023), but was first seen in north-west Minas Gerais in 2013, in Paracatu (WikiAves 2023). There are also records in the Triângulo Mineiro and the north-east of the state (WikiAves 2023). Listed for the São Francisco basin in Minas Gerais (Diniz *et al*. 2012), and the only records in the north-west of the state are from this watershed (WikiAves 2023).

JABIRU *Jabiru mycteria*
Endangered in Minas Gerais. One photographed on 27 April 2014, flying over Feio stream near its confluence with the Verde River, João Pinheiro (WA 1589749). In Vazante, one flew over the Escuro River on 8 May 2014. Occasionally recorded in north-west Minas Gerais (WikiAves 2023), where also reported at Fazenda Brejão (Faria *et al*. 2009), the municipality of Arinos (Machado *et al*. 1998) and around Unaí and Cabeceira Grande (Lopes *et al*. 2008a).

WOOD STORK *Mycteria americana*
Vulnerable in Minas Gerais. On 10 May 2014, one photographed on the Escuro River, at the border between Vazante and Paracatu (WA 5218874). On 24 July 2014, three in flight along Escurinho stream. Also mentioned for Arinos, Formoso, Brasilândia de Minas and João Pinheiro (Machado *et al*. 1998).

ROSEATE SPOONBILL *Platalea ajaja*
Vulnerable in Minas Gerais. Three on 24 July 2014 flying over the Escuro River, municipalities of Vazante and Paracatu; one was photographed (WA5218872). Rare in central Brazil, usually seen alone or in small groups (pers. obs.). Also recorded in Arinos, Brasilândia de Minas and Vazante (Machado *et al*. 1998).

BLACK HAWK-EAGLE *Spizaetus tyrannus*
Endangered in Minas Gerais. One sound-recorded on 8 May 2014, in flight over riparian forest at the Escuro River, at the border of Paracatu and Vazante. In the north-west of the state, listed previously only for Fazenda Brejão (Faria *et al*. 2009, WikiAves 2023).

SOUTH AMERICAN SNIPE *Gallinago paraguaiae*
One sound-recorded at night on 3 August 2014, at a *vereda* in the headwaters of the Santo Antônio River in João Pinheiro. Apparently unusual in north-west Minas Gerais (WikiAves 2023), with records in Unaí and Cabeceira Grande (Lopes *et al*. 2008a). Remains hidden in tall grasses, vocalising only occasionally, including at night, making it difficult to observe and perhaps explaining the small number of records in the region (pers. obs.).

GILDED HUMMINGBIRD *Hylocharis chrysura*
One seen and sound-recorded on 26 July 2014 in *campo sujo* near the Paracatu River (WA 1687375). Apparently migratory in the region, being recorded only sporadically in July–August in Minas Gerais (WikiAves 2023). This record is the first for the north-west of the state.

OCELLATED CRAKE *Micropygia schomburgkii*
Endangered in Minas Gerais and Near Threatened in Brazil. On 29 April 2014, sound-recorded in João Pinheiro, with three present in *campo sujo*. Can be common in tall grassland (Lopes *et al*. 2010b, Mazzoni *et al*. 2012, Alteff & Marçal-Júnior 2019). In Minas Gerais, recent records available only for Serra da Canastra National Park (Vasconcelos *et al*. 2006), the Triângulo Mineiro (Lopes *et al*. 2010b, Alteff & Marçal-Júnior 2019), the centre-east (Mazzoni *et al*. 2012) and in the north-west at São Gonçalo do Abaeté (WikiAves 2023).

GREY-BREASTED CRAKE *Laterallus exilis*
One sound-recorded on 24 July 2014 in a *vereda* with a few buriti palms *Mauritia flexuosa*, near the Escuro River, Vazante. The first record for north-west Minas Gerais, in which state the species was recorded for the first time only recently (Lopes *et al*. 2010a). Other records in João Pinheiro in 2018 and Paracatu in 2019 (WikiAves 2023).

UNIFORM CRAKE *Amaurolimnas concolor*
A pair sound-recorded on 26 April 2014 in João Pinheiro, along Mutuca stream, in gallery forest with associated *vereda*. On 28 April 2014, one was heard at a separate locality with the same habitat, again along Mutuca stream. A rare species, these are the first records for north-west Minas Gerais and the São Francisco basin. Recorded in Distrito Federal (Bagno & Marinho-Filho 2001, Lopes *et al*. 2012), the municipality of Uberlândia, Triângulo Mineiro region (Alteff & Marçal-Júnior 2019), and around Emas National Park, Goiás, all in the Paranaíba basin, usually in similar habitats (pers. obs.).

SUNGREBE *Heliornis fulica*
Data Deficient in Minas Gerais. A female photographed on 24 July 2014 on the Escuro River, at the border between Vazante and Paracatu (WA1580754). Usually on rivers and dams flanked by forests, as in the Triângulo Mineiro and southern Goiás (pers. obs.). Not previously recorded in the São Francisco basin (Diniz *et al*. 2012), but subsequently reported at Pompéu, in central Minas Gerais (Souza *et al*. 2018).

PAVONINE CUCKOO *Dromococcyx pavoninus*
Sound-recorded on 1 August 2014, when three were heard in *cerradão* in João Pinheiro. Previously reported for the São Francisco watershed, but my record is the first for north-west Minas Gerais. The species is rare in Minas Gerais, and most records are in the Atlantic Forest, in the east and south (Mazzoni *et al*. 2018, WikiAves 2023). The closest recent record was in 2017 in Campo Alegre de Goiás (WikiAves 2023), south-east Goiás.

ISSN-2513-9894
(Online)

BUFF-FRONTED OWL *Aegolius harrisii*
Two at Mutuca stream in João Pinheiro, in gallery forest with associated *vereda*, using open areas in the surrounds, on 28 July–1 August 2014, being sound-recorded on 31 July 2014 (WA 1687324). Uncommon (Stotz *et al*. 1996) with no previous records in north-west Minas Gerais. Not mentioned for the São Francisco basin in Minas Gerais by Diniz *et al*. (2012), but recorded around Januária since 2004 (by A. Whittaker; Ubaid *et al*. 2012). Records in central Brazil are outside the generally known distribution (BirdLife International 2023), despite recent records in several states, e.g., Minas Gerais, São Paulo (Ubaid *et al*. 2012, Santos *et al*. 2014), Goiás, Distrito Federal and Tocantins (WikiAves 2023), with other extensions to its range reported in south, south-east and north-east Brazil (Santos 2009, Ubaid *et al*. 2012, Ruiz-Esparza *et al*. 2017).

SWALLOW-WINGED PUFFBIRD *Chelidoptera tenebrosa tenebrosa*
One photographed in riparian forest on the Escuro River on 24 July 2014, at the border of Paracatu and Vazante. In João Pinheiro, an adult in riparian forest along Feio stream on 29 July 2014. Its range also encompasses the Triângulo Mineiro and north-east of the state (BirdLife International 2023). My records extend its distribution *c*.200 km east, are the first for the São Francisco basin and for the north-west of the state. Further records in João Pinheiro were made in November 2015 (WikiAves 2023).

CHESTNUT-EARED ARACARI *Pteroglossus castanotis*
Endangered in Minas Gerais. One photographed in *cerradão* in Paracatu on 8 May 2014 (WA 1601921), eating fruits of *Schefflera macrocarpa* (Araliaceae). Usually in gallery forest, with or without *vereda*, and also anthrogenic sites nearby (pers. obs.). Occasionally, in orchards in rural, even urban areas, as in the Triângulo Mineiro, where observed visiting *Roystonea oleracea* (Arecaceae), an exotic palm (pers. obs.). In Minas Gerais restricted to the north-west and Triângulo Mineiro (BirdLife International 2023). In the north-west recorded in the municipalities of Arinos, Uruana de Minas, Natalândia (WikiAves 2023), Unaí and Cabeceira Grande (Mazzoni *et al*. 2015).

GOLDEN-GREEN WOODPECKER *Piculus chrysochloros*
A male seen and heard on 5 August 2014 in riparian forest along the Santo Antônio River in João Pinheiro. Previously mentioned for Fazenda Brejão (Faria *et al*. 2009) and Fazenda Três Rios in Unaí (Lopes *et al*. 2008a). The record at Fazenda Três Rios in 2003 (Lopes *et al*. 2008a) extended its geographic range (BirdLife International 2023). Subsequently, my record expanded its distribution *c*.150 km to the south. One of the southernmost records is in the municipality of Divinópolis, central Minas Gerais (Del-Rio *et al*. 2013).

BARRED FOREST FALCON *Micrastur ruficollis*
One sound-recorded on 8 May 2014 and found again on 24 July 2014, in riparian forest along the Escuro River in Paracatu, in the region's largest forest fragment. These are the first records for the north-west of the state, and one of the few for the São Francisco basin (Kirwan *et al*. 2001).

CACTUS PARAKEET *Eupsittula cactorum*
Found in diverse habitats, such as forest edge, *cerrado sensu stricto*, *vereda* and anthropogenic sites; two were photographed on 26 April 2014 (WA 1606856). Sporadically recorded in João Pinheiro, Paracatu and Vazante, generally alone or in flocks, max. 7 individuals. Endemic to Brazil (Sick 1997), and previously considered endemic to the Caatinga (Pacheco 2003).

ISSN-2513-9894 (Online)

First reported in north-west Minas Gerais, in the municipality of Lagoa Grande, in 2001 (WikiAves 2023), extending its distribution *c.*100 km to the west (vs. BirdLife International 2023). There are records in several municipalities of the north-west (WikiAves 2023), including in Unaí, Cabeceira Grande and Brasilândia de Minas (Faria *et al*. 2009, Mazzoni *et al*. 2015).

BLUE-AND-YELLOW MACAW *Ara ararauna*
Vulnerable in Minas Gerais. Observed in diverse habitats, with a total of 32 individuals in the wet season (over 15 days), and 41 in the dry season (in 15 days). Makes long daily movements between foraging areas and roosts. Observed alone or in flocks of variable size, with a group of four photographed on 3 May 2014 in João Pinheiro (WA 5269172). Uncommon (Stotz *et al*. 1996) and loss of habitat, together with trapping of adults, and poaching of eggs and nestlings, have reduced its populations.

POINT-TAILED PALMCREEPER *Berlepschia rikeri*
Near Threatened in Minas Gerais. Seen on 25 July 2014 at a *vereda* in the headwaters of the Paracatu River in Vazante. Tied to palms, often in *veredas*, but can use other habitats (Lopes & Faria 2014). Recorded in the region since June 1993, in the municipality of Vazante (Vasconcelos *et al*. 2006), and also reported for Unaí and Cabeceira Grande (Lopes *et al*. 2008a).

RUSSET-MANTLED FOLIAGE-GLEANER *Syndactyla dimidiata*
Endangered in Minas Gerais. An adult at Mutuca stream on 28 July 2014, in gallery forest with associated *vereda*. On 2 August 2014, one in the headwaters of the Santo Antônio River, in the same habitat, documented with photographs and a sound-recording. Endemic to forested habitats in the Cerrado (Silva & Bates 2002, Lopes & Gonzaga 2014), uncommon and little known (Stotz *et al*. 1996, Lopes & Gonzaga 2014). Previously recorded around Unaí and Cabeceira Grande (Lopes *et al*. 2008a).

CHOTOY SPINETAIL *Schoeniophylax phryganophilus petersi*
One photographed and sound-recorded on 23 July 2014 in *cerrado sensu stricto* in Paracatu (WA1580765). There is also a record from Fazenda Brejão (Faria *et al*. 2009). *S. p. petersi* was described from the São Francisco basin (Vasconcelos *et al*. 2006, Lopes *et al*. 2008a) but has since been recorded in the Paranaíba basin, in the Altiplano Leste, Paranoá, south-east Distrito Federal. In northern Goiás, recorded in Posse, Flores de Goiás and Alto Paraíso de Goiás, in the Tocantins watershed (WikiAves 2023). Further afield, also found in Piauí, north-east Brazil (Santos *et al*. 2010).

CINEREOUS-BREASTED SPINETAIL *Synallaxis hypospodia*
Two sound-recorded on 11 May 2014 near the Escuro River, in *campo sujo* with swampy environments nearby. On 25 July 2014, it was found again at the same site. The first records for north-west Minas Gerais, where recorded since in Uruana de Minas in 2015–16 and Vazante in 2017 (WikiAves 2023).

BLACK-TAILED FLYCATCHER *Myiobius atricaudus snethlagei*
In João Pinheiro one sound-recorded in *cerradão* on 5 August 2014. Rare with few records in north-west Minas Gerais: in Uruana de Minas in 2012 and Arinos in 2014 (WikiAves 2023).

MINAS GERAIS TYRANNULET *Phylloscartes roquettei*
Endangered at state, national and global levels. In total, six individuals at two sites. In João Pinheiro, photographed on 26 April 2014 (WA 1569691) on the edge of *cerradão*, with many ground bromeliads. On 28 July 2014, recorded again at the same locality, with Reiser's Tyrannulet *Phyllomyias reiseri*, apparently in a mixed-species flock. Also recorded on 30 April 2014 in *cerradão* with bamboo in the understorey, where Blackish-blue Seedeater *Amaurospiza moesta* was seen nearby. In Paracatu, seen and sound-recorded in *cerradão* on 8 May 2014 (WA 1687382). Observed foraging in a *Eucalyptus* plantation with some native vegetation (WA 4782324). Uses diverse forest habitats, but my records in *cerradão* enlarge its occupany (Lopes *et al*. 2008b), from dry forests (Silva & Oren 1992, Olmos 2005, Lopes *et al*. 2010a), riparian, gallery and mesophytic semi-deciduous forests (Raposo *et al*. 2002, Kirwan *et al*. 2004, Lopes *et al*. 2008b, Santos *et al*. 2009). Also recorded at Fazenda Brejão, in riparian forest along the Paracatu River (Faria *et al*. 2009), and around Unaí and Cabeceira Grande (Mazzoni *et al*. 2015). In the municipality of Paracatu, also reported at Morro Bom Sucesso (Lopes *et al*. 2008b). Endemic to Brazil and, until recently, thought to be restricted to the São Francisco and Jequitinhonha basins (BirdLife International 2023), but there are recent records in the Paranaíba and Tocantins basins (Alteff & Alquezar 2020).

EARED PYGMY TYRANT *Myiornis auricularis*
In Paracatu, four on 24 July 2014 in riparian forest along the Escuro River and in *cerradão*, of which one was sound-recorded. Endemic to the Atlantic Forest (Vale *et al*. 2018), but in January 2012 it was found outside the biome in the municipality of São Gotardo, Triângulo Mineiro (pers. obs.). My record is the first for north-west Minas Gerais, *c*.200 km north of São Gotardo.

CHILEAN ELAENIA *Elaenia chilensis*
Migratory species which moves north from southern South America post-breeding, with records in Amazonas, Acre and in almost every state in north-east Brazil (Pacheco *et al*. 2021, WikiAves 2023). Some of a flock of *c*.10 were photographed and sound-recorded in João Pinheiro on 6 May 2014 in *cerradão* and nearby silviculture with some native plants, as well as a *Eucalyptus* plantation. Mostly seen in Brazil during February–April (Sick 1997), but with records in September–December in Minas Gerais, where it was considered rare until recently (WikiAves 2023). My record is the first for north-west Minas Gerais. Other records in June and August 2019 in northern Goiás and Distrito Federal, respectively (pers. obs.).

SUIRIRI FLYCATCHER *Suiriri suiriri suiriri*
S. s. suiriri is Data Deficient in Minas Gerais. Four in João Pinheiro on 30 July 2014 in *cerrado sensu stricto*. Some were sound-recorded and photographed, showing the white belly, and were seen alongside yellow-bellied individuals (the usual subspecies in the region *S. s. burmeisteri*) as also described by Faria *et al.* (2009), who collected two specimens of the nominate at Fazenda Brejão.

CHAPADA FLYCATCHER *Guyramemua affine*
Vulnerable in Minas Gerais, Data Deficient in Brazil, and Near Threatened globally. Two pairs in *campo sujo* in the headwaters of the Santo Antônio River, João Pinheiro, on 5–6 May 2014, documented with photographs and sound-recordings (WA 4783718). There was a *vereda* nearby, as in the municipality of Patrocínio, Triângulo Mineiro, where I found a nest with two chicks ready to fledge on 30 April 2012 (pers. obs.). Endemic to the Cerrado (Silva & Bates 2002), common in grassland but can also use habitats with a higher density

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of woody plants, as in *cerrado sensu stricto* (pers. obs.). In north-west Minas Gerais, records in São Gonçalo do Abaeté and Brasilândia de Minas (WikiAves 2023), including at Fazenda Brejão (Faria *et al*. 2009).

REISER'S TYRANNULET *Phyllomyias reiseri*
Data Deficient in Minas Gerais and Endangered in Brazil. In total, seven found at three sites: in João Pinheiro, on 26 April 2014 at the edge of *cerradão* with many ground bromeliads, and photographed on 5 August 2014 (WA 1569652) on a *Pterodon pubescens* (Fabaceae) in *cerradão* near a silviculture with an understorey of native plants; in Paracatu, one sound-recorded on 24 July 2014 (WA 1573499), in the region's largest forest remnant, in *cerradão* with bamboo, as well as in riparian forest along the Escuro River. Often in seasonal deciduous forest with limestone outcrops (Silva & Oren 1992, Sick 1997, Kirwan *et al*. 2001, Pacheco & Olmos 2006, Lopes *et al*. 2010a, Dornelas *et al*. 2012), but also occurs in gallery forest (Clay *et al*. 1998), as in the municipality of Estrela do Sul, Triângulo Mineiro (pers. obs.). Not seen in deciduous forest with limestone outcrops during this study, but the only area with such formations, in the municipality of Paracatu *c*.12 km from the study area, is being mined. All of my records in Minas Gerais were close to silviculture, even at the edge of *Eucalyptus* plantations. Endemic to the Cerrado (Silva & Bates 2002), rare and poorly known. Not listed for the north-west of the state, my records extend its range *c*.250 km to the east (BirdLife International 2023), with a record in the municipality of Estrela do Sul, *c*.150 km south-east. There is a record in the Atlantic Forest biome, in Poções, Bahia, where a nest was discovered on 10 December 2016 (WikiAves 2023).

RUFOUS-TAILED ATTILA *Attila phoenicurus*
One heard in João Pinheiro on 2 August 2014, in the headwaters of the Santo Antônio River in gallery forest with associated *vereda*. Uncommon (Stotz *et al*. 1996) and typically recorded in Atlantic Forest, but considered migratory, visiting the Cerrado and Amazonia between March and November (Lopes & Schunk 2022). A new species for the São Francisco basin, extending its geographic range *c*.260 km to the east (Lopes & Schunk 2022). In Minas Gerais, most of the recent records are in the south (Lopes & Schunk 2022, WikiAves 2023).

BLACK-COLLARED SWALLOW *Pygochelidon melanoleuca*
Critically Endangered in Minas Gerais and Near Threatened at national level. Typical of river rapids formed by rocky outcrops. Six at the Santo Antônio River, João Pinheiro, on 3 August 2014; one was photographed (WA 1588784). In the dry season, often seen alone or in small groups (2–6 individuals), probably searching for appropriate nest sites along the river, as they were observed entering crevices in rocks, where the species is known to breed (Silva *et al*. 2017). Elsewhere, in Catalão, Goías, a pair was seen collecting nest material on 15 July 2010, on a tributary of the São Marcos River, Paranaíba watershed (pers. obs.). Not mentioned for the São Francisco basin in Minas Gerais by Diniz *et al*. (2012), but had been seen in 2011 on the Abaeté River, São Gonçalo do Abaeté (Silva *et al*. 2017).

SOLITARY BLACK CACIQUE *Cacicus solitarius*
On 29 July 2014, an adult photographed and sound-recorded in João Pinheiro in riparian forest along Feio stream (WA 1580757). Generally found in riparian forests or swampy areas nearby (pers. obs.). Rare in north-west Minas Gerais, but also found at Fazenda Brejão (Faria *et al*. 2009) and the municipality of Uruana de Minas (WikiAves 2023).

ISSN-2513-9894
(Online)

GREYISH SALTATOR *Saltator coerulescens*
One photographed in riparian forest near the mouth of Feio stream, João Pinheiro, on 29 July 2014 (WA1580756). Another at the ecotone between *vereda* and *cerrado sensu stricto*, in the headwaters of the Paracatu River. Recorded at Fazenda Brejão (Faria *et al*. 2009) and in several municipalities in north-west Minas Gerais (WikiAves 2023) including Unaí and Cabeceira Grande (Mazzoni *et al*. 2015).

SCARLET-THROATED TANAGER *Compsothraupis loricata*
Observed in João Pinheiro, Vazante and Paracatu, in riparian and gallery forests and open areas around watercourses, generally in flocks of up to 15. Sound-recorded and photographed. Endemic to Brazil (Sick 1997); with increased field work its distribution has been extended over time. The species was not found in north-west Minas Gerais around Unaí and Cabeceira Grande by Mattos *et al*. (1991) and Lopes *et al*. (2008a), but it was discovered in this region in 2012 (Mazzoni *et al*. 2015). In south-east Goiás (municipalities of Catalão, Davinópolis and Campo Alegre de Goiás) I failed to find the species during almost two years of intensive fieldwork (2009–10; pers. obs.), but in 2013 it was recorded in Catalão and Davinópolis (WikiAves 2023).

ORANGE-FRONTED YELLOW FINCH *Sicalis columbiana*
A pair in *campo sujo* at João Pinheiro on 29 April 2014 and 5 May 2014 was the first record for north-west Minas Gerais. Previously recorded in the north of the state, mainly in the São Francisco basin, but has since been found at other localities in the north-west of the state and in the Distrito Federal (WikiAves 2023), including records in the Paranaíba basin (pers. obs.). Not recorded during surveys prior to 2009 in the municipalities of Unaí, Cabeceira Grande and Brasilândia de Minas (Lopes *et al*. 2008a, Faria *et al*. 2009, Mazzoni *et al*. 2015), but there are recent records in Arinos, Uruana de Minas, Brasilândia de Minas, Paracatu and São Gonçalo do Abaeté, all in north-west Minas Gerais (WikiAves 2023). Not mentioned for Distrito Federal by Bagno & Marinho-Filho (2001), but was found there in 2017 (WikiAves 2023).

BLACKISH-BLUE SEEDEATER *Amaurospiza moesta*
Vulnerable in Minas Gerais. A pair on 30 April 2014 in João Pinheiro, where a male was photographed (WA1580750) and sound-recorded, in *cerradão* with bamboo in the understorey. Recorded in Presidente Olegário and São Gonçalo do Abaeté (Lopes *et al*. 2011), and is potentially widespread, if sporadic, virtually throughout the Cerrado biome (Lopes *et al*. 2011).

Closing remarks and recommendations for conservation

The municipality of João Pinheiro is one of the few areas in Brazil with records of Brazilian Merganser *Mergus octosetaceus*, which was found there in 2011 (WikiAves 2023); it is Critically Endangered at state, national and global levels (Copam 2010, MMA 2022, BirdLife International 2023). The Santo Antônio River should be surveyed for it. Another species that should be searched for in the same area is Great-billed Seed Finch *Sporophila maximiliani*, as I briefly saw a female *Sporophila* that was perhaps this species along Feio stream, near its confluence with the Verde River. Given the species' habitat preferences (Ubaid *et al*. 2018), flooded and swampy areas, riparian and gallery forests, and *veredas*, the area of my sighting was certainly suitable for it.

Major threats to biodiversity conservation in north-west Minas Gerais are posed by agricultural expansion, fire, drainage, use of water for irrigation, pollution of water

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resources by pesticides, use of mercury in mining, and deforestation (Drummond *et al*. 2005). When developed sustainably, silviculture apparently is less impactful on biodiversity than large-scale crop and livestock farming, requiring less intensive human intervention. However, when species of *Pinus* are used, especially with grassland nearby, more intense management is needed to prevent the spread of the trees into otherwise natural areas.

The creation of additional conservation units in the region should be a priority, especially as there are still quite large remnants of natural vegetation in a good state of conservation that harbour rare and threatened species. To date, the only conservation unit in the region is Paracatu State Park (6,400 ha). Therefore, further conservation units should be designated with the aim of protecting a representation of the avifauna and its rarer species against future environmental changes. Among conservation units compatible with current regional land use are wildlife refuges or sustainable-use areas such as Reservas Particulares do Patrimônio Natural (see Law 9985, 18 July 2000, which established the Brazilian National System of Conservation Units). Environmental compensation funds from potentially polluting enterprises should be used to create new conservation units, as decreed by CONAMA Resolution 371, 5 April 2006 and Decree 45175, 17 September 2009.

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Appendix

List of 293 bird species recorded during two visits to the municipalities of João Pinheiro, Vazante and Paracatu, north-west Minas Gerais, Brazil. Status: VU = Vulnerable, EN = Endangered, CR = Critically Endangered, NT = Near Threatened, DD = Data Deficient. [1]State list (Fundação Biodiversitas 2007, Copam 2010), [2]National list (ICMBio 2014, Mma 2022), [3]Global list (BirdLife International 2023). Study sites: 1 = João Pinheiro municipality 1, 2 = João Pinheiro municipality 2, 3 = Vazante and Paracatu municipalities.

Taxon name	English name	Status	Sites
RHEIFORMES			
Rheidae			
Rhea americana	Greater Rhea	NT[3]	1,3
TINAMIFORMES			
Tinamidae			
Crypturellus undulatus	Undulated Tinamou		1,3
Crypturellus parvirostris	Small-billed Tinamou		1,2,3
Rhynchotus rufescens	Red-winged Tinamou		3
Nothura maculosa	Spotted Nothura		1,3
Taoniscus nanus	Dwarf Tinamou	EN[1],EN[2],EN[3]	2
ANSERIFORMES			
Anhimidae			
Anhima cornuta	Horned Screamer		1,2,3
Anatidae			
Dendrocygna viduata	White-faced Whistling Duck		1
Dendrocygna autumnalis	Black-bellied Whistling Duck		1,3
Cairina moschata	Muscovy Duck		1,2,3
Amazonetta brasiliensis	Brazilian Teal		1,2,3
GALLIFORMES			
Cracidae			
Penelope superciliaris	Rusty-margined Guan		1,2,3
Crax fasciolata	Bare-faced Curassow	EN[1],VU[3]	1,2,3
COLUMBIFORMES			
Columbidae			
Patagioenas speciosa	Scaled Pigeon		3
Patagioenas picazuro	Picazuro Pigeon		1,2,3
Patagioenas cayennensis	Pale-vented Pigeon		1,2,3
Patagioenas plumbea	Plumbeous Pigeon		1,2,3
Leptotila verreauxi	White-tipped Dove		1,2,3
Leptotila rufaxilla	Grey-fronted Dove		1,2,3
Zenaida auriculata	Eared Dove		2,3
Claravis pretiosa	Blue Ground Dove		1,3
Uropelia campestris	Long-tailed Ground Dove		1,2
Columbina talpacoti	Ruddy Ground Dove		1,2,3
Columbina squammata	Scaled Dove		1,2,3
CUCULIFORMES			
Cuculidae			
Guira guira	Guira Cuckoo		1,2,3
Crotophaga ani	Smooth-billed Ani		1,2,3
Tapera naevia	Striped Cuckoo		1,2,3

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Taxon name	English name	Status	Sites
Dromococcyx pavoninus	Pavonine Cuckoo		1
Piaya cayana	Squirrel Cuckoo		1,2,3
NYCTIBIIFORMES			
Nyctibiidae			
Nyctibius griseus	Common Potoo		3
CAPRIMULGIFORMES			
Caprimulgidae			
Nyctidromus albicollis	Common Pauraque		1,2,3
Hydropsalis torquata	Scissor-tailed Nightjar		1,2,3
Podager nacunda	Nacunda Nighthawk		1,3
Chordeiles acutipennis	Lesser Nighthawk		1,2
APODIFORMES			
Apodidae			
Streptoprocne zonaris	White-collared Swift		3
Chaetura meridionalis	Sick's Swift		1
Tachornis squamata	Fork-tailed Palm Swift		1,2,3
Trochilidae			
Florisuga fusca	Black Jacobin		1,3
Phaethornis ruber	Reddish Hermit		2,3
Phaethornis pretrei	Planalto Hermit		1,3
Colibri serrirostris	White-vented Violetear		1,2,3
Heliactin bilophus	Horned Sungem		1,2
Anthracothorax nigricollis	Black-throated Mango		2,3
Calliphlox amethystina	Amethyst Woodstar		2
Chlorostilbon lucidus	Glittering-bellied Emerald		1,2,3
Thalurania furcata	Fork-tailed Woodnymph		1,2,3
Eupetomena macroura	Swallow-tailed Hummingbird		1,2,3
Aphantochroa cirrochloris	Sombre Hummingbird		1
Chionomesa fimbriata	Glittering-throated Emerald		1,2,3
Hylocharis chrysura	Gilded Hummingbird		3
GRUIFORMES			
Aramidae			
Aramus guarauna	Limpkin		1
Rallidae			
Rufirallus viridis	Russet-crowned Crake		2,3
Laterallus melanophaius	Rufous-sided Crake		1
Laterallus exilis	Grey-breasted Crake		3
Micropygia schomburgkii	Ocellated Crake	EN[1],NT[2]	1
Mustelirallus albicollis	Ash-throated Crake		1,3

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Taxon name	English name	Status	Sites
Amaurolimnas concolor	Uniform Crake		1
Aramides cajaneus	Grey-necked Wood Rail		1,3
Heliornithidae			
Heliornis fulica	Sungrebe	DD[1]	3
CHARADRIIFORMES			
Charadriidae			
Vanellus chilensis	Southern Lapwing		1,2,3
Scolopacidae			
Gallinago paraguaiae	South American Snipe		2
Jacanidae			
Jacana jacana	Wattled Jacana		1,3
CICONIIFORMES			
Ciconiidae			
Jabiru mycteria	Jabiru	EN[1]	1,3
Mycteria americana	Wood Stork	VU[1]	1,3
SULIFORMES			
Anhingidae			
Anhinga anhinga	Anhinga		1,3
Phalacrocoracidae			
Nannopterum brasilianum	Neotropic Cormorant		1,2,3
PELECANIFORMES			
Ardeidae			
Tigrisoma lineatum	Rufescent Tiger Heron		1,3
Nycticorax nycticorax	Black-crowned Night Heron		1,3
Butorides striata	Striated Heron		1
Ardea cocoi	Cocoi Heron		1,3
Ardea alba	Great Egret		1,2,3
Syrigma sibilatrix	Whistling Heron		2,3
Egretta thula	Snowy Egret		1,2,3
Threskiornithidae			
Mesembrinibis cayennensis	Green Ibis		1,2,3
Phimosus infuscatus	Bare-faced Ibis		3
Theristicus caudatus	Buff-necked Ibis		1,2,3
Platalea ajaja	Roseate Spoonbill	VU[1]	1,3
CATHARTIFORMES			
Cathartidae			
Coragyps atratus	Black Vulture		1,2,3
Cathartes aura	Turkey Vulture		1,2,3
Cathartes burrovianus	Lesser Yellow-headed Vulture		1,3

Taxon name	English name	Status	Sites
ACCIPITRIFORMES			
Accipitridae			
Elanus leucurus	White-tailed Kite		3
Leptodon cayanensis	Grey-headed Kite		1,3
Spizaetus tyrannus	Black Hawk-Eagle	EN[1]	3
Busarellus nigricollis	Black-collared Hawk		1,3
Rostrhamus sociabilis	Snail Kite		1
Accipiter bicolor	Bicoloured Hawk		2
Geranospiza caerulescens	Crane Hawk		1,3
Heterospizias meridionalis	Savanna Hawk		1,2,3
Urubitinga urubitinga	Great Black Hawk		3
Rupornis magnirostris	Roadside Hawk		1,2,3
Geranoaetus albicaudatus	White-tailed Hawk		2
Buteo brachyurus	Short-tailed Hawk		2,3
STRIGIFORMES			
Tytonidae			
Tyto furcata	American Barn Owl		1,2,3
Strigidae			
Megascops choliba	Tropical Screech Owl		1,2,3
Bubo virginianus	Great Horned Owl		2,3
Glaucidium brasilianum	Ferruginous Pygmy Owl		1,2,3
Athene cunicularia	Burrowing Owl		1,2,3
Aegolius harrisii	Buff-fronted Owl		1
Asio clamator	Striped Owl		3
TROGONIFORMES			
Trogonidae			
Trogon surrucura	Surucua Trogon		1,3
CORACIIFORMES			
Alcedinidae			
Megaceryle torquata	Ringed Kingfisher		1,3
Chloroceryle amazona	Amazon Kingfisher		1,2,3
Chloroceryle americana	Green Kingfisher		1,3
GALBULIFORMES			
Galbulidae			
Galbula ruficauda	Rufous-tailed Jacamar		1,2,3
Bucconidae			
Chelidoptera tenebrosa	Swallow-winged Puffbird		1,3
Nonnula rubecula	Rusty-breasted Nunlet		1,2,3
Nystalus maculatus	Spot-backed Puffbird		1,2,3
Nystalus chacuru	White-eared Puffbird		1,2

Taxon name	**English name**	**Status**	**Sites**
PICIFORMES			
Ramphastidae			
Ramphastos toco	Toco Toucan		1,2,3
Pteroglossus castanotis	Chestnut-eared Aracari	EN[1]	3
Picidae			
Picumnus albosquamatus	White-wedged Piculet		1,2,3
Melanerpes candidus	White Woodpecker		1,2,3
Veniliornis passerinus	Little Woodpecker		1,2,3
Veniliornis mixtus	Checkered Woodpecker		1
Campephilus melanoleucos	Crimson-crested Woodpecker		1,2,3
Dryocopus lineatus	Lineated Woodpecker		1,2,3
Celeus flavescens	Blond-crested Woodpecker		3
Piculus chrysochloros	Golden-green Woodpecker		2
Colaptes melanochloros	Green-barred Woodpecker		1,2,3
Colaptes campestris	Campo Flicker		1,2,3
CARIAMIFORMES			
Cariamidae			
Cariama cristata	Red-legged Seriema		1,2,3
FALCONIFORMES			
Falconidae			
Herpetotheres cachinnans	Laughing Falcon		1,2,3
Micrastur ruficollis	Barred Forest Falcon		3
Micrastur semitorquatus	Collared Forest Falcon		3
Caracara plancus	Crested Caracara		1,2,3
Milvago chimachima	Yellow-headed Caracara		1,2,3
Falco sparverius	American Kestrel		1,3
Falco femoralis	Aplomado Falcon		1,2,3
PSITTACIFORMES			
Psittacidae			
Brotogeris chiriri	Yellow-chevroned Parakeet		1,2,3
Pionus maximiliani	Scaly-headed Parrot		1,2,3
Alipiopsitta xanthops	Yellow-faced Parrot	NT[2],NT[3]	1,2,3
Amazona aestiva	Turquoise-fronted Parrot	NT[2]	1,2,3
Forpus xanthopterygius	Blue-winged Parrotlet		1,3
Eupsittula aurea	Peach-fronted Parakeet		1,2,3
Eupsittula cactorum	Cactus Parakeet		1,2,3
Orthopsittaca manilatus	Red-bellied Macaw		1,2,3
Ara ararauna	Blue-and-yellow Macaw	VU[1]	1,2,3
Diopsittaca nobilis	Red-shouldered Macaw		1,2,3
Psittacara leucophthalmus	White-eyed Parakeet		2,3

Taxon name	English name	Status	Sites
PASSERIFORMES			
Thamnophilidae			
Formicivora rufa	Rusty-backed Antwren		1,2,3
Dysithamnus mentalis	Plain Antvireo		3
Herpsilochmus longirostris	Large-billed Antwren		1,2,3
Herpsilochmus atricapillus	Black-capped Antwren		1
Thamnophilus doliatus	Barred Antshrike		1
Thamnophilus torquatus	Rufous-winged Antshrike		1,2,3
Thamnophilus pelzelni	Planalto Slaty Antshrike		1,2,3
Thamnophilus caerulescens	Variable Antshrike		2,3
Taraba major	Great Antshrike		1,3
Melanopareiidae			
Melanopareia torquata	Collared Crescentchest		1,2
Dendrocolaptidae			
Sittasomus griseicapillus	Olivaceous Woodcreeper		1,3
Campylorhamphus trochilirostris	Red-billed Scythebill		1,2,3
Lepidocolaptes angustirostris	Narrow-billed Woodcreeper		1,2,3
Xenopidae			
Xenops rutilans	Streaked Xenops		3
Furnariidae			
Berlepschia rikeri	Point-tailed Palmcreeper		3
Furnarius figulus	Wing-banded Hornero		1
Furnarius leucopus	Pale-legged Hornero		1,2
Furnarius rufus	Rufous Hornero		1,2,3
Syndactyla dimidiata	Russet-mantled Foliage-gleaner	EN[1]	1,2
Clibanornis rectirostris	Chestnut-capped Foliage-gleaner		1,2,3
Phacellodomus rufifrons	Rufous-fronted Thornbird		1,2,3
Phacellodomus ruber	Greater Thornbird		1,2,3
Cranioleuca vulpina	Rusty-backed Spinetail		1
Certhiaxis cinnamomeus	Yellow-chinned Spinetail		1,3
Schoeniophylax phryganophilus	Chotoy Spinetail		3
Synallaxis scutata	Ochre-cheeked Spinetail		1,2
Synallaxis hypospodia	Cinereous-breasted Spinetail		3
Synallaxis albescens	Pale-breasted Spinetail		1,2,3
Synallaxis frontalis	Sooty-fronted Spinetail		1,2,3
Pipridae			
Neopelma pallescens	Pale-bellied Tyrant-Manakin		1,2,3
Antilophia galeata	Helmeted Manakin		1,2,3
Tityridae			
Pachyramphus polychopterus	White-winged Becard		3

Taxon name	English name	Status	Sites
Onychorhynchidae			
Myiobius atricaudus	Black-tailed Flycatcher		2
Platyrinchidae			
Platyrinchus mystaceus	White-throated Spadebill		3
Rhynchocyclidae			
Leptopogon amaurocephalus	Sepia-capped Flycatcher		1,2,3
Phylloscartes roquettei	Minas Gerais Tyrannulet	EN[1],EN[2],EN[3]	1
Tolmomyias sulphurescens	Yellow-olive Flycatcher		1,2,3
Todirostrum cinereum	Common Tody-Flycatcher		1,3
Poecilotriccus latirostris	Rusty-fronted Tody-Flycatcher		1,2,3
Myiornis auricularis	Eared Pygmy Tyrant		3
Hemitriccus striaticollis	Stripe-necked Tody-Tyrant		1,2,3
Hemitriccus margaritaceiventer	Pearly-vented Tody-Tyrant		1,2,3
Tyrannidae			
Euscarthmus meloryphus	Tawny-crowned Pygmy Tyrant		2
Camptostoma obsoletum	Southern Beardless Tyrannulet		1,2,3
Elaenia flavogaster	Yellow-bellied Elaenia		1,2,3
Elaenia chilensis	Chilean Elaenia		2
Elaenia cristata	Plain-crested Elaenia		1,2,3
Elaenia chiriquensis	Lesser Elaenia		2
Suiriri suiriri	Suiriri Flycatcher	DD[1]	1,2,3
Myiopagis caniceps	Grey Elaenia		1,2,3
Myiopagis viridicata	Greenish Elaenia		1,3
Capsiempis flaveola	Yellow Tyrannulet		1,3
Phaeomyias murina	Mouse-coloured Tyrannulet		1,2,3
Phyllomyias reiseri	Reiser's Tyrannulet	DD[1],EN[2]	1,2,3
Phyllomyias fasciatus	Planalto Tyrannulet		1,2,3
Attila phoenicurus	Rufous-tailed Attila		2
Myiarchus ferox	Short-crested Flycatcher		1,2,3
Myiarchus tyrannulus	Brown-crested Flycatcher		1,2,3
Sirystes sibilator	Sibilant Sirystes		1,3
Casiornis rufus	Rufous Casiornis		1,2,3
Pitangus sulphuratus	Great Kiskadee		1,2,3
Philohydor lictor	Lesser Kiskadee		1,3
Machetornis rixosa	Cattle Tyrant		1,2
Myiodynastes maculatus	Streaked Flycatcher		3
Megarynchus pitangua	Boat-billed Flycatcher		1,2,3
Myiozetetes cayanensis	Rusty-margined Flycatcher		1,3
Myiozetetes similis	Social Flycatcher		1,2,3
Tyrannus melancholicus	Tropical Kingbird		1,2,3

Taxon name	English name	Status	Sites
Guyramemua affine	Chapada Flycatcher	VU[1],DD[2],NT[3]	2
Sublegatus modestus	Southern Scrub Flycatcher		1,2
Colonia colonus	Long-tailed Tyrant		1,2,3
Arundinicola leucocephala	White-headed Marsh Tyrant		1,3
Fluvicola nengeta	Masked Water Tyrant		1,3
Pyrocephalus rubinus	Vermilion Flycatcher		1,3
Gubernetes yetapa	Streamer-tailed Tyrant		1,3
Myiophobus fasciatus	Bran-coloured Flycatcher		1,2,3
Cnemotriccus fuscatus	Fuscous Flycatcher		1,3
Lathrotriccus euleri	Euler's Flycatcher		1,2,3
Contopus cinereus	Tropical Pewee		1
Xolmis velatus	White-rumped Monjita		1,3
Nengetus cinereus	Grey Monjita		1,2,3
Vireonidae			
Cyclarhis gujanensis	Rufous-browed Peppershrike		1,2,3
Hylophilus amaurocephalus	Grey-eyed Greenlet		2
Vireo chivi	Chivi Vireo		2
Corvidae			
Cyanocorax cristatellus	Curl-crested Jay		1,2,3
Cyanocorax cyanopogon	White-naped Jay		1,3
Hirundinidae			
Pygochelidon cyanoleuca	Blue-and-white Swallow		3
Pygochelidon melanoleuca	Black-collared Swallow	CR[1],NT[2]	2
Stelgidopteryx ruficollis	Southern Rough-winged Swallow		1,2,3
Progne tapera	Brown-chested Martin		1,2,3
Progne chalybea	Grey-breasted Martin		1,3
Tachycineta albiventer	White-winged Swallow		1,2
Troglodytidae			
Troglodytes musculus	Southern House Wren		1,2,3
Cantorchilus leucotis	Buff-breasted Wren		1,2,3
Polioptilidae			
Polioptila dumicola	Masked Gnatcatcher		1,2,3
Donacobiidae			
Donacobius atricapilla	Black-capped Donacobius		1,3
Turdidae			
Turdus leucomelas	Pale-breasted Thrush		1,2,3
Turdus rufiventris	Rufous-bellied Thrush		1,2,3
Turdus amaurochalinus	Creamy-bellied Thrush		1,3
Turdus albicollis	White-necked Thrush		3

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Taxon name	English name	Status	Sites
Mimidae			
Mimus saturninus	Chalk-browed Mockingbird		1,2,3
Passeridae			
Passer domesticus	House Sparrow		2,3
Motacillidae			
Anthus chii	Yellowish Pipit		3
Fringillidae			
Euphonia chlorotica	Purple-throated Euphonia		1,2,3
Passerellidae			
Ammodramus humeralis	Grassland Sparrow		1,2,3
Arremon flavirostris	Saffron-billed Sparrow		2,3
Zonotrichia capensis	Rufous-collared Sparrow		1,2,3
Icteridae			
Psarocolius decumanus	Crested Oropendola		1,2,3
Cacicus solitarius	Solitary Black Cacique		1
Cacicus haemorrhous	Red-rumped Cacique		3
Icterus jamacaii	Campo Troupial		1,3
Icterus pyrrhopterus	Variable Oriole		1,3
Molothrus bonariensis	Shiny Cowbird		1,3
Gnorimopsar chopi	Chopi Blackbird		1,2,3
Parulidae			
Geothlypis aequinoctialis	Masked Yellowthroat		3
Setophaga pitiayumi	Tropical Parula		1,3
Myiothlypis flaveola	Flavescent Warbler		1,2
Basileuterus culicivorus	Golden-crowned Warbler		1,2,3
Cardinalidae			
Piranga flava	Hepatic Tanager		2
Amaurospiza moesta	Blackish-blue Seedeater	VU[1]	1
Thraupidae			
Charitospiza eucosma	Coal-crested Finch	NT[3]	1
Nemosia pileata	Hooded Tanager		1,2,3
Compsothraupis loricata	Scarlet-throated Tanager		1,2,3
Emberizoides herbicola	Wedge-tailed Grass Finch		1,2,3
Hemithraupis guira	Guira Tanager		1,2,3
Tersina viridis	Swallow Tanager		1,2,3
Dacnis cayana	Blue Dacnis		1,2,3
Saltatricula atricollis	Black-throated Saltator		1,2,3
Saltator maximus	Buff-throated Saltator		3
Saltator coerulescens	Greyish Saltator		1,3
Saltator similis	Green-winged Saltator		1,2,3

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Taxon name	English name	Status	Sites
Coereba flaveola	Bananaquit		1,2,3
Volatinia jacarina	Blue-black Grassquit		1,2,3
Eucometis penicillata	Grey-headed Tanager		1,3
Coryphospingus pileatus	Pileated Finch		1,2,3
Coryphospingus cucullatus	Red-crested Finch		1,3
Tachyphonus rufus	White-lined Tanager		1,2,3
Ramphocelus carbo	Silver-beaked Tanager		1,2,3
Sporophila plumbea	Plumbeous Seedeater		1,2
Sporophila collaris ochrascens	Rusty-collared Seedeater		1
Sporophila nigricollis	Yellow-bellied Seedeater		1,2,3
Sporophila caerulescens	Double-collared Seedeater		1,2,3
Thlypopsis sordida	Orange-headed Tanager		1,3
Cypsnagra hirundinacea	White-rumped Tanager		1,3
Conirostrum speciosum	Chestnut-vented Conebill		1,3
Sicalis citrina	Stripe-tailed Yellow Finch		2
Sicalis flaveola	Saffron Finch		1,3
Sicalis columbiana	Orange-fronted Yellow Finch		1,2
Neothraupis fasciata	White-banded Tanager	NT[3]	1,2
Schistochlamys melanopis	Black-faced Tanager		1,2,3
Schistochlamys ruficapillus	Cinnamon Tanager		1,2
Thraupis sayaca	Sayaca Tanager		1,2,3
Thraupis palmarum	Palm Tanager		1,2,3
Stilpnia cayana	Burnished-buff Tanager		1,2,3

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The composite identity of *Muscicapa virens* Linnaeus, and a neotype designation for Eastern Wood Pewee *Contopus virens* (Tyrannidae)

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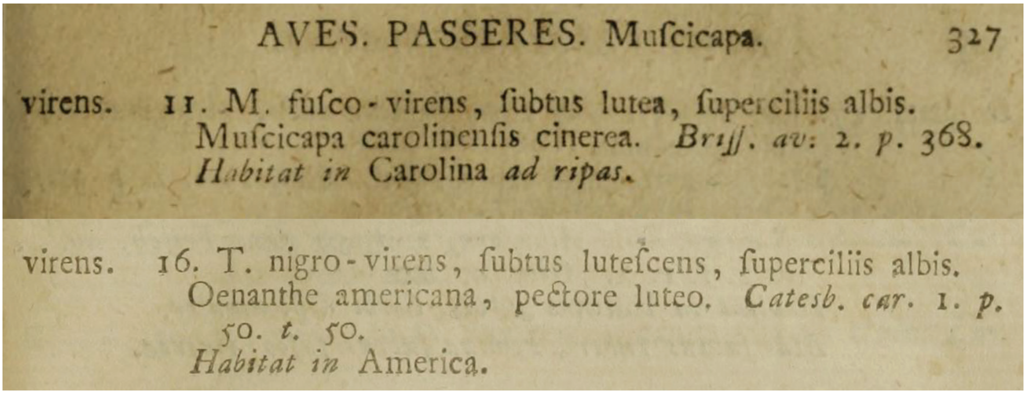
Summary.—I reviewed the material basis of *Muscicapa virens* Linnaeus, 1766, long presumed to be the original description of Eastern Wood Pewee *Contopus virens* (Linnaeus), type species of the genus *Contopus* Cabanis, 1855, and found it to be an unidentifiable taxonomic composite. Linnaeus' (1766) account was partly based on Brisson's (1760) 'Gobe-mouche Cendré de la Caroline', which was based on (1) a non-extant specimen that, as demonstrated herein, was probably a species in the genus *Empidonax* Cabanis, 1855, and (2) Catesby's (1731) 'little brown Fly-catcher', which was also a taxonomic composite. Linnaeus (1766) also included a novel character in his original description of *M. virens*—a white supercilium ('*superciliis albis*')—which is lacking in Eastern Wood Pewee, and was probably miscopied from Catesby's (1731) description of 'Red-eyed Fly-catcher' (= Red-eyed Vireo *Vireo olivaceus* Linnaeus, 1766), which appeared on the same plate as the 'little brown Fly-catcher'. In light of these ambiguities, after a thorough review of literature and relevant primary sources, I designate a neotype specimen for *C. virens* (Linnaeus) that stabilises nomenclature in accordance with prevailing use.

For more than two centuries, scholars have consistently cited *Muscicapa virens* Linnaeus, 1766 (Tyrannidae) as the original description of Eastern Wood Pewee *Contopus virens* (Linnaeus), a common migratory species that breeds in eastern North America and winters in South America (e.g., Wilson 1810: 81, Nuttall 1831: 285, Baird *et al*. 1858: 190, AOU 1886: 234, 1931: 210, 1983: 449, 1998: 392, Watt *et al*. 2020, Chesser *et al*. 2022, Pyle 2022). However, in his original description, Linnaeus (1766: 327) included a conspicuous character not present in *C. virens*—a white supercilium, or line above the eye ('*superciliis albis*', Fig. 1,



AVES. PASSERES. Muſcicapa. 327

virens. 11. M. fuſco-virens, ſubtus lutea, ſuperciliis albis.
Muſcicapa carolinenſis cinerea. *Briſſ. av: 2. p. 368.*
Habitat in Carolina *ad ripas.*

virens. 16. T. nigro-virens, ſubtus luteſcens, ſuperciliis albis.
Oenanthe americana, pectore luteo. *Catesb. car. 1. p. 50. t. 50.*
Habitat in America.

Figure 1. (top) Original description of *Muscicapa virens* Linnaeus, 1766, courtesy of the Harvard University Botany Library. (bottom) Original description of *Turdus virens* Linnaeus, 1758, courtesy of the Peter H. Raven Library, Missouri Botanical Garden. Both images downloaded from Biodiversity Heritage Library (www.biodiversitylibrary.org, accessed 13 March 2023).

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top). This rendered his description of *M. virens* nearly identical to *Turdus virens* Linnaeus, 1758 (Fig. 1, bottom), now known as Yellow-breasted Chat *Icteria virens* (Linnaeus, 1758), although these distantly related species are extremely unlikely to be confused in the field or museum.

To investigate this anomaly, I reviewed the material basis of *M. virens* by carefully scrutinising the original description and its nested set of cited works (i.e., Catesby 1731, Klein 1750, Brisson 1760). I compared measurements of specimens reported by those authors to an original dataset of comparable measurements, taken by me from study skins of eight morphologically similar flycatcher (Tyrannidae) species that occur in eastern North America, where the type material of *M. virens* was presumably collected. I also examined a high-resolution digital reproduction of Catesby's original painting of the 'little brown Fly-catcher' and compared it to different editions of his published plates. Collectively, these lines of enquiry exposed the ambiguous (composite) identity of *M. virens* Linnaeus, 1766, which is the type species of the genus *Contopus* Cabanis, 1855.

Morphological data

I measured study skins (n = 519) of the following eight species in the bird collection of the Delaware Museum of Nature & Science, Wilmington (DMNH, formerly Delaware Museum of Natural History): (1) *Contopus virens* (Linnaeus, 1766); (2) Eastern Phoebe *Sayornis phoebe* (Latham, 1790); (3) Acadian Flycatcher *Empidonax virescens* (Vieillot, 1818); (4) Willow Flycatcher *E. traillii* (Audubon, 1828); (5) Olive-sided Flycatcher *Contopus cooperi* (Nuttall, 1831); (6) Least Flycatcher *Empidonax minimus* (Baird & Baird, 1843); (7) Yellow-bellied Flycatcher *E. flaviventris* (Baird & Baird, 1843); and (8) Alder Flycatcher *E. alnorum* Brewster, 1895.

For each specimen, I recorded (1) tail length, measured with a ruler to the nearest 1 mm, from the insertion point of the two central rectrices to the tip of the longest rectrix; (2) bill length, measured with digital callipers to the nearest 0.01 mm, from the bill tip to the posterior edge (corner) of the gape (i.e., Brisson's 1760 method); (3) wing length (flattened), measured with a ruler to the nearest 1 mm, from the carpal joint to the tip of the longest primary remex; and (4) tarsometatarsus length, measured with digital callipers to the nearest 0.01 mm, from the intertarsal joint to the distal end of the final leg scale.

I also compiled a large dataset of body mass measurements (n = 2,649) for the same eight species, by downloading records from VertNet.org (accessed 13 March 2023). Each mass datum was associated with a vouchered specimen in one of 29 different institutions (see Acknowledgements). I sorted the mass data by taxon and removed obvious outliers (i.e., likely data entry errors) from the tails of each distribution. I combined *Empidonax traillii* and *E. alnorum* into a single taxon ('*E. traillii sensu lato*') because study skins of these sibling species cannot be confidently identified without a description of voice (e.g., Stein 1963, Pyle 2022), which was missing from most study skin labels. I plotted the data and generated figures with the program R-Studio (R Core Team 2020).

The material basis of *C. virens* (Linnaeus)

There is no evidence that Linnaeus (1766) personally examined a specimen before writing his brief description of *M. virens*, and no specimen is known in the Linnaean collection in the Uppsala University Museum of Evolution (UUZM) at Uppsala, Sweden (Wallin 2001). Rather, he based his description (primarily, but apparently not exclusively; see below) on Brisson's (1760) 'Le Gobe-mouche Cendré de la Caroline … *Muscicapa Carolinensis cinerea*', which he cited (Fig. 1, top: '*Briss. Av.* 2. p. 368'). Brisson (1760) placed

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stars next to the names of species of which he personally examined specimens (Allen 1910: 322), but his account of 'Le Gobe-mouche Cendré de la Caroline' was not so denoted (Brisson 1760: 368). This implies that Brisson's (1760) account was derivative, i.e., based on material examined by Catesby (1731) and / or Klein (1750), the only authors he cited. However, Brisson (1760) also reported measurements of a (presumably mounted) specimen that did not appear in those works, from which we may deduce that, despite the omission of stars, his account *was* actually based in part on original material (i.e., a syntype of *M. virens* Linnaeus, 1766). Notwithstanding, no specimen associated with Brisson's (1760) description is known, and a manual search of study skins and mounted specimens in the Muséum national d'Histoire naturelle, Paris (MNHN), in January 2023, failed to produce a specimen or any new information (P. Boussès *in litt*. 2023).

Without a specimen, we must rely on Brisson's (1760: 368) text description and measurements of 'Le Gobe-mouche Cendré de la Caroline' to establish its identity—just as Linnaeus (1766) did when writing his description of *M. virens* (but with the benefit of hindsight). Brisson's (1760) description of the colour of the bill ('Le demi-bec supérieur est noir, l'inférieur est jaune' = 'The [maxilla] is black, the [mandible] is yellow') eliminates *S. phoebe*, which has a black mandible. However, his description of the plumage is too vague to reliably distinguish among *C. virens* and multiple *Empidonax* species, which vary seasonally in colour (due to wear and fading) and exhibit a range of inter-individual colour variation within each species. Any of these species could plausibly be said to have ash-coloured dorsal plumage ('cendré foncé'), dirty yellowish-white ventral plumage ('d'un blanc sale & jaunâtre'), and wingbars ('les moyennes sont de la même couleur [brown] & bordées extérieurement de blanc'). Most of Brisson's (1760) reported measurements are also unreliable because they may be influenced (distorted) by the preparator. The distance between the bill tip and the end of the tail, and the length of the wings relative to the tail, may be adjusted to suit the preparator's stylistic preferences; and toe measurements cannot be replicated without knowing their degree of curvature.

Only two measurements reported by Brisson (1760) are more or less reliable (stable) and amenable to modern comparisons. His measurement of tail length, which was presumably recorded from the point of insertion to the tip of the longest rectrix ('sa queue deux pouces' = 54.1 mm, if 1 pouce = *c*.27.07 mm; Débarbat 1799), falls below the range of *C. virens* (*n* = 49, range = 55–66 mm) and within that of multiple *Empidonax* species (Fig. 2). Brisson's (1760) bill length measurement, recorded from the tip of the bill to the corner of the gape ('Son bec depuis son bout jusqu'àux coins de la bouche a huit lignes de long' = 18 mm, if 1 ligne = *c*.2.256 mm), also fails to identify his specimen as *C. virens* (Fig. 3). This suggests that Brisson's (1760) syntype of *M. virens* may have been one of the *Empidonax*—not Eastern Wood Pewee.

Next, we must examine Catesby (1731) and Klein (1750) to assess if they described any original specimens unambiguously identifiable as Eastern Wood Pewee (i.e., that might serve as a lectotype to rescue the name *C. virens*, since Brisson's syntype was probably an *Empidonax*). Of these, Klein (1750) lacked original material and merely cited Catesby (1731). Notably, Brisson (1760) stated that his syntype was a nearly identical match ('avec un figure assez exacte') to the upper bird figured on Pl. 54 of Catesby (1731), which he called the 'Petite preneur de mouches brun' (i.e., a French translation of 'little brown Fly-catcher'). Following tradition, many authors have identified Catesby's (1731) '*Muscicapa Fusca* / The little brown Fly-catcher' as an Eastern Wood Pewee (e.g., Reveal 2009: 300). However, there are several reasons to doubt this identification.

The species was not listed in specimen manifests sent by Catesby to Hans Sloane (1660–1753) in May 1723 and March 1724, which suggests that no specimen was preserved

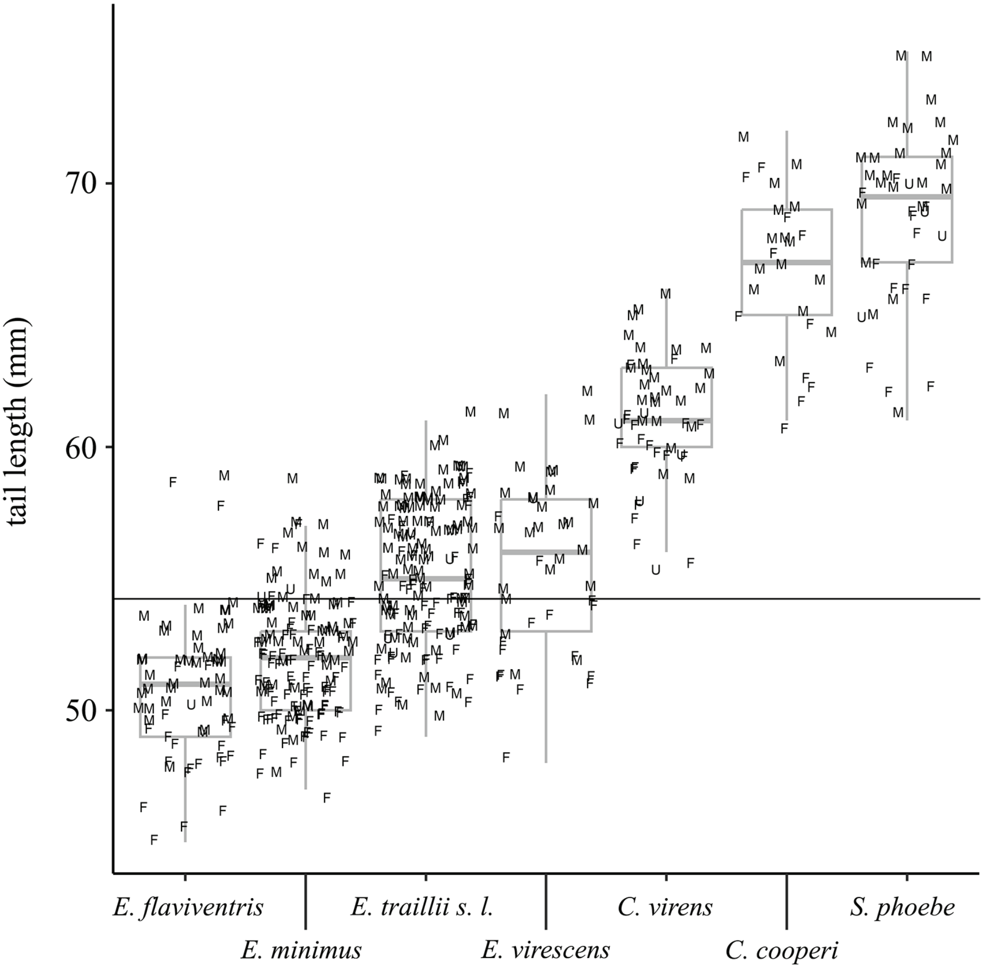

Figure 2. Tail length variation among eight tyrant flycatcher (Tyrannidae) species that occur regularly in eastern North America (*Empidonax* spp., *Contopus virens*, *C. cooperi*, *Sayornis phoebe*), from a sample of study skins in the DMNH collection (*n* = 507). Data from study skins of *Empidonax alnorum* and *E. traillii* were combined into a single category (*E. traillii s. l.*, see text). The sex class of each specimen is shown (F = female, M = male, U = unknown) and the horizontal line denotes the reported tail length ('deux pouces' = 54.1 mm) of 'Le Gobe-mouche Cendré de la Caroline' (Brisson 1760).

(Nelson 2017). Therefore, any identification must be made solely on the basis of Catesby's text description and plate, which contradict each other in morphological characters. The bird in Catesby's original watercolour (Fig. 4), which served as the model for his plate, lacks the ventral 'Tincture of yellow' mentioned in Catesby's (1731: 54) text, and also lacks the relatively prominent wingbars of Eastern Wood Pewee. In this respect, Catesby's 'little brown Fly-catcher' bears a closer resemblance to *S. phoebe*, which has paler (less prominent) wingbars than *C. virens*. Catesby's (1731: 54) reported body mass ('nine Penny-weight' = 14 g, if 1 dwt = 1.555174 g) fails to resolve this ambiguity (Fig. 5). Published (hand-coloured) prints of Catesby's plate vary widely in coloration between the first (1731) and third (1771) editions. The colourists of the third edition apparently attempted to reconcile the composite characters of Linnaeus (1766) and Catesby (1731) by giving the 'little brown Fly-catcher' a white supercilium (Fig. 6).

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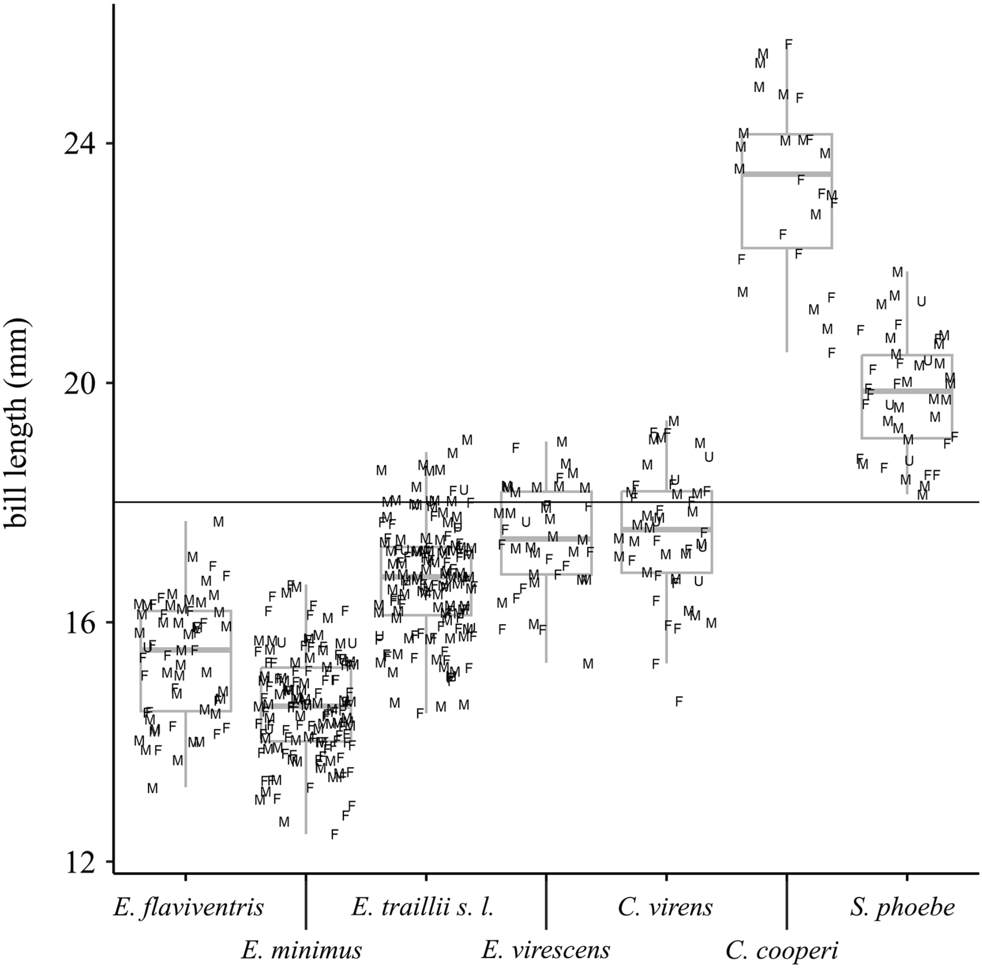

Figure 3. Bill length variation among eight tyrant flycatcher (Tyrannidae) species that occur regularly in eastern North America (*Empidonax* spp., *Contopus virens*, *C. cooperi*, *Sayornis phoebe*), from a sample of study skins in the DMNH collection ($n = 499$). Data from *Empidonax alnorum* and *E. traillii* were combined into a single category (*E. traillii s. l.*, see text). The sex class of each specimen is shown (F = female, M = male, U = unknown) and the horizontal line denotes the reported bill length ('huit lignes' = 18 mm) of 'Le Gobe-mouche Cendré de la Caroline' (Brisson 1760).

The white supercilium ('*superciliis albis*') was not mentioned by Brisson (1760), Klein (1750) or Catesby (1731). Apparently, it was an original addition by Linnaeus (1766). Although its inclusion rendered the description of *M. virens* superficially similar to the description of *Turdus virens* Linnaeus, 1758, which confused some early American ornithologists (see below), it seems more likely that Linnaeus (1766) miscopied it from Catesby's (1731) 'Red-eyed Fly-catcher' (= Red-eyed Vireo *Vireo olivaceus* Linnaeus, 1766), which appeared directly below the 'little brown Fly-catcher' on Pl. 54, and of which Catesby (1731: 54) wrote: 'From the Bill, over the Eyes, runs a dusky white Line' (Fig. 4). Either way, the composite *M. virens* included characters from species in at least two passerine families (i.e., Tyrannidae, and Vireonidae or Icteriidae). One of the syntypes was probably an *Empidonax* (Brisson 1760), and the other may have been a specimen of *Sayornis phoebe* (Catesby 1731). Furthermore, none of the original material can be unambiguously identified as the species now known as Eastern Wood Pewee.

Figure 4. Original painting of (top) 'The Small brown flycatcher / *Muscicapa Fusca*' and (bottom) 'The green flycatcher / *Muscicapa virescens*' executed by Catesby *c*.1722–26, which served as the model for Catesby (1731, Pl. 54). The latter species (= Red-eyed Vireo *Vireo olivaceus*) appeared under the name 'Red-eyed Fly-catcher' in Catesby (1731) and has a prominent white supercilium (image used with permission of the Royal Collection Trust / © His Majesty King Charles III 2022).

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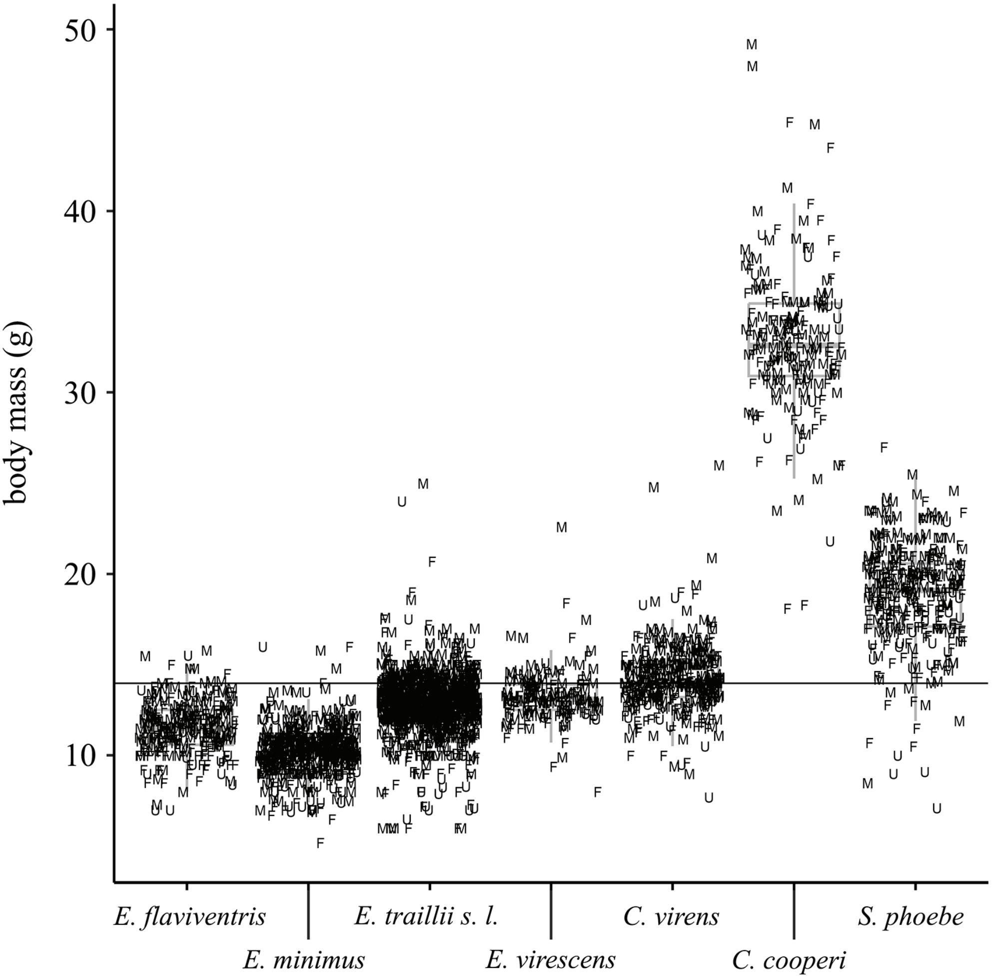

Figure 5. Body mass variation among eight tyrant flycatcher (Tyrannidae) species that occur regularly in eastern North America (*Empidonax* spp., *Contopus virens*, *C. cooperi*, *Sayornis phoebe*), from a large sample of specimens (*n* = 2,649) in multiple collections (see Acknowledgements), downloaded from www.VertNet.org (accessed 13 March 2023). Data from *Empidonax alnorum* and *E. traillii* were combined into a single category (*E. traillii s. l.*, see text). The sex class of each specimen is shown (F = female, M = male, U = unknown) and the horizontal line denotes the reported mass ('nine Penny-weight' = 14 g) of the 'little brown Fly-catcher' (Catesby 1731: 54).

Consequences of the composite *M. virens*

European authors of the late 18th century were confounded by the composite descriptions. In his account of the 'Cinereous [Flycatcher]', Latham (1783: 350) gave a brief and practically verbatim copy of Catesby's (1731: 54) description of 'little brown Fly-catcher'. Latham (1783) mentioned that he had examined a specimen in the British Museum ('Br. Mus.'), but virtually all of the specimens he described are believed to have perished by the early 19th century, 'probably [because] they were inadequately prepared, were always mounted, and, from a lack of appreciation of their priceless value, were allowed to decay, through a want of proper curatorial knowledge' (Sharpe 1906: 79). Pennant's (1785: 387) description of 'Cinereous [Flycatcher]', which was prepared prior to, and cited by, Latham (1783), included two composite characters: (1) 'eyes red', and (2) 'over each eye a

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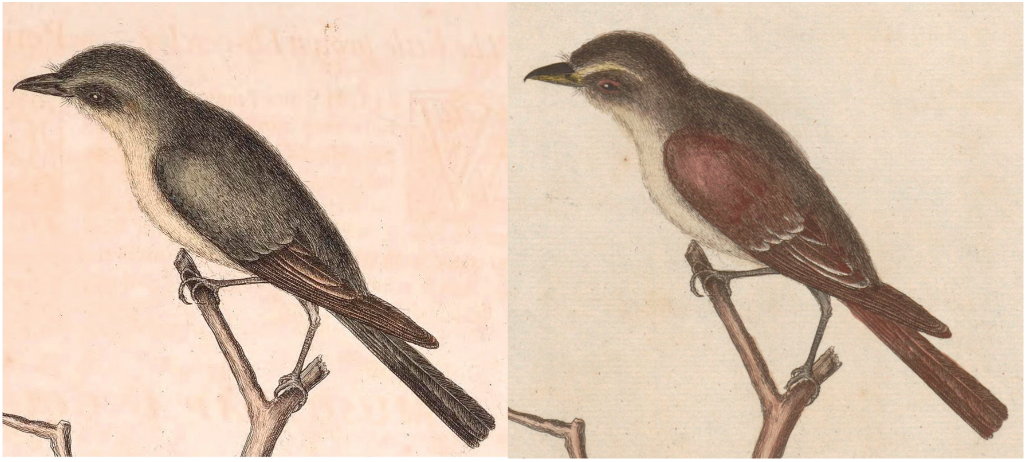

Figure 6. Colour variation in different editions of *The natural history of Carolina, Florida, and the Bahama Islands* (Catesby 1731, Pl. 54): (left) first edition, published in 1731; (right) third edition, published in 1771 by Benjamin White. Colourists for the third edition evidently attempted to reconcile the discrepancies between Pl. 54 and Catesby's (1731) text. Both images appear courtesy of Smithsonian Institution Libraries and Biodiversity Heritage Library (www.biodiversitylibrary.org, accessed 13 March 2023).

faint white line'. This suggests that Pennant (1785) may have consulted the third edition of Catesby (1731), published in 1771, which featured significant alterations to the colours of Pl. 54 (Fig. 6); or he may have directly miscopied characters from Catesby's (1731) 'Red-eyed Fly-catcher', like Linnaeus (1766) probably did. Gmelin (1789: 936), in his own description of *M. virens*, did not cite Linnaeus (1766) but nevertheless copied his original Latin description verbatim (including '*superciliis albis*'). Gmelin (1789) also cited Brisson (1760), whose description was likely based on an *Empidonax* specimen (see above).

Were ornithologists in America also confused by these composite taxonomic descriptions? Benjamin Smith Barton (1766–1815), Professor of Natural History at the University of Pennsylvania, taught the first university-based course in ornithology in North America in 1802. He brought his students to the 'Philadelphia Museum' of Charles Willson Peale (1741–1827), where hundreds of mounted birds were displayed in glass cases, and conveniently arranged according to the Linnaean system (Miller 1988: 473, Halley in press). Was there a specimen of Eastern Wood Pewee in the Philadelphia Museum by that time? Did Peale and / or Barton distinguish *C. virens* from the morphologically similar *Empidonax* species?

The earliest source that may refer to Eastern Wood Pewee is an entry in Peale's diary, dated 8 June 1788, written during a collecting trip to Annapolis, Maryland: 'before Dinner I preserved [a specimen of] … ~~unknown~~ nondescript (but commonly called Peewe)' (Miller 1983: 498). This bird remains unidentified because the name 'Pewee' (and its alternate spellings) was then colloquially used for the species now called Eastern Phoebe, although Peale noted in an unpublished lecture (*c.*1799) that '[*Sayornis phoebe* had] always been known in [his] family as sausy bird' (i.e., not 'Pewee'). Peale's lecture contained no description of Eastern Wood Pewee, but it may have appeared on the (now missing) page immediately before his description of *S. phoebe*, which Peale listed under the name 'Black Cap Flycatcher … *Muscicapa fusca* Linn. [*sic*, = Gmelin]') (Halley in press).

Barton's (1799) published works and unpublished manuscripts provide no indication that he distinguished Eastern Wood Pewee from the sympatric *Empidonax* species, despite having access to Peale's collection. An unpublished note, probably written in the mid-1790s, reveals that Barton initially assumed that *Turdus virens* and *M. virens* were the same species

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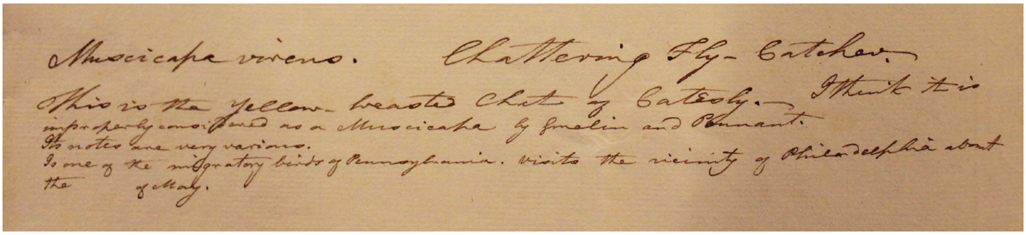

Muscicapa virens. Chattering Fly-Catcher.
This is the yellow-breasted Chat of Catesby. I think it is
improperly considered as a Muscicapa by Gmelin and Pennant.
Its notes are very various.
Is one of the migratory birds of Pennsylvania. visits the vicinity of Philadelphia about
the of May.

Figure 7. Unpublished note written by Benjamin Smith Barton (1766–1815), probably in the 1790s, before publication of Barton (1799): ‘*Muscicapa virens*. Chattering Fly-catcher. This is the yellow-breasted chat of Catesby. I think it is improperly considered a *Muscicapa* by Gmelin and Pennant. Its notes are very various. [It] is one of the migratory birds of Pennsylvania, visits the vicinity of Philadelphia about the [blank] of May.’ Reproduced courtesy of the American Philosophical Society (APS) Library (coll. Mss.B.B284d), Philadelphia, PA (Matthew R. Halley)

(Fig. 7). Apparently, he was fooled by the superficial similarity of their descriptions and assumed that Linnaeus (1758 and 1766, respectively) had inadvertently described the same species twice, in two different genera. However, by the time Barton (1799: 19) published his famous calendar of bird migration, he seems to have corrected this error and was using the name ‘*M. viridis* [J. F. Gmelin, 1789]’ for Yellow-breasted Chat (not *M. virens*).

Which species of flycatchers (Tyrannidae) did Barton (1799) distinguish in his calendar? First, he listed the arrival of ‘*Muscicapa fusca* (G.) [= J. F. Gmelin, 1789] … Black-headed Fly-Catcher. (Pewe.)’ on 12 March 1791, which he (according to information in his Appendix) associated with the ‘*Muscicapa nunciola* of Bartram’ (i.e., ‘the pewit, or black cap flycatcher’, Bartram 1791). This clearly refers to Eastern Phoebe, the earliest of the flycatchers to arrive on spring migration, which Peale also associated with the name ‘*Muscicapa fusca* Linn.’ (see above, Halley in press). The name *M. phoebe* Latham, 1790 later gained priority for Eastern Phoebe after *M. fusca* J. F. Gmelin, 1789, which had been based on Catesby’s (1731, Pl. 53) ‘*Muscicapa nigrescens* / The Blackcap Fly-catcher’, was found to be preoccupied by *M. fusca* Statius Müller, 1776, which now refers to Scaly-breasted Thrasher *Allenia fusca*.

Next, Barton (1799) recorded the arrival of ‘*Muscicapa fusca* (Catesby) … Warbling Wren, or Green Wren’ on 28 April 1791, which he considered synonymous with Bartram’s (1791) ‘*Muscicapa cantatrix*, the little domestic flycatcher or green wren’. This seems unlikely to refer to any member of Tyrannidae (which do not ‘warble’) and is clearly not Eastern Wood Pewee, which is neither ‘green’ nor particularly ‘domestic’ (i.e., frequently found in towns and gardens). This may be a reference to Eastern Warbling Vireo *Vireo gilvus* Vieillot, 1808, which better fits Barton’s (1799) morphological and behavioral descriptions. In any case, unlike later authors, Barton (1799) evidently did not associate Catesby’s (1731) unidentifiable ‘little brown Fly-catcher’ with any species now classified in Tyrannidae.

Finally, Barton (1799) recorded the arrival of ‘*Muscicapa rapax* of Bartram … Olive coloured Fly-catcher, or Lesser Pewe’ on 18 May 1791, of which he wrote: ‘[it is] the Lesser Crested Fly-Catcher of Mr. Pennant: the *Muscicapa acadica* of Gmelin. It is a very useful little bird, destroying numbers of the common house-fly and other troublesome insects. It continues with us until late in September, when it retires southerly to pass the winter’ (Barton 1799: 19). Bartram’s (1791) ‘*M. rapax*, the lesser pewit, or brown and greenish flycatcher’, and the species in the cited accounts of Pennant and Gmelin, were vaguely described and unidentifiable, although likely referring to *C. virens* or one of the similar *Empidonax*. In summary, there is no evidence that Peale, Bartram (1791), Barton (1799) or any American author of the 18th century, distinguished the species now known as Eastern Wood Pewee from the morphologically similar *Empidonax* species.

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Louis Pierre Vieillot (1748–1830), the French ornithologist, also visited the Philadelphia Museum during his travels in eastern North America from 1793–1798, and later described 'Le Moucherolle Plaintif, *Muscicapa querula*' Vieillot, 1808, which was probably either *C. virens* or one of the similar *Empidonax*. His description was based on a (presumably non-extant) specimen in his own collection ('De ma collection', Vieillot 1808: 68, Pl. 39), however, and not on a specimen in the Philadelphia Museum. The name *M. querula* Vieillot, 1808, has traditionally been cited as a junior synonym of *M. virens* (e.g., Watt *et al*. 2020). However, in hindsight, Vieillot's (1808) text description and plate were too vague to distinguish *C. virens* from the similar *Empidonax* species, and he provided no reliable measurements (see above) that would be helpful to resolve this issue. Although he did not list any synonyms of *M. querula*, Vieillot (1808: 68) stated that, except for being yellower on the ventral surface ('les parties inférieures du corps qui sont d'un blanc jaunâtre'), his specimen was practically identical to Catesby's (1731) 'little brown Fly-catcher'. He even suspected that they were the same species and the difference was due to Catesby's colourists taking creative liberties ('il est vraisemblable que cette difference provient du coloriste de la figure publiée par cet auteur', Vieillot 1808: 68). Therefore, Vieillot's (1808) *M. querula* cannot be unambiguously identified as an Eastern Wood Pewee or confidently disentangled from the enigmatic 'little brown Fly-catcher' of Catesby (1731).

To my knowledge, the oldest convincing evidence that ornithologists were in possession of a specimen of Eastern Wood Pewee is found in an unpublished essay written by Peale in 1805–06, entitled 'A Walk Through the Philad[elphi]a Museum' (Historical Society of Pennsylvania [HSP], coll. 0481). By this time, Alexander Wilson (1766–1813) was busy creating the artwork and text accounts for his forthcoming work, *American ornithology* (1808–14), and he occasionally visited the Philadelphia Museum to make drawings of Peale's specimens, and to inform the elder ornithologist of his progress. Referring to a mounted specimen in the Philadelphia Museum collection, Peale wrote:

> 'Here is another species considerably like the *M. fusca* [J. F. Gmelin, 1789 = *Sayornis phoebe*], but a smaller bird, whose manners also very much resemble it. Mr. Wilson [who is fond] of Natural History & a very accurate observer, gave me this account. But this species [is] only found in [the] thickest woods, they visit us about one month latter [*sic*] than the other. This bird has not been described.' (HSP, coll. 0481)

Peale was likely referring to the species that Wilson (1810: 81, Pl. 13) later described under the name '*Wood* Pewee Flycatcher' (my italics), distinguishing it from the common 'Pewee' (i.e., Eastern Phoebe), which arrives in Philadelphia more than a month earlier than Eastern Wood Pewee during spring migration. Wilson's description of its voice is also a good match for Eastern Wood Pewee ('calling out in a feeble tone, *peto wāy*; *peto wāy*; *pee way*'). For his 'Wood Pewee Flycatcher', Wilson (1810) recycled the scientific name '*Muscicapa rapax*', which Bartram (1791) and Barton (1799: 19) had previously applied to the 'Lesser crested Flycatcher' of Pennant (1785: 386), based on a non-extant and unidentified specimen from Nova Scotia. However, Wilson (1810) did not cite Bartram (1791) or Barton (1799). Therefore, according to the Code (ICZN 1999, Art. 11.6), the name *M. rapax* Wilson, 1810, is technically available because (1) 'A name which when first published in an available work [e.g., *M. rapax* Barton 1799] was treated as a junior synonym of a name then used as valid [*M. acadica* J. F. Gmelin, 1789] is not thereby made available' (i.e., *M. rapax* Barton is unavailable); and (2) Bartram's (1791) nomenclature is also unavailable, because it was suppressed on account of his occasional use of trinomials (ICZN 1957). However, although it is available, *M. rapax* Wilson, 1810, is not free from taxonomic entanglement because the

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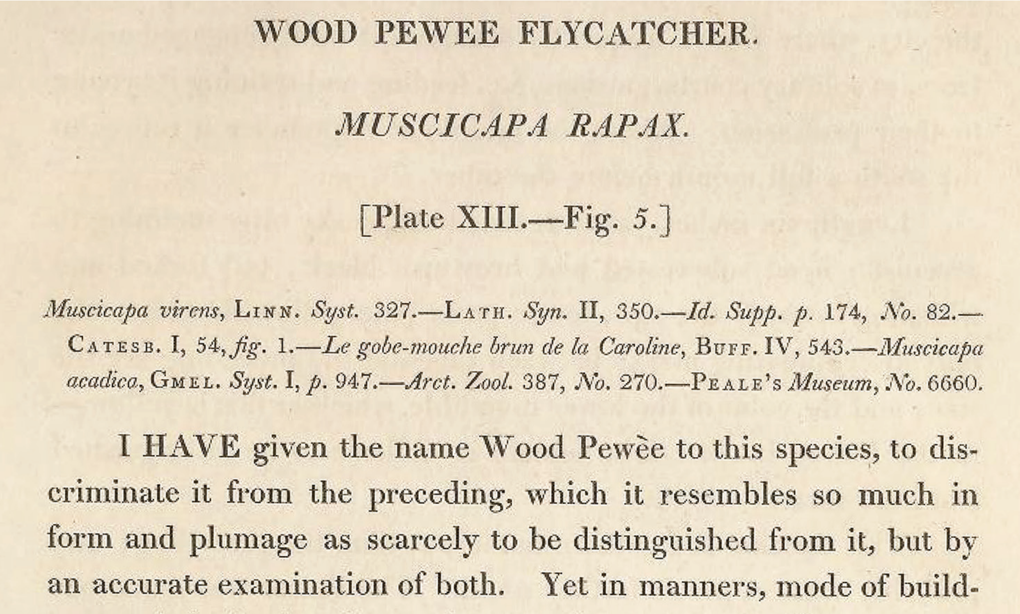

WOOD PEWEE FLYCATCHER.

MUSCICAPA RAPAX.

[Plate XIII.—Fig. 5.]

Muscicapa virens, Linn. *Syst.* 327.—Lath. *Syn.* II, 350.—*Id. Supp. p.* 174, *No.* 82.—Catesb. I, 54, *fig.* 1.—*Le gobe-mouche brun de la Caroline*, Buff. IV, 543.—*Muscicapa acadica*, Gmel. *Syst.* I, *p.* 947.—*Arct. Zool.* 387, *No.* 270.—Peale's *Museum*, *No.* 6660.

I HAVE given the name Wood Pewèe to this species, to discriminate it from the preceding, which it resembles so much in form and plumage as scarcely to be distinguished from it, but by an accurate examination of both. Yet in manners, mode of build-

Figure 8. First page of the original description of *Muscicapa rapax* Wilson, 1810. Courtesy of Smithsonian Institution Libraries and Biodiversity Heritage Library (www.biodiversitylibrary.org, accessed 13 March 2023).

composite '*Muscicapa virens* Linn.', and the unidentifiable *M. acadica* J. F. Gmelin, 1789, were listed among its synonyms (Fig. 8).

The type material of *M. rapax* Wilson, 1810, is also untraceable. Wilson (1810: 81) cited 'Peale's Museum, No. 6660' among the synonyms of *M. rapax*, which referred to a specimen or specimens in the Philadelphia Museum. Two data-deficient specimens of '*Myiochanes virens* (Linn.)' in the Museum of Comparative Zoology, Harvard University, Cambridge, MA (MCZ), which came from the historic Boston Museum collection, are alleged to have originated in Peale's collection (Faxon 1915: 144). However, there are lingering doubts about the provenance of this material (see Halley 2022: 234). Upon the dispersal of Peale's collection in the mid-19th century, some material was reportedly purchased by Moses Kimball (1809–95), which passed temporarily to the Boston Society of Natural History, then spent several years stored in a barn in Massachusetts. By the time the collection was accessioned at MCZ, in the early 20th century, the original mounts and labels had been disassociated from the specimens and an untold number were lost (Faxon 1915). Another portion of the Philadelphia Museum collection was sold to the circus promoter P. T. Barnum (1810–91) and subsequently destroyed in a fire at his 'American Museum' in New York City (Anon. 1865). There are no known contemporaneous catalogues or inventories of the Kimball and Barnum allotments, so we cannot be confident that any MCZ specimen was actually mounted in the Philadelphia Museum, let alone that it was the same specimen to which Wilson (1810) referred in his *M. rapax* account. After his death in 1813, the Philadelphia Museum continued to acquire new specimens until at least September 1839, when the last ornithological entry was made in the accessions ledger (HSP, coll. 0481); and there is evidence that the Peales periodically replaced older specimens of common local species, which were occasionally damaged by insects, to keep the exhibits looking fresh (see Miller 1988).

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Figure 9. DMNH 85602, the neotype of *Muscicapa virens* Linnaeus, 1766; see text for provenance (Matthew R. Halley)

Neotypification of *M. virens* Linnaeus, 1766

The name *Contopus virens* (Linnaeus) has been used for the Eastern Wood Pewee for more than 200 years, and is recognised as the type species of *Contopus* Cabanis, 1855. However, Brisson's (1760) measurements match a specimen in the genus *Empidonax*, unidentifiable to species, and Catesby's (1731) plate and description exhibit an inconsistent suite of characters, precluding identification. The bird in Catesby's original painting lacks prominent wingbars, and therefore resembles *Sayornis phoebe* more than *C. virens*. Furthermore, Linnaeus (1766) evidently miscopied a conspicuous plumage character—a white supercilium ('*superciliis albis*')—from a species in a different family (Vireonidae), the 'Red-eyed Fly-catcher' (= *Vireo olivaceus*), which appeared on the same plate as Catesby's (1731: 54) 'little brown Fly-catcher'. Therefore, despite its long use, the original description of *M. virens* Linnaeus, 1766, is not unambiguously identifiable. Its known type material evidently consisted of specimens from multiple passerine families and genera (Tyrannidae: *Empidonax*, *Sayornis*; and Vireonidae: *Vireo*, or Icteriidae: *Icteria*) and no specimen is extant or traceable. None of the type material can be unambiguously identified as the species now known as Eastern Wood Pewee. To my knowledge, this situation has not been previously discussed in literature, nor has any previous author designated a lectotype or neotype of *M. virens*.

Therefore, to fix the taxonomic identity of Eastern Wood Pewee *C. virens* (Linnaeus), in accordance with prevailing use, I hereby designate a neotype for *M. virens* Linnaeus, 1766. The neotype is an adult female (DMNH 85602) in the collection of the Delaware Museum of Nature & Science, Wilmington, DE, USA (Fig. 9). This action stabilises nomenclature and prevents confusion arising from alternative identifications. It satisfies the requirements for neotype designation in the Code (ICZN 1999) by clarifying the taxonomic application (status) of the name (Art. 75.3.1), describing, illustrating and referencing the defining characters of *C. virens* and its neotype (Art. 75.3.2), providing data sufficient to ensure recognition of the neotype specimen (Art. 75.3.3), providing grounds for believing that all original type material has been lost and is untraceable (Art. 75.3.4), showing that traits of the

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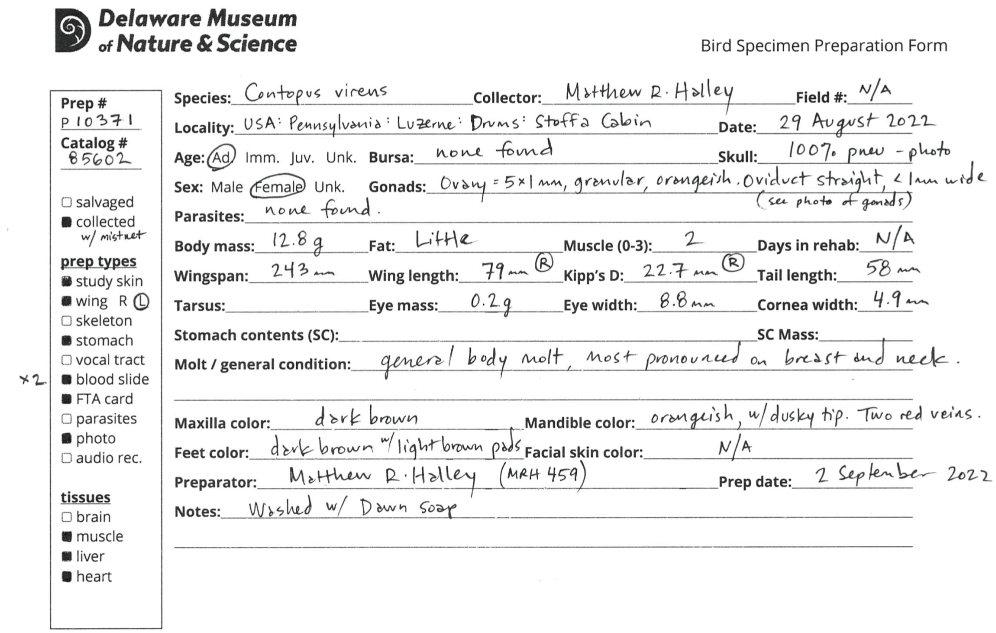

Delaware Museum of Nature & Science

Bird Specimen Preparation Form

Prep # P10371
Catalog # 85602

☐ salvaged
● collected w/ mistnet

prep types
● study skin
● wing R [✓ L]
☐ skeleton
● stomach
☐ vocal tract
×2 ● blood slide
● FTA card
☐ parasites
● photo
☐ audio rec.

tissues
☐ brain
● muscle
● liver
● heart

Species: Contopus virens
Collector: Matthew R. Halley
Field #: N/A
Locality: USA: Pennsylvania: Luzerne: Drums: Stoffa Cabin
Date: 29 August 2022
Age: [✓ Ad] Imm. Juv. Unk.
Bursa: none found
Skull: 100% pneu - photo
Sex: Male [✓ Female] Unk.
Gonads: Ovary = 5×1 mm, granular, orangeish. Oviduct straight, < 1 mm wide (see photo of gonads)
Parasites: none found.
Body mass: 12.8 g
Fat: Little
Muscle (0-3): 2
Days in rehab: N/A
Wingspan: 243 mm
Wing length: 79 mm Ⓡ
Kipp's D: 22.7 mm Ⓡ
Tail length: 58 mm
Tarsus:
Eye mass: 0.2 g
Eye width: 8.8 mm
Cornea width: 4.9 mm
Stomach contents (SC):
SC Mass:
Molt / general condition: general body molt, most pronounced on breast and neck.
Maxilla color: dark brown
Mandible color: orangeish, w/ dusky tip. Two red veins.
Feet color: dark brown w/ light brown pads
Facial skin color: N/A
Preparator: Matthew R. Halley (MRH 459)
Prep date: 2 September 2022
Notes: Washed w/ Dawn soap

Figure 10. Original data form used during preparation of DMNH 85602, neotype of *Muscicapa virens* Linnaeus, 1766 (Matthew R. Halley)

neotype are included in the original description (Art. 75.3.5), choosing a neotype collected on the breeding grounds of *C. virens*, in eastern North America, where the syntypes that served as the models for Brisson (1760) and Catesby (1731) were presumably collected (Art. 75.3.6), and depositing the neotype in a recognised scientific institution (Art. 75.3.7).

Collection of the neotype.—DMNH 85602 is an adult female (study skin and spread left wing) collected on private property ('Stoffa Cabin') at 274 Freedom Road, Drums, Luzerne County, Pennsylvania, USA (41°1′0.62″N, 75°56′29.86″W). At 08.00 h, on the morning of 29 August 2022, I captured the bird in a mist-net. I drew approximately 50 μL of blood via brachial venipuncture into a microhematocrit capillary tube. I immediately smeared blood droplets on two glass slides, then fixed them in pure methanol. I also applied blood drops to an FTA card, which I stored in a sealed plastic bag with silica desiccant beads. I euthanised the bird via cardiac compression, then transported the body on ice to DMNH, where I placed it in a storage freezer (–20°C) until I prepared the specimen.

The type locality ('Stoffa Cabin') is a mixed deciduous-conifer woodland with a colonial history of human disturbance including residential development and selective logging. It is located near the headwaters of the Little Nescopeck Creek, and named for a cabin constructed there in the 1980s by my grandfather, Francis J. Stoffa, Sr. (1931–99). Eastern Wood Pewee is a common summer resident and breeder in the woods at Stoffa Cabin, and I heard its familiar song during field work there on 13 August 2022 (one singer), 28 August (two) and 29 August 2022 (two, both singing after I collected DMNH 85602). On those dates, I did not detect any species except those that breed regularly on the property. I did not hear *C. virens* when I returned to the site for several hours of field work on 24 September. Therefore, it is likely that DMNH 85602 was a member of the breeding population at Stoffa Cabin, collected just prior to its migration, and not a southbound migrant collected at a stopover site, although this is not known for certain. In this case, choosing a breeder for the neotype is not imperative because no geographic variation is known or described in the

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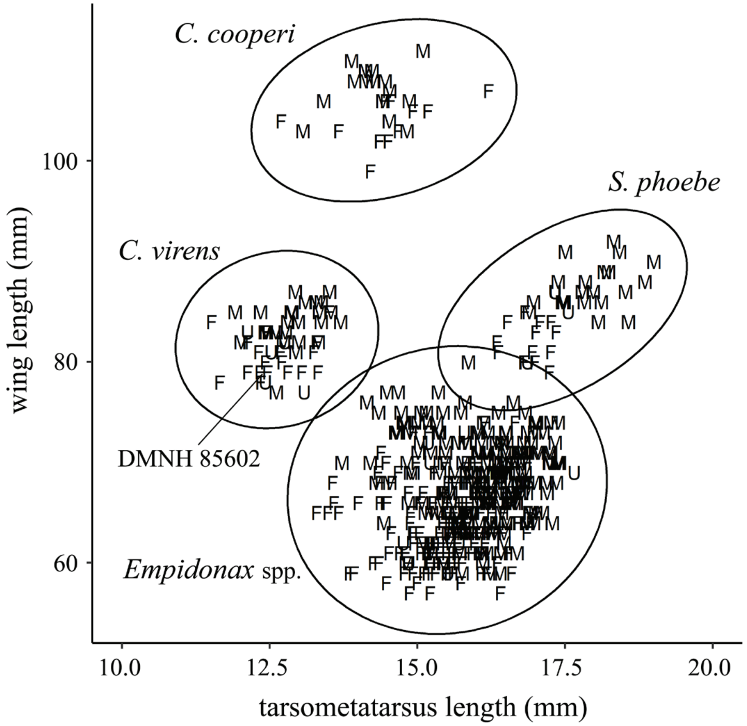

Figure 11. Variation in wing and tarsometatarsus length among eight tyrant flycatcher (Tyrannidae) species that occur regularly in eastern North America (*Empidonax* spp., *Contopus virens*, *C. cooperi*, *Sayornis phoebe*), from a sample of study skins in the DMNH collection (*n* = 519). Data from *Empidonax alnorum* and *E. traillii* were combined into a single category (*E. traillii s. l.*, see text). The sex class of each specimen is shown (F = female, M = male, U = unknown). The neotype of *C. virens* (DMNH 85602) falls clearly within the *C. virens* cluster. Ellipses were estimated using the 'geom_mark_ellipse' function in the 'ggforce' package in R-Studio (R Core Team 2020).

monotypic *C. virens* (Watt *et al.* 2020) nor is there evidence that Catesby's (1731) or Brisson's (1760) original descriptions were based on breeding birds.

Preparation of the neotype.—Four days later (2 September 2022), I prepared the study skin and sampled tissues (Fig. 10, prep. = MRH459). The bird was undergoing general body moult, most pronounced on the breast and neck. I did not find any parasites, despite fumigation with ethyl acetate and ruffling of each feather tract. I measured the wings and tail from the fresh (pliable) body with a metric ruler or dial callipers, as noted. Max. wingspan was 243 mm (ruler); the length of the closed and flattened right wing from the carpal joint to the tip of the longest primary was 79 mm (ruler); with the wing closed, the distance between the tips of the longest primary and first secondary ('Kipp's distance'; Kipp 1959) was 22.7 mm (callipers); the length of the tail, from the insertion point of the two central rectrices to the tip, was 58 mm (ruler). I measured the wing length again on 22 March 2023, by which time the study skin had been dried for over six months; it had decreased slightly to 78.5 mm.

The ovary measured 5 × 1 mm (ruler), was an orangey colour and had a granular texture. The oviduct was straight and < 1 mm wide (ruler). The skull was 100% pneumatised. No bursa was found. The stomach was saved and refrozen for a forthcoming dissection. There was a small amount of fat in the dorsal tract and around the furcula. Measured with dial callipers, the widest diameter of the (wet) left eye was 8.8 mm, after removal from the skull, and the diameter of the corneal 'bulge' was 4.9 mm. I collected samples of the breast muscle, liver, and heart tissue (DMNH P10371) in 95% ethanol and placed them in the

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storage freezer (–20ºC). I also deposited backup tissues at the Academy of Natural Sciences of Drexel University (Philadelphia, PA).

Diagnosis.—Eastern Wood Pewee *C. virens* (Linnaeus) is distinguished morphologically from the five *Empidonax* (Tyrannidae) that regularly occur in eastern North America (see above) by its combination of a longer wing and shorter tarsometatarsus (Fig. 11, Pyle 2022: 257), and, from *Sayornis phoebe*, by its shorter tarsometatarsus (Fig. 11) and pale mandible (vs. black in *S. phoebe*).

Acknowledgements

This paper is dedicated to the memory of Francis J. Stoffa, Sr. (1931–99), who imparted his curiosity about birds to his grandson. My grandmother, Dorothy Mae (Murman) Stoffa, kindly permitted me to collect specimens at Stoffa Cabin. The neotype (DMNH 85602) was collected under US Fish & Wildlife Service permit no. MBPER0036206 and Pennsylvania Game Commission permit no. 55967. I am grateful to Guy M. Kirwan, Edward C. Dickinson, and Frank Steinheimer for commenting on early drafts of the manuscript. Patrick Boussès assisted by searching the MNHN collection for Brisson's (1760) type material. Mass data obtained via VertNet.org were sourced from specimens in the following institutions: California Academy of Sciences, San Francisco (CAS); Chicago Academy of Sciences (CHAS); Carnegie Museum of Natural History, Pittsburgh (CM); Cleveland Museum of Natural History (CMNH); Charles R. Conner Museum, Moscow (CRCM); California State University, Chico Vertebrate Museum (CSUC); Cornell University Museum of Vertebrates, Ithaca (CMUV); Denver Museum of Nature & Science (DMNS); University of Kansas Biodiversity Institute, Lawrence (KU); Natural History Museum of Los Angeles County (LACM); Museum of Comparative Zoology, Harvard University, Cambridge (MCZ); Bell Museum of Natural History, St Paul (MMNH); Museum of Southwestern Biology, Albuquerque (MSB); Museum of Vertebrate Zoology, University of California, Berkeley (MVZ); Natural History Museum, Tring (NHMUK); Museum of Biological Diversity, Ohio State University, Columbus (OSUM); Royal Ontario Museum, Toronto (ROM); South Australian Museum, Adelaide (SAMA); Texas A&M University Biodiversity Research and Teaching Collections, College Station (TCWC); University of Arkansas Collections Facility, Fayetteville (UAFMC); Museum of the North, University of Alaska Fairbanks (UAM); University of British Columbia Beaty Biodiversity Museum, Vancouver (UBCBBM); University of California, Los Angeles (UCLA); University of Michigan Museum of Zoology, Ann Arbor (UMMZ); University of Washington Burke Museum of Natural History and Culture, Seattle (UWBM); University of Wyoming Museum of Vertebrates, Laramie (UWYMV); Western Foundation of Vertebrate Zoology, Camarillo (WFVZ); Western New Mexico University, Silver City (WNMU); and Yale University Peabody Museum, New Haven (YPM). Many thanks to the curatorial staff of these collections.

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What's so special about New Guinea birds?[1]

by Jared Diamond (text) & K. David Bishop (photographs)

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http://zoobank.org/urn:lsid:zoobank.org:pub:17F6CFD6-31F0-4865-B0F4-269D9B54256C

Summary.—I discuss why the tropical island of New Guinea has long been important in the development of our understanding of birds. There are two sets of reasons: New Guinea's birds, and its geography and peoples. New Guinea birds include: the famous birds of paradise, bowerbirds, and megapodes, which evolved in New Guinea (or New Guinea plus Australia) and are still concentrated there; pigeons, parrots, and kingfishers, which are especially species-rich and diverse in New Guinea and radiated there, whether or not they originally evolved there; and many groups that are morphologically and ecologically similar to European groups, such as 'wrens', 'creepers', and 'nuthatches', but that proved to be 'lookalikes' that evolved independently in New Guinea / Australia, just as numerous marsupial mammals and placental mammals converged on similar morphologies. Finally, the poisonous pitohuis and ifrit independently acquired the same neurotoxin as did South American poison-dart frogs; and a melampitta roosts and nests underground. The advantages offered by the island itself include: its equatorial location and its high mountains, so that New Guinea offers the entire range of habitats from coral reefs and rainforests through alpine grassland and glaciers on one short transect; the 'right size' (sufficient species to illuminate but not too many species so as to confuse); a simple geographic layout comprising a central mountain chain and its lowland ring; hundreds of islands of three types; virtually complete knowledge of the composition of its resident avifauna at the level of species; and the encyclopedic knowledge of birds among traditional New Guinea peoples. As examples of phenomena of general biological interest that New Guinea birds have illuminated, I discuss elevational sequences of congeners, culture in bowerbirds, evolution of 'aggressive mimicry' of larger bird species by smaller birds, brown-and-black mixed-species foraging flocks, and selection for and against overwater dispersal. These birds, landscapes, and topics are illustrated by photographs by K. David Bishop.

The tropical island of New Guinea has long played a pre-eminent role in ornithology, and in field biology in general (Wallace 1869, D'Albertis 1880, Mayr 1942, Diamond 1973, Beehler 2020). That pre-eminence caused New Guinea to be chosen as the site for the British Ornithologists' Union 1909 Jubilee Expedition (Wollaston 1912, Ogilvie-Grant 1915), and for the Archbold Expeditions of 1933–59 (e.g., Archbold & Rand 1940, Rand 1942). New Guinea's exploration was described by Wichmann (1909–12) and Souter (1964); its biological exploration by Frodin (2007); its ornithological exploration by Beehler & Mandeville (2017);

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[1] This paper is an invited submission designed to partner a lecture that Prof. Diamond gave to the Club and the Linnean Society of London, originally planned to celebrate the occasion of the Club's 1,000th meeting since the inaugural assembly, held on 5 October 1892, and reported in the first issue of *Bull. Brit. Orn. Cl.* Unfortunately, this plan was one of the many casualties of the Covid-19 pandemic. Ultimately it was not possible for the presentation to go ahead until 6 October 2022, by which time it became the 1,005th meeting (see *Bull. Brit. Orn. Cl.* 142: 383–384). A recording of Prof. Diamond's address is available to view at https://www.youtube.com/watch?v=yJBGS7boZ6k.

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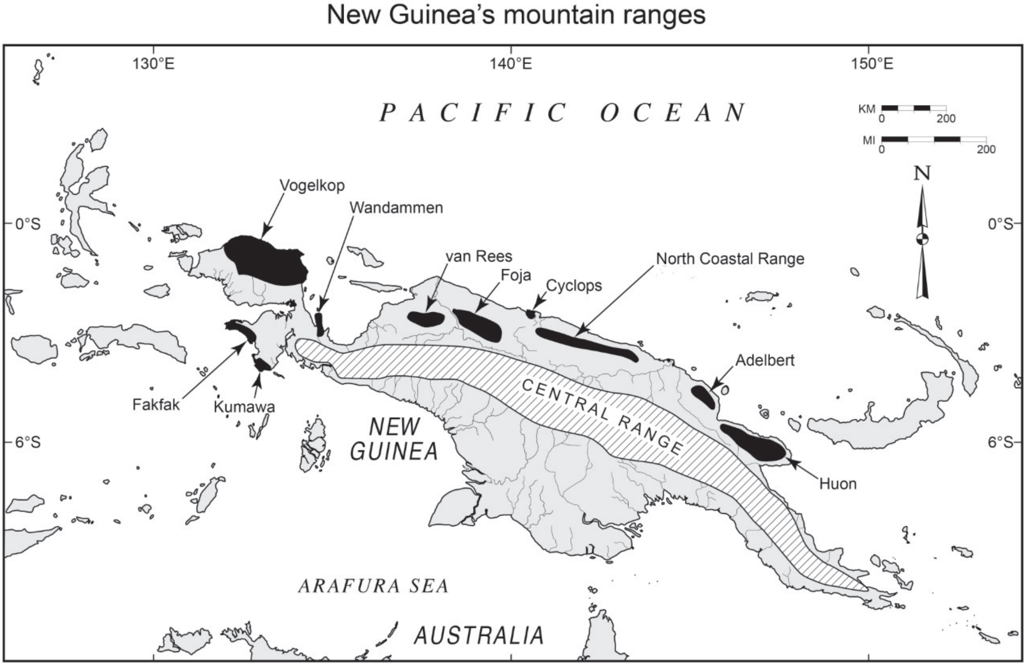

Map 1. New Guinea's mountain ranges: the Central Range running from west to east, and ten lower and much smaller outlying ranges along the north and north-west coasts.

and its ecology by Gressitt (1982) and Marshall & Beehler (2007). Illustrated guidebooks to its birds include Rand & Gilliard (1967), Coates (1985, 1990), Pratt & Beehler (2015) and Gregory (2017). Beehler & Pratt's (2016) book is a recent comprehensive systematic, taxonomic and distributional account to the level of subspecies.

In this paper I explain the two sets of factors that have made New Guinea a magnet for ornithologists: the island's remarkable groups of bird species; and advantages resulting from New Guinea's geography and peoples. I'll then present five examples to illustrate New Guinea's contributions to our understanding of biology.

My own first visit to New Guinea was in 1964. Since then, I have made a total of 31 expeditions, each lasting 1–5 months, to New Guinea and adjacent islands (e.g., Diamond 1969, 1972a, 1974, Diamond & Raga 1978). The 21 expeditions since 1986 have been conducted jointly with K. David Bishop, who has co-authored with me all of the publications resulting from those expeditions (e.g., Diamond & Bishop 1994, 1999, 2015, 2022) and who has provided all of the photographs for this article. These expeditions have been equally divided between the two halves into which New Guinea is divided politically: in the west, the Indonesian province of Indonesian New Guinea, alias Irian Jaya and now named Papua; and in the east, the independent nation of Papua New Guinea. Localities explored ornithologically during these expeditions have included a range of elevations from sea level to 4,000 m; both the northern and the southern watersheds; all main sections of the Central Range and the lowlands; and all ten of New Guinea's outlying mountain ranges (Map 1). Geographic highlights included the discovery and first ascents of the previously unidentified highest peaks of four of the outliers (e.g., Diamond 1969, Diamond & Bishop 2015). An ornithological highlight was the rediscovery, in Indonesian New Guinea's Foja Mts., of the long-lost Golden-fronted Bowerbird *Amblyornis flavifrons*, previously known only from four skins of uncertain

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provenance that appeared in a Paris hat shop in 1895 (Diamond 1982a). Some other results of these expeditions will be described below.

Remarkable New Guinea birds

Three famous families.—If you ask any ornithologist or birdwatcher which birds first come to mind at the mention of New Guinea, the answer will surely be 'birds of paradise' (Paradisaeidae) (Gilliard 1969, Cooper & Forshaw 1977, Frith & Beehler 1998). They are widely regarded as the world's most beautiful birds, and as the most extreme avian examples of sexual selection and male ornamental plumage (Figs. 1–3). While one species in the family (Trumpet Manucode *Phonygammus keraudrenii*) and three riflebird allospecies (genus *Ptiloris*) extend to Australia's east coast, and two others are endemic to the Moluccas, this family of 22 species or superspecies is otherwise confined to New Guinea and its satellite islands, especially to the mountains of New Guinea. (Throughout, I take as my unit of analysis the isolated full species, or the superspecies consisting of two or more allopatric allospecies. More often in the recent ornithological literature, individual allospecies are treated as separate species. The

Figure 1. Wilson's Bird of Paradise *Cicinnurus respublica* (K. David Bishop)

Figure 2. King of Saxony Bird of Paradise *Pteridophora alberti* (K. David Bishop)

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latter definition recognises 39–45 rather than 22 species of Paradisaeidae; Rand & Gilliard 1967, Gilliard 1969, Cooper & Forshaw 1977, Frith & Beehler 1998, Gregory 2017.)

Male plumage decorations of birds of paradise include tail feathers up to 1 m long, feathers reduced to long wires protruding from the tail or the head, profuse soft plumes, and (in King of Saxony Bird of Paradise *Pteridophora alberti*) a pair of highly modified feathers consisting of erectile wires each supporting a row of several dozen hard blue squares resembling glued pieces of plastic (Fig. 2). The *Pteridophora* male decorations are so extraordinary and un-birdlike that, when they were first described in 1894 by A. B. Meyer, the bird of paradise monographer Bowdler Sharpe dismissed the report by saying that any fool could see that the specimen was a human artifact. Males of two genera of birds of paradise, *Parotia* and *Diphyllodes* = *Cicinnurus*, construct terrestrial display courts as do bowerbirds.

Figure 3. Blue Bird of Paradise *Paradisornis rudolphi* (K. David Bishop)

The bowerbirds (Ptilonorhynchidae), confined to New Guinea and Australia, are nearly as famous and distinctive among New Guinea birds as birds of paradise (Gilliard 1969, Cooper & Forshaw 1977, Frith & Frith 2004). The terrestrial display courts built and decorated by male bowerbirds are the most elaborate structures constructed by any animal: stick huts up to several metres in diameter, or stick towers up to a few metres tall, decorated with up to hundreds of fruits, flowers, mushrooms, snail shells, beetle elytrae, pandanus leaves, and (near human settlements) stolen car keys, ballpoint pens, and other shiny or colourful objects (Fig. 4). Gilliard (1969) recognised that, in the course of bowerbird evolution, females' attention has become transferred from male ornamental plumage to male bowers: the duller the male's ornamental plumage, the more elaborate the bower's structure and decorations. Female bowerbirds choose a male with which to mate on the basis of bower quality (Borgia 1985); hence males devote spare time to pilfering and wrecking bowers of rival males, to reduce rivals' sex appeal.

The remaining New Guinea-centred or New Guinea-plus-Australia-centred family that I will mention (extending to islands east and west of New Guinea) consists of the megapodes alias mound-builders or brush-turkeys (Megapodiidae). These are the world's only birds whose eggs are incubated by heat sources other than the parents' body heat: variously, fermentation heat of decaying vegetation scraped together into huge mounds (Fig. 5), volcanic heat, or sunbaked sand (Jones *et al.* 1995). On hatching, chicks dig their way up to the surface, never encounter their parents, forage and feed entirely precocially, and eventually may make overland or overwater dispersal flights.

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Figure 4. Bower of Vogelkop Bowerbird *Amblyornis inornata* in the Arfak Mts. (K. David Bishop)

Figure 5. Dusky Scrubfowl *Megapodius freycinet* and its egg incubator mound (K. David Bishop)

Three worldwide families that radiated.—Those three families for which New Guinea is famous are still confined to New Guinea plus Australia and (Megapodiidae) some other islands, and surely evolved there. We now turn to three families or orders with worldwide distributions but that are especially speciose and diverse in New Guinea and must have radiated there, whether or not their distant origins were in New Guinea: pigeons (Columbidae), parrots (Psittaciformes) and kingfishers (Halcyonidae and Alcedinidae) (Beehler & Pratt 2016).

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Figure 6 (left). Victoria Crowned Pigeon *Goura victoria* (K. David Bishop)
Figure 7 (right). Red-breasted Pygmy Parrot *Micropsitta bruijnii* (K. David Bishop)

With 41 New Guinea species or superspecies (50 if allospecies are counted separately), pigeons reach their greatest morphological and ecological diversity in New Guinea. The region's pigeons range from the world's largest extant species (the crowned pigeon *Goura* superspecies: Fig. 6) to one of the world's smallest (Dwarf Fruit Dove *Ptilinopus nainus*). Distinctive groups of New Guinea pigeons besides *Goura* include fruit doves and fruit pigeons (*Ptilinopus* and *Ducula*), cuckoo-doves (*Macropygia* and *Reinwardtoena*), the extreme supertramp Nicobar Pigeon (*Caloenas nicobarica*) nesting colonially on small or remote islands, and 12 ground pigeons including the distinctive monotypic genera *Trugon* and *Otidiphaps* as well as *Goura* and *Caloenas*.

With 37 New Guinea species or superspecies (47 if allospecies are counted separately), parrots also reach, even more conspicuously, their greatest morphological, ecological and taxonomic diversity in New Guinea plus Australia (Forshaw & Cooper 1973). Again, New Guinea parrots range from one of the world's largest (Palm Cockatoo *Probosciger aterrimus*) to the world's smallest (*Micropsitta* pygmy parrots, barely *c*.8 cm long: Fig 7). Parrot groups or families confined to or centred on New Guinea and Australia, besides the pygmy parrots, are the cockatoos and the lories (the latter with brush tongues as specialisations for feeding on nectar and pollen) (Joseph *et al*. 2012, 2020).

Finally, New Guinea's 19 kingfishers (or 27 including allospecies) are also diverse in morphology, ecology and taxonomy (Forshaw 1987). They include river and lake kingfishers, a saltwater species (Beach Kingfisher *Todiramphus saurophagus*), and a large majority of woodland species; one of the world's largest kingfishers (Blue-winged Kookaburra *Dacelo leachii*, mass 350 g), as well as one of the smallest (Little Kingfisher *Ceyx pusillus*, 14 g); one of the world's few nocturnal kingfishers (Hook-billed Kingfisher *Melidora macrorrhina*); the bizarre Shovel-billed Kingfisher *Clytoceyx rex*, which excavates prey from the ground

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Figure 8 (left). Brown-headed Paradise Kingfisher *Tanysiptera danae* (K. David Bishop)
Figure 9 (right). Papuan Treecreeper *Cormobates placens* (K. David Bishop)

with its enormous bill; and the five species or superspecies (*c.*9 allospecies) of paradise kingfishers *Tanysiptera* (Fig. 8), with greatly elongated central tail feathers like those of male *Astrapia* and *Epimachus* birds of paradise, suggesting a role in sexual selection—but the long tail feathers of *Tanysiptera* are shared by both sexes, so their function remains unknown.

Convergent lookalikes.—In apparent contrast to the obviously distinctive groups of New Guinea bird species, many other New Guinea (and Australian) bird species are morphologically and ecologically similar to European groups already familiar to Australia's first British colonists and scientists: warblers, wrens, creepers, nuthatches, sallying flycatchers, robins, and nightjars (Figs. 9–10). Among New Guinea's and Australia's mammals as well, along with unequivocal members of European rat and bat families are many other mammals morphologically and ecologically similar to other European mammals such as cats, moles, wolves and flying squirrels. However, it was immediately obvious that the New Guinea and Australian mammalian lookalikes were not members of European mammal families because they all gave birth to undeveloped offspring in a pouch. That identified them as a very distinct mammalian branch (marsupials), whereas all European mammals are placental mammals giving birth to more developed young. But New Guinea and Australian lookalike bird species do not share any distinctive morphological feature like a pouch. It remained for late 20th-century DNA studies to prove that apparently familiar groups of New Guinea and Australian birds are not closely related to their European lookalikes (Sibley & Ahlquist 1990). Instead, like marsupials, they

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Figure 10. Emperor Fairywren *Malurus cyanocephalus* (K. David Bishop)

represent independent radiations superficially very similar in morphology and behaviour to European bird groups. New Guinea and Australian 'wrens' (Fig. 10), 'warblers' and 'creepers' (Fig. 9), etc. are now recognised as belonging to separate bird families confined to New Guinea and Australia, plus in some cases neighbouring islands. The superficial resemblance between the New Guinea / Australian and European bird families exemplifies the phenomenon of convergent evolution: 'The repeated evolution of similar phenotypes in response to similar environmental conditions…is referred to…as convergent evolution when similar phenotypes evolve in distantly related forms' (Losos *et al*. 2014: 455). A familiar obvious example of this phenomenon is the evolution of superficially similar large swift marine carnivores among mammals, cartilaginous fishes, teleost fishes and reptiles to give rise to dolphins, sharks, tuna and the extinct ichthyosaurs, respectively.

Two surprises.—Finally, among remarkable birds that make New Guinea special, I will mention two species or groups of species that had been described already in the 19th century, and are common or locally common, but whose unexpected properties or behaviours were recognised only recently. One of the two surprises is that in 1990 Dumbacher *et al*. (1992) discovered that Hooded Pitohui *Pitohui dichrous* (Fig. 11) and some other common New Guinea species contain the neurotoxin homobatrachotoxin, previously known only in South American poison-dart frogs. Although such chemical defence agents are widespread among other vertebrate classes and insects, this was one of the first cases documented among birds. Several of the toxic New Guinea species are so similar to each other in their orange-brown and / or black plumage that they were considered congeneric with *P. dichrous*, but they proved to be only pseudo-pitohuis not closely related to *P. dichrous* (Dumbacher *et al*. 2008, Jønsson *et al*. 2008, Dumbacher 2014). Hence, they are convergent in plumage, as well as in their independent evolution of toxicity. (The toxin is probably acquired from beetles consumed in the diet, rather than synthesised by the birds themselves: Dumbacher *et al*. 2004.) As I shall discuss below, most toxic New Guinea bird species associate in mixed-

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Figure 11. Hooded Pitohui *Pitohui dichrous* (K. David Bishop)

species flocks of deceptively similar brown and / or black species of which some are toxic and others not, and which may thus constitute examples of Müllerian mimicry and Batesian mimicry.

My other example of a surprising discovery in a species described a century ago involves Greater Melampitta *Megalampitta gigantea*, a large black bird previously known only from six specimens collected without any field observations. Puzzling peculiarities of the specimens were their stiffened and spiny but heavily worn tail and wing feathers; an exposed bony spur at the wing bend; and egg cases of feather mites covering the head. In 1981 I discovered in New Guinea's Fakfak Mts. (Diamond 1983), and confirmed at other New Guinea locations in subsequent years, that this melampitta is a locally common specialist of limestone karst terrain with abundant deep narrow vertical sinkholes. According to my New Guinea field companions, the melampitta roosts and nests underground in the sinkholes, which are too deep and narrow for a short-winged bird like the melampitta to exit just by flying vertically upwards. Instead, the bird may scurry up a sinkhole's rock face by propping itself with its stiffened wings and tail, whose feathers thereby become abraded. The function of the wing's bony spur remains unknown, as does the reason for infestation with feather mites.

Advantages of New Guinea itself

Those are some of the advantages offered to ornithologists by New Guinea's remarkable birds. Let us now consider six advantages offered by New Guinea's geography and peoples.

Equatorial location and elevation.—New Guinea lies on the equator, but its mountains rise to nearly 5,000 m. As a result, New Guinea is one of only three places in the world where there is permanent snow on the equator, because New Guinea has equatorial mountains high enough to support glaciers. (The other two are the Andes of South America, and Mt.

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Kilimanjaro and a few other mountains of East Africa.) New Guinea's glaciated highest peaks lie just 100 km from the coast. Already when the Dutch explorer Jan Carstenz sailed past New Guinea in 1623, he could see white in the sky that he correctly inferred meant high snow-capped mountains. (The only other place in the world with equatorial glaciers sufficiently near the coast that one can stand on a coral reef and see snow is Colombia's Sierra Nevada de Santa Marta.) However, the difficulties of overland travel in New Guinea are so great that it was not until 1909 that a Dutch military expedition reached the snowline, and only in 1962 did a team led by the Austrian mountaineer Heinrich Harrer (famed for his first ascent of the notoriously difficult Eiger North Face in the Swiss Alps) succeed in climbing New Guinea's highest peak (Wichmann 1909–12, Souter 1964).

The height of those snow-capped equatorial mountains means that in New Guinea, within a distance of 100 km as the crow flies, one traverses a range of habitats similar to the range encountered at sea level as one proceeds 7,500 km from the equator to the Arctic Circle. The succession of habitats encountered in New Guinea, proceeding inland from the coast, is: coral reefs, sand beaches, mangrove and swamp forests, lowland rainforest, hill forest dominated by *Castanopsis* and *Lithocarpus* oaks, montane forest dominated by southern beech (*Nothofagus*), subalpine forest with conifers, alpine grassland with cycads and tree ferns, alpine rock fields, and finally the snow (Figs. 12–18). That range of habitats contributes to New Guinea's biological richness: each elevational band has its own distinct species. New Guinea even has a small endemic alpine avifauna. The New Guinea bird species with the highest elevational range is Snow Mountain Robin *Petroica archboldi*, discovered only in 1938, with an elevational floor of 3,850 m (Rand 1942). While the climax vegetation of most of New Guinea below the treeline is various types of forest, there are also extensive swamps, lakes and (in dry areas of the southern lowlands) savanna. The only major habitat type lacking in New Guinea is desert.

The right size.—New Guinea is often described as the world's largest tropical island. With approximately 515 breeding species or superspecies on its mainland (621 if allospecies are counted separately), New Guinea is rich: the size of its resident avifauna is comparable to those of North America, Europe or Australia (Salvadori 1880–82, Mayr 1941, Rand & Gilliard 1967, Coates 1985, 1990, Pratt & Beehler 2015, Beehler & Pratt 2016).

Of course, South America is much larger and much richer. I recall a conversation soon after my first visit to New Guinea, when I chatted with a well-known ornithologist specialising in South American birds. After I had given him a brief summary of the New Guinea avifauna, he commented, "Didn't you feel that New Guinea is impoverished, depauperate?" No, I don't, and here's why.

It's a misnomer for an ornithologist to call New Guinea the largest tropical island. Instead, New Guinea rates as the smallest continent. If one's distinction between an 'island' and a 'continent' is based solely on landmass area, such a distinction would be completely arbitrary. But to a biologist, there is a non-arbitrary distinction: a continent is a landmass large enough for many of its species to have been generated by speciation and radiation within the landmass, rather than by colonisation one species at a time from other landmasses. By that criterion, New Guinea clearly is for birds a continent: its avifauna includes many radiations of endemic subgenera (e.g., groups of *Rhipidura* fantails), genera (*Melanocharis* berrypeckers) and families (e.g., Cnemophilidae satinbirds). Its 515 species or superspecies constitute a database large enough to test major questions of biology, but small enough that in a decade or two an ornithologist can observe most of New Guinea's species and learn the distributions of all of them. While South America of course offers a far larger database of about 3,000 species, that includes so many species with highly local or poorly known distributions that no ornithologist can observe or understand all of them in a lifetime

ISSN-2513-9894 (Online)


12


13


14


15


17


16

Figure 12. Coastal forest (K. David Bishop)

Figure 13. Lowland rainforest (K. David Bishop)

Figure 14. David Bishop and Jared Diamond at a native-built vine suspension bridge over the upper Digul River, 215 m elevation (K. David Bishop)

Figure 15. Small aircraft dropping down to land at a one-way bush airstrip, Yolban, 1,250 m (K. David Bishop)

Figure 16. Moss forest, Arfak Mts. (K. David Bishop)

Figure 17. Alpine grassland with cycads, Mt. Doma (K. David Bishop)

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of study. That's why I say that New Guinea is just the right size for an ornithologist: big and rich enough, but not too big or too rich.

Simple geographic layout.—The mountains of New Guinea comprise a single central chain running west to east, on which differentiation has created west / east chains of subspecies or allospecies, plus ten outlying mountains along the north and north-west coasts, with endemic subspecies and allospecies but only two endemic species (Diamond 1985: see Maps 1–2). The lowlands of New Guinea consist of a ring enclosing that central chain—a ring around which differentiation has created three main lowland regions (northern, southern, and far western), each with endemic subspecies or allospecies, or chains of them (see Map 3). That is a much simpler geography than South America offers for reconstructing evolutionary history.


Figure 18. Alpine pools at 4,000 m below the summit of Mt. Mandala (K. David Bishop)

Hundreds of islands of three types.—Much of New Guinea's underwater shallow continental shelf was dry land at Pleistocene times of low sea level. Rising sea level at the end of the Pleistocene, and repeatedly during the Pleistocene, submerged lower parts of the shelf and isolated the higher parts as land-bridge islands of various elevations and areas, which were formerly part of Pleistocene Greater New Guinea (Diamond 1972b, Diamond & Bishop 2020: see Map 4). When those land bridges to modern New Guinea were intact during the Pleistocene, the islands could be reached not only by flightless mammals, but also by New Guinea's several hundred bird species unable or unwilling to colonise over water (Diamond 1972b). With the severing of the land bridges at the end of the Pleistocene, populations of non-water-crossing species on the islands became isolated and subject to the risk of extinction without the possibility of recolonisation. They thus constitute a convenient test system for understanding species differences in risk of extinction as isolated populations (Diamond 1972b).

Hundreds of other 'oceanic' islands lying beyond New Guinea's continental shelf could be colonised only by species capable of crossing water barriers (e.g., Mayr & Diamond 2001). Some of those oceanic islands lie on volcanic arcs at tectonic plate boundaries and have periodically been defaunated by volcanic eruptions. That has led to the evolution of a group of *c*.20 species without parallel in the Caribbean or elsewhere in the world: so-called supertramps with high dispersal ability, specialised for colonising small or remote or recently defaunated islands, and absent from large, central, species-rich islands (Diamond 1974, 1975).

Completeness of species-level cataloguing.—Knowledge of the composition of New Guinea's resident endemic avifauna can be considered near-complete at the level of species/superspecies. The next-to-most-recent discoveries were of one monotypic

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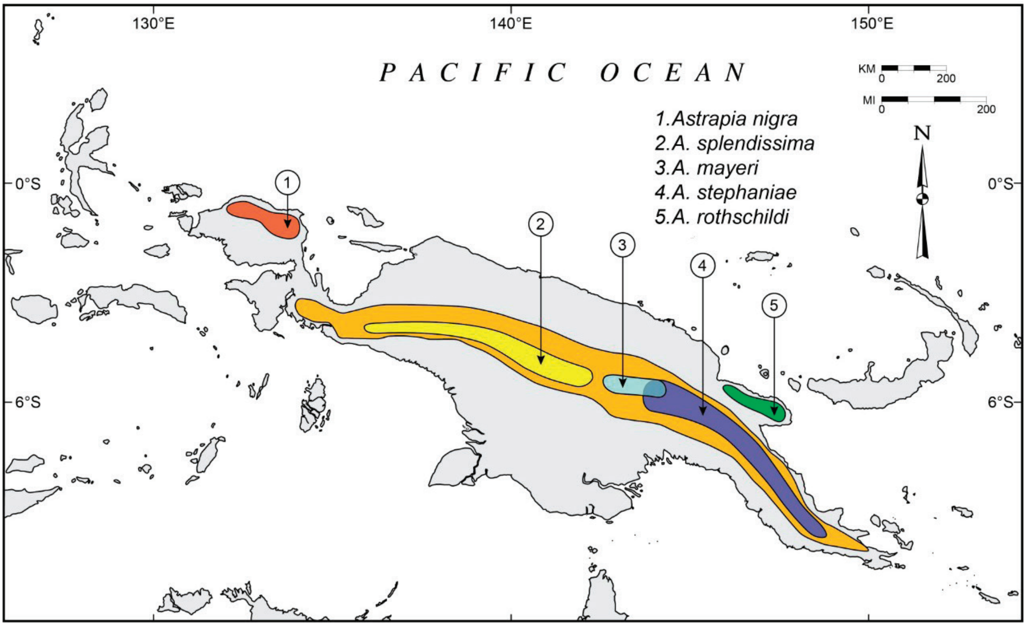
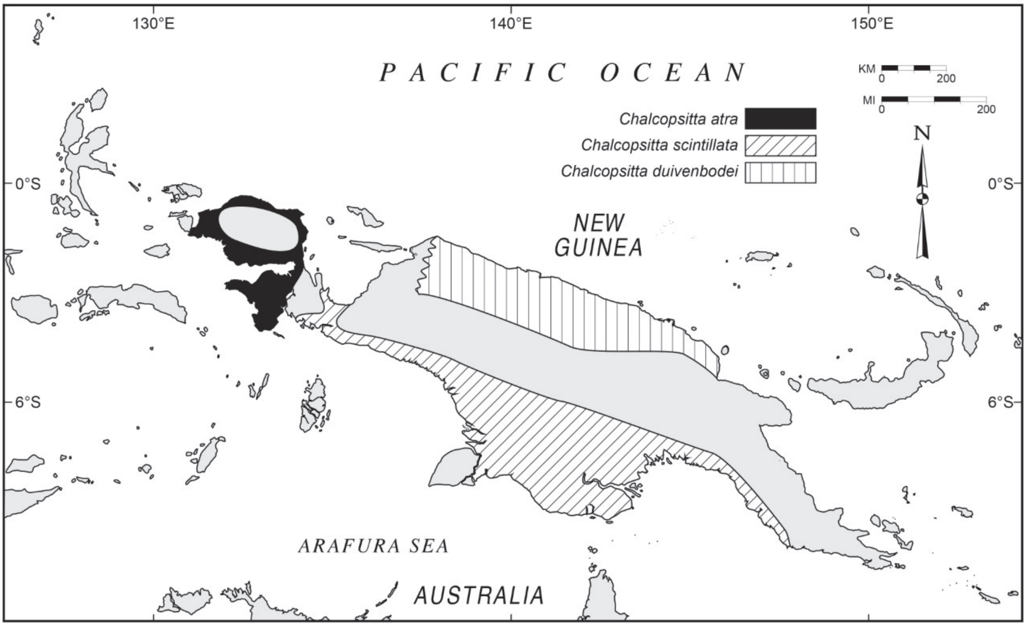


Map 2. Speciation in *Astrapia* birds of paradise. The five allospecies of the *Astrapia* superspecies have differentiated from west to east along the Central Range, plus one each on the two highest outlying ranges (*A. nigra* on the Vogelkop, and *A. rothschildi* on Huon). All five allospecies are allopatric, except that the easternmost population of *A. mayeri* and the westernmost of *A. stephaniae* overlap, with elevational exclusion in the zone of sympatry.



Map 3. Speciation in New Guinea's lowlands, as illustrated by the three allospecies of the parrot superspecies *Chalcopsitta*. Speciation in the lowlands consists of differentiation in the lowland ring around the Central Range, usually with one or more isolates each in the northern, southern and western lowlands.

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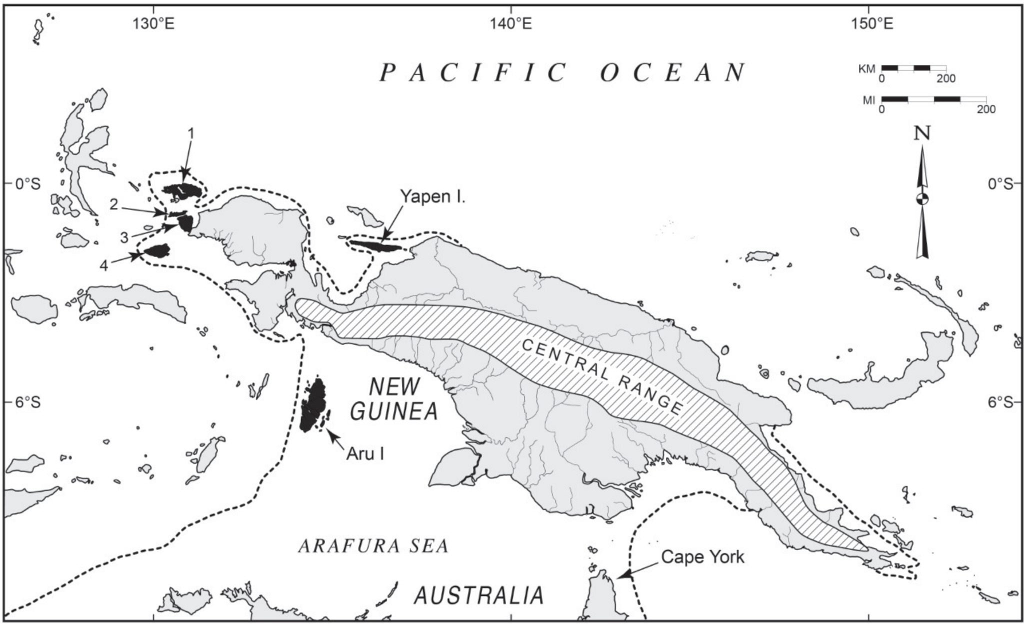

Map 4. New Guinea's six largest land-bridge islands. The dashed line around New Guinea and northern Australia marks the edge of New Guinea's continental shelf, corresponding to the 200-m depth contour in the ocean today. When sea level dropped by nearly 200 m at Pleistocene times of low sea level, the Arafura Sea became dry land, New Guinea and Australia were joined in a single landmass, and Greater New Guinea extended to the edge of the continental shelf. At the end of the Pleistocene, as glaciers melted around the world, rising sea level flooded the continental shelf and converted the six highest portions of the shelf into land-bridge islands: Yapen, Aru, 1 = Waigeo, 2 = Batanta, 3 = Salawati, 4 = Misool. Many of those modern-day islands' bird populations arrived overland during the Pleistocene. Islands lying beyond the edge of the continental shelf are oceanic islands, which lacked a recent land connection to New Guinea and have derived their birds entirely by overwater colonisation.

genus (Archbold's Bowerbird *Archboldia papuensis*) and four species unrelated to known superspecies (Brass's Friarbird *Philemon brassi*, *Petroica archboldi*, Black-breasted Mannikin *Lonchura teerinki*, and possibly Archbold's Owlet-nightjar *Aegotheles archboldi* whose status is still debated), discovered in 1938–39 by the Third Archbold Expedition in a biologically unexplored large area of western New Guinea: Rand 1942). The most recent discovery was of Satin Berrypecker *Melanocharis citreola* in the outlying Kumawa Mts. (Mila *et al*. 2021). Two other recently discovered taxa have been described as endemic allospecies rather than as subspecies: Long-bearded Honeyeater *Melionyx princeps* (Mayr & Gilliard 1951) and Wattled Smoky Honeyeater *Melipotes carolae* (Beehler *et al*. 2007). Some other allopatric populations discovered since 1939 may also prove to be allospecies rather than subspecies, and numerous previously known allopatric populations are regarded as allospecies, rather than subspecies, by recent authors (e.g., Beehler & Pratt 2016).

Of course, there have been, and will continue to be, innumerable discoveries about distributions and biology. However, it seems that our knowledge of New Guinea's resident endemic avifauna at the level of the species or superspecies is much more complete than is true of South America, where distinct new species continue to be discovered annually, and occasionally even new genera.

New Guinea peoples.—Traditionally, New Guinea peoples were either (a minority) hunter / gatherers or (a majority) subsistence farmers with protein-poor crops and few domestic animals, hence dependent on hunting and gathering for much of their dietary

ISSN-2513-9894 (Online)


19


20


21


22

Figure 19. Dugout canoe on the Elevala tributary of the Fly River (K. David Bishop)

Figure 20. Huli man (K. David Bishop)

Figure 21. Man wearing phallocarp at Yolban, 1,250 m (K. David Bishop)

Figure 22. Traditional highland sweet potato farm (K. David Bishop)

protein (Figs. 19–23). As a result, traditional New Guineans are walking encyclopedias of information about local birds, with up to 200 local-language names for local bird species or groups of species (Majnep & Bulmer 1977, Diamond & Bishop 1999). Routinely, whenever I arrive at a New Guinea village to study birds, I devote much time to learning names of bird species in the local language, of which New Guinea has about 1,000, because it is essential for tapping into New Guineans' encyclopedic knowledge of local bird species, and to find species of particular interest. That requires knowledge of local-language names. Questions about '*Phonygammus keraudrenii*' or 'Bicoloured Mouse-Warbler' will produce no response; one must instead ask about the '*isawanotaba*' or the '*kri-kro*', having first figured out those names' English or Latin equivalents.

As examples: when Jack Dumbacher discovered by accident (as a result of his reaction to being scratched) that *Pitohui dichrous* (Fig. 11) is poisonous, and he reported his 'discovery' to local New Guineans, after their initial response (in effect, 'Of course, are you Europeans

Figure 23. Children at Yolban, 1,250 m (K. David Bishop)

so stupid that you don't even know *that*?') they proceeded to tell Dumbacher about other bird species known to them, but not to Europeans, to be poisonous. My local guide Robert Uropka in New Guinea's Star Mts. described to me, along with 165 other bird species, a bird he called the *densiki* in his Ketengban language, and which he said is rare and very similar to but smaller and greyer and with a more cocked tail than the abundant *sewi*, which I had already identified as Grey-streaked Honeyeater *Ptiloprora perstriata*. Robert twice succeeded in finding for me a *densiki*, which proved to be the rare and little-known Leaden Honeyeater *P. plumbea*, a sibling species of *P. perstriata*. Those are the only two occasions in my life that I have seen *P. plumbea*.

Those six advantages—equatorial location and elevation, the right size, simple geographic layout, hundreds of islands of three types, completeness of species-level cataloguing, and New Guinea peoples—have made New Guinea ideal terrain for studying evolution, speciation, community ecology, behaviour, sexual selection, and other fields and topics of biology.

What have we learned?

We've now discussed some of New Guinea's remarkable bird species, and some of New Guinea's advantages for bird studies. What have those birds and those advantages taught us? I'll give five examples of conclusions of general biological interest.

Elevational sequences.—One of the ecological segregating mechanisms by which related or congeneric species co-exist on New Guinea's mountains depends on elevation. The New Guinea montane avifauna includes dozens of pairs, a dozen triplets, several quartets, and one quintet of taxonomically related and ecologically otherwise similar species that co-exist by inhabiting different elevations, often occupying mutually exclusive elevational ranges (Diamond 1972a, 1973, Freeman & Freeman 2014). For instance, Mt.

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Karimui's north-west ridge in 1965 supported two abundant and territorial warbler species of the genus *Crateroscelis*, with no elevational overlap at all: *C. murina* from the lowlands to 1,643 m and *C. robusta* from 1,646 m to 2,320 m. Such sequences are also frequent among Andean birds (Terborgh 1971).

The distributions of many pairs of populations have been interpreted as constituting 'snapshots' of successive intermediate stages in speciation (Diamond 1972a, 1973). They suggest that these elevational sequences arise via allopatric speciation of eastern and western populations along New Guinea's Central Range (Map 2), rather than through sympatric speciation along an elevational gradient. Map 5 depicts seven stages in that suggested allopatric evolution of one species into a sympatric species pair co-existing by elevational segregation. This hypothesis, based on distributional evidence, remains to be tested by molecular phylogenetic approaches. The seven distributional stages are as follows.

In the presumed first stage, one species without close relatives is distributed continuously from the western to the eastern end of the Central Range, with no consistent variation in elevational range (e.g., Blue-capped Ifrit *Ifrita kowaldi*).

In the presumed second stage, a species' western and eastern populations become separated by a large distributional gap, due perhaps either to local extinctions or to a distributional barrier across the Central Range such as the Strickland Gorge (e.g., Papuan Treecreeper *Cormobates placens*; Fig. 9).

In the presumed third stage, the western and eastern populations are still separated by a distributional gap, but have now evolved slightly different elevational ranges and sufficient morphological and genetic differences to be classified as distinct allospecies of a superspecies, rather than as subspecies of an allospecies or species (e.g., Short-bearded Honeyeater *Melionyx nouhuysi* in the west, Long-bearded Honeyeater *M. princeps* in the east).

In the presumed fourth stage, the western and / or eastern population expand eastwards and/or westwards, respectively, to approach each other's ranges without yet having achieved sympatry (e.g., Western *Paramythia olivacea* and Eastern Crested Berrypeckers *P. montium*).

In the presumed fifth stage, geographic expansion has proceeded further, to the point where western and eastern forms have achieved partial sympatry, with truncated and mutually exclusive elevational ranges in the zone of sympatry, but with each species occupying a broader elevational range in its own zone of allopatry (e.g., Green-backed *Pachycephalopsis hattamensis* and White-eyed Robins *P. poliosoma*).

In the presumed sixth stage, one taxon has completely overrun the geographic range of the second, with the two species still co-existing by elevational segregation, but the first taxon still maintains a zone of allopatry where it occupies a wider elevational range.

In the presumed seventh stage, the two taxa are now geographically fully sympatric as an elevationally segregating species pair, with neither species existing in allopatry, and both species widely distributed geographically from west to east over the Central Range. This whole process may then repeat itself to generate an elevationally segregated species trio (stage eight), quartet, or quintet.

Culture in bowerbirds.—Culture may be defined as the set of behaviours that characterise a local population of a species, and which are transmitted not genetically but instead by learning and copying among individuals. Culture was previously considered unique to humans. When Jane Goodall and other field biologists studying chimpanzees, gorillas and other animal species observed differences in behaviour between conspecific but geographically separated populations (such as in tool use by chimpanzee populations), their interpretation of the differences as cultural was initially dismissed by other biologists.

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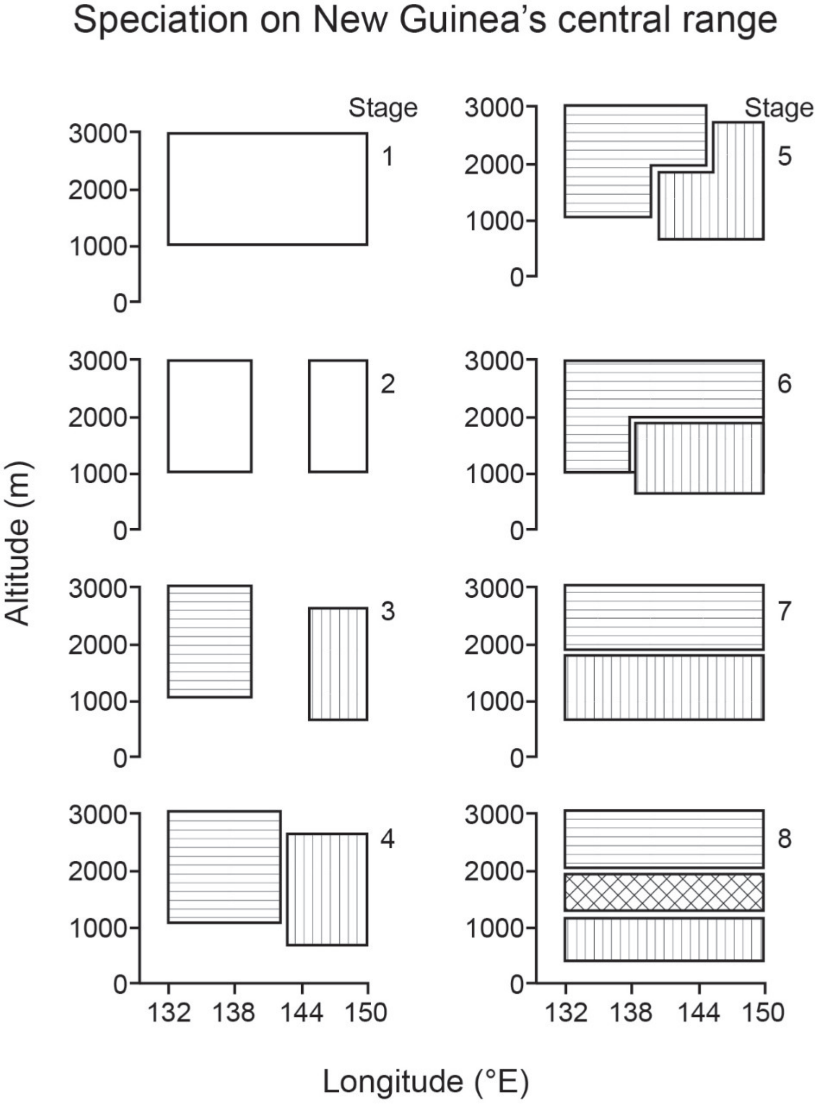

Map 5. Speciation on New Guinea's Central Range. This figure depicts eight postulated stages in the evolutionary transformation of one species, initially distributed from the west to east end of the Central Range, into two (stage seven) or even three (stage eight) fully sympatric species co-existing with elevational segregation. Each of the eight subfigures depicts the actual elevational and longitudinal distribution of one taxon, or of a pair or a triplet of closely related taxa (distinguished by horizontal, vertical, or cross-hatching), on the Central Range. Each subfigure is interpreted as constituting a 'snapshot' of one stage in speciation. In each subfigure, longitudinal distribution is shown along the horizontal axis, and elevational distribution along the vertical axis. For example, stage four depicts two taxa with allopatric but abutting geographic distributions and slightly different elevational ranges; stage five depicts two taxa each with largely allopatric geographic distributions and mutually exclusive elevational ranges in the zone of sympatry; and stage seven shows two fully sympatric taxa both distributed from the west to the east end of the Central Range, with mutually exclusive elevational ranges everywhere. See text for discussion.

Gradually, though, it has become accepted that behavioural differences between conspecific animal populations may indeed be cultural.

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(Online)

Amblyornis bowerbirds provide a good example. Bowers of Vogelkop Bowerbird *A. inornata* differ drastically between mountains (Diamond 1986a). In the Arfak, Tamrau and Wandammen Mts. bowers are stick 'huts' up to 2 m in diameter, decorated with many coloured objects (red, pink, orange, yellow, green, blue and purple fruits, flowers, mushrooms and butterfly wings, as well as black, brown, grey and white objects) (Fig. 4). Bowers of the same species in the Kumawa and Fakfak Mts. are instead stick towers up to 2.4 m tall, usually decorated only with black, white, grey and brown objects. Those differences led Gibbs (1994) to conclude that the former populations could not be conspecific with the latter. But the two sets of populations are nearly identical morphologically, and they are similar genetically too (Kusmierski *et al*. 1997). Furthermore, there are differences in bower style even between three sites less than 10 km apart in the Kumawa Mts.: bowers in one area were decorated with fruits and flowers of four colours, in another with black, grey and white objects plus propped-up pandanus leaves, and in still another area with neat rectangular rows of pieces of buff-coloured clay. These differences are not due to differences in local availability of those objects: coloured fruits and flowers, and uncoloured stones and snail shells, are widely available; and when bowerbirds of a population decorating only with uncoloured natural objects were offered coloured poker chips, they discarded the chips, but coloured chips were promptly incorporated into the bowers of a population using coloured natural objects (Diamond & Bishop 2015).

Local bower style appears to be learned and transmitted by observation in both male and female bowerbirds (Diamond 1986b). Young males build crude bowers with locally inappropriate decorations and form, take up to seven years to develop the locally appropriate bower style, resemble females in plumage, and exploit that resemblance to enter bowers of adult males and elicit the adult male's display, thereby giving young males the opportunity to learn by closely observing mature bower design and display. Females sometimes form groups to visit bowers, thereby giving young females the opportunity to learn taste in bowers from older females.

'Aggressive mimicry'.—Over a century and a half ago, the great Alfred Russel Wallace (1869), co-discoverer of evolution and natural selection with Darwin, described a striking case of apparent visual mimicry between species of two different bird families: honeyeaters (Meliphagidae) and orioles (Oriolidae). Wallace attributed the apparent mimicry to the putative advantage that 'weak' orioles gained in deterring attack by aggressive crows and hawks, as a result of resembling the 'strong' pugnacious honeyeaters. But Wallace's interpretation was dismissed by Stresemann (1914) and forgotten. In recent years, however, interest in 'aggressive mimicry' has exploded, stimulated by discoveries of cases involving not only species that are taxonomically remote and obviously unrelated, but also between confamilial species that had previously been considered closely related. Especially shocking to European and North American ornithologists has been genetic evidence demonstrating that three pairs of confamilial species so similar that they had always been considered closest relatives—Middle Spotted *Dendrocopos medius* and Lesser Spotted Woodpeckers *D. minor*, Hairy *Picoides villosus* and Downy Woodpeckers *P. pubescens*, and Greater *Tringa melanoleuca* and Lesser Yellowlegs *T. flavipes*—are not close relatives but instead mimics or convergent (Weibel & Moore 2002, 2005, Gibson & Baker 2012, Prum 2014).

I re-appraised Wallace's classic example and concluded that Wallace was half-right (Diamond 1982b). Orioles (genus *Oriolus*) are predominantly yellow-and-black Afro-Eurasian species that, on invading the Indonesian archipelago and New Guinea, encountered a superspecies of big brown honeyeaters known as friarbirds (genus *Philemon*). The Indonesian and New Guinea orioles differ drastically in plumage from extralimital orioles, in being brown like friarbirds. Among Indonesian islands and New Guinea, both

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orioles and friarbirds exhibit marked geographic variation in plumage, but variation is parallel, such that on each island the oriole and the friarbird resemble each other. For example, geographic differences in patches of bare black facial skin in friarbirds are paralleled by corresponding patches of black feathers in orioles. While on each island the friarbird is larger than the oriole, paradoxically the more *dissimilar* the friarbird and oriole are in size (i.e., the larger the local friarbird relative to the oriole), the more *perfect* is the local plumage resemblance. David Bishop and I have often been confused in the field by species pairs that are merely 'quite similar' in plumage, as on New Guinea. On islands such as Seram and Buru, where the species pairs are virtually identical in plumage, they are very difficult to distinguish not only in the field, but even as specimens in museum trays: indeed, some museum specimens proved to be misidentified. Further complicating the picture is that the New Guinea oriole, which is 'quite similar' to the larger New Guinea friarbird, shares New Guinea with the smaller Streak-headed Honeyeater *Pycnopygius stictocephalus*, whose plumage is even more similar to the New Guinea oriole's than the New Guinea oriole's plumage is to the New Guinea friarbird's! All of these resemblances are even more confusing in the field than in museums, because of vocal mimicry and similarity in posture, movements and flight.

Hence, I agree that Wallace was partially correct: Indonesian and New Guinea orioles do mimic friarbirds. We can confidently refer to mimicry of friarbirds by orioles, rather than mutual convergence between friarbirds and orioles, because the friarbirds are typical honeyeaters in their brown plumage and bare facial skin, whereas Indonesian and New Guinea orioles are unique within the family Oriolidae in plumage and in their black facial patches resembling the friarbirds' black facial skin areas. The evidence for mimicry is now much stronger than that available to Wallace, who encountered only two pairs of island populations (on Seram and Buru), whereas we now know seven pairs. Especially convincing is the study of Jønsson *et al*. (2016), who obtained molecular data for all *Philemon* species and all brown *Oriolus* species, constructed molecular phylogenies, measured plumage reflectance, and calculated durations of co-existence.

What advantage do orioles gain by mimicking friarbirds? And why is plumage mimicry more perfect, the more dissimilar the model (i.e., the friarbird) is to the mimic (i.e., the oriole) in size? Here, like Stresemann (1914), I disagree with Wallace: crows and bird-hunting hawks are much too rare in habitats used by orioles and friarbirds to be a significant selective factor. Instead, I believe that selection involves attacks among friarbirds, orioles and Streak-headed Honeyeaters themselves, and the many other bird species congregating at fruiting and flowering trees where they feed on fruit and nectar. These feeding assemblages are 'veritable riots of interindividual aggression', to quote Beehler (1980: 516). Larger birds devote much time and energy to driving off smaller birds that overlap in diet and that can be safely attacked. Smaller birds that resemble larger birds would be less likely to be attacked by larger birds, and in turn would be more intimidating to even smaller species. That would explain why plumage mimicry of friarbirds by orioles is more perfect, the relatively larger is the friarbird: larger size makes the friarbird more dangerous to the smaller oriole, and in turn makes a friarbird-mimicking oriole more intimidating to even smaller birds.

These expectations are supported by my field observations in New Guinea. The New Guinea friarbird, oriole and Streak-headed Honeyeater all drive off smaller species overlapping in diet, but do not waste time and energy attacking species with quite different diets. However, it is striking that in 500 hours of observation at fruiting and flowering trees in many different areas of New Guinea, I have never seen the New Guinea friarbird attack the smaller New Guinea oriole, nor the oriole attack the smaller Streak-headed Honeyeater.

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Mimicry serves the function of deception. A pervasive question in mimicry studies is: who is intended to be the deceived victim? In studies of poisonous butterfly species and their non-poisonous mimics, the answer is clear: the deceit is aimed at predators of butterflies. The poisonous New Guinea pitohuis that I discussed earlier are unpalatable to humans and ectoparasites, and presumably also to snakes, hawks and other predators on bird nests and adult birds (Dumbacher *et al*. 2008). There are now dozens of cases of apparent mimicry of larger birds by smaller birds (Prum 2014), discussed under the title 'interspecific social dominance mimicry' = ISDM. Is the intended victim of deceit the larger model species itself, or other potential competitors of the mimic? This question of the relative importance of different potential victims of deceit remains to be established not only for New Guinea friarbirds, orioles and honeyeaters, but also for all putative cases of ISDM (Prum 2014).

Brown-and-black flocks.—Itinerant mixed-species foraging flocks are known from many parts of the world: throughout the year in the tropics, and in the winter in temperate zones. They consist especially of small (<40 g) midstorey insectivores, often sharing a single predominant colour or colour-mixture. New Guinea also possesses such small insectivore flocks, especially of flycatchers and warblers.

But, in addition, New Guinea has another type of flock, consisting of medium-sized or large (40–220 g) species, most feeding on both fruit and arthropods, and at any moment concentrated at a given height anywhere from the understorey to the lower canopy. All constituent species are passerines; all are forest species; and most are strictly endemic to New Guinea and its large land-bridge islands, hence the flocks are absent from New Guinea-region oceanic islands, Australia, and all other sites outside the New Guinea region. Notably, flock members are either brown or black in both sexes (ranging to grey in cuckooshrike member species), or black in the male and brown in the female. Brown-and-black flocks have been studied especially by the late Harry Bell (1982, 1983) and by me (Diamond 1987). In New Guinea, brown-and-black flocks occur everywhere in lowland forests, up to elevations only occasionally above 1,200 m in the mountains.

Flock leaders are drawn from six species: Papuan Babbler *Garritornis isidorei* and five species of pitohuis or pseudo-pitohuis. Those are the sole flock species that regularly forage in intraspecific groups of five or more and maintain a constant stream of contact calls. Among the babblers, Harry Bell identified a leader individual with a distinctive leader call. These leader species constitute a hierarchy: the babbler is the leader species whenever it is present in the flock; if the babbler is absent, then the 'second-choice' leader is the pseudo-pitohui Rusty Shrikethrush *Pseudorectes ferrugineus*, which would otherwise follow the babbler; if both of those species are absent, the 'third-choice leader' becomes Variable Pitohui *Pitohui kirhocephalus*/*P. uropygialis*; and if all three of those species are absent, then the leader is *P. dichrous* (Fig. 11) or two pseudo-pitohui species. This means that at least some flock members are known to be poisonous.

Another regular flock member is New Guinea's lowland Spangled Drongo *Dicrurus bracteatus* or (above the lowlands) Drongo Fantail *Chaetorhynchus papuensis* (now revealed by molecular studies to be related to fantails [Irestedt *et al*. 2008], but formerly believed to be a drongo because of its similarity to drongos in behaviour). Drongos are notorious elsewhere in the world for following mixed flocks of birds, large mammals or people. (I was once momentarily frightened, while walking alone in a remote New Guinea forest, to sense something black following me; it proved to be *Chaetorhynchus*!) Still other regular flock members are one or more of at least 16 bird of paradise species, and one or more of all seven New Guinea forest species of cuckooshrikes (genera *Coracina* and *Edolisoma*).

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As for the function of joining brown-and-black flocks, the observable or suggested benefits include the usual ones suggested for mixed-species flocking elsewhere in the world: flushing prey, kleptoparasitism, benefitting from other species as sentinels, confusing predators, improved foraging efficiency, and acting as a 'gang' to overwhelm the defences of solitary territorial species.

Neotropical mixed flocks converge on a single colour or colour mix, perhaps to promote flock cohesion and predator confusion (Moynihan 1968). Why do New Guinea brown-and-black flocks instead converge on two alternative colours? One speculation is that the answer may involve the flock's long co-evolutionary history with birds of paradise, of which females are often brown (to aid crypsis at the nest?) and males are often glossy black (display plumage for sexual selection?). While some bird of paradise species have brightly coloured males, individuals that join flocks are mainly females and female-plumaged immature males.

Obviously, we still have much to learn about brown-and-black flocks, especially about their poisons, the functions of their two colours, and the roles and histories of their birds of paradise.

Selection for and against overwater dispersal.—Except for four flightless species—the three species of cassowaries, and New Guinea Flightless Rail *Megacrex inepta*—all New Guinea bird species are capable of flight, and many are outstandingly strong fliers. Nevertheless, New Guinea bird species differ enormously in their ability to colonise distant islands overwater.

At one extreme are the already mentioned so-called supertramps that specialise in living on oceanic islands requiring overwater colonisation to found populations. They dominate the avifaunas of Krakatoa-like recently defaunated volcanic islands, of which there are many in the New Guinea region along the Bismarck Volcanic Arc (fig. 1.2 of Mayr & Diamond 2001). For example, Long Island, defaunated by a volcanic eruption in the late 1600s, now has an avifauna dominated by ten supertramp species (Diamond 1974). Another set of islands dominated by supertramps are small islands where population extinctions are frequent, and where frequent recolonisations are necessary to maintain populations. Supertramps also occupy remote islands difficult for other species to reach. They have evolved high dispersal ability, and probably large reproductive outputs, at the expense of competitive ability. This may explain why they are absent on species-rich New Guinea itself, and on large and / or nearby islands in the same region. A human equivalent of avian supertramps is the Polynesians, who colonised every island of the tropical Pacific Ocean, no matter how remote, but who are confined to outlying islands on archipelagos closer to New Guinea, such as Rennell, Bellona and Sikaiana of the Solomons, whose central islands are all occupied by Melanesians.

At the same extreme of high overwater dispersal ability are species whose geographic ranges encompass islands scattered over thousands of kilometers of ocean, such as Buff-banded Rail *Hypotaenidia philippensis*, the *Megapodius* [*reinwardt*] superspecies, and Pacific Imperial Pigeon *Ducula pacifica*. On many remote islands that they have colonised, these species have evolved local endemic allospecies, many of which in the cases of *Hypotaenidia* and *Megapodius* went on to evolve flightlessness (Steadman 2006).

At the opposite extreme are several hundred New Guinea species absent from every oceanic island in the region (i.e., islands lacking a land connection to New Guinea at Pleistocene times of low sea level) (Diamond 1972b). The only islands of the New Guinea region, other than New Guinea itself, on which these species may occur are the larger so-called land-bridge islands, i.e., islands on New Guinea's shallow continental shelf, which were part of New Guinea at Pleistocene times of low sea level (Map 4). These 'land-bridge

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relict species' reached the islands overland when they were part of Pleistocene Greater New Guinea. Their island populations have subsequently been subject to differential extinction: more extinctions on smaller land-bridge islands with smaller populations, and extinction even on large islands for species with small populations due to low population density (e.g., New Guinea Harpy Eagle *Harpyopsis novaeguineae*, now absent even on the largest islands, and confined to New Guinea itself).

An initially surprising feature of the land-bridge relict fauna is that it includes many notably strong fliers, whose ecology on New Guinea involves daily long overland flights of dozens of kilometres and many hours. These surprising species include nomadic fruit pigeons, parrots and other species that fly long distances in search of fruiting and flowering trees, and three species of swifts whose foraging is entirely aerial. Yet these species are never seen flying overwater. The land-bridge relict species are entirely absent, even as visitors, from all oceanic islands more than 10 km from the New Guinea mainland—a distance that they could cover in a flight of ten minutes. Hence their absence from those islands is not because they are incapable of reaching them: it is because they *choose* not to fly overwater.

These facts illustrate that overwater dispersal is subject to natural selection, which variously either favours or opposes overwater dispersal depending on the species. The land-bridge relict fauna consists mainly of New Guinea forest species, although swifts are an exception. Their selection against dispersal may arise in part because their low reproductive potential makes them poor colonists even if they did reach islands. Hence any individuals inclined to disperse overwater would be selected out of the mainland population, and would also fail to found offshore island populations.

Disadvantage of New Guinea bird studies

I have discussed the advantages that New Guinea's remarkable birds, its geography, and its peoples offer to visiting ornithologists. I have provided examples of the questions of broad interest that New Guinea birds lend themselves to exploring. But I will conclude by acknowledging a disadvantage of field work in New Guinea. After one has come to know New Guinea, the rest of the world seems boring by comparison.

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Subspeciation in the Ruby-throated Bulbul *Rubigula dispar*

by Alex J. Berryman & Nigel J. Collar

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Summary.—Ruby-throated Bulbul *Rubigula dispar*, currently Vulnerable on the IUCN Red List owing to trade pressure, is considered monotypic across its range on three Sundaic islands in Indonesia: Sumatra, Java and Bali. However, examination of photographs and museum specimen labels and measurement of 37 Sumatran and 50 Javan specimens indicate that birds from Sumatra differ from those on Java (type locality) and Bali in exhibiting a variably red (not pale yellow) iris and a slightly longer bill and wing. Consequently, we propose subspecies rank for the Sumatran population. We recommend that the two taxa be maintained pure in captivity and that any releases of confiscated birds take place on the correct island based on eye colour.

Ruby-throated Bulbul *Rubigula dispar* (Horsfield, 1821) is endemic to the Greater Sunda Islands of South-East Asia, where it occurs on Sumatra, Java and Bali in Indonesia, inhabiting a range of wooded habitats (apparently preferring degraded areas) in lowlands below 1,000 m (Eaton *et al*. 2021). The species is currently listed as Vulnerable on the IUCN Red List because of perceived significant pressure from the Indonesian songbird trade (Eaton *et al*. 2015, Chng *et al*. 2016), which is suspected of causing declines exceeding 30% in the last ten years (BirdLife International 2022).

Although treated as a species for the first *c.*140 years of its taxonomic existence, in the second half of the 20th century *Rubigula dispar* was lumped as a subspecies of Black-capped Bulbul *Pycnonotus melanicterus* (now *R. melanictera*) along with the forms *flaviventris*, *gularis* and *montis* (e.g. Rand & Deignan 1960, MacKinnon 1988, Sibley & Monroe 1990, Inskipp *et al*. 1996). In the present century, however, a five-species treatment of these taxa proposed by Fishpool & Tobias (2005) has been widely adopted in regional and global classifications (e.g. Dickinson & Christidis 2014, Eaton *et al*. 2021, Clements *et al*. 2022, Gill *et al*. 2022, HBW & BirdLife International 2022). This arrangement—originally made based on external morphology—has since been affirmed by molecular data (Shakya & Sheldon 2017).

When treated specifically, *R. dispar* has always been considered monotypic (Fishpool & Tobias 2005, Dickinson & Christidis 2014, del Hoyo & Collar 2016, Eaton *et al*. 2016, 2021). Recently, however, a difference in iris colour between Sumatran and Javan / Bali birds has been noted (Eaton *et al*. 2021; J. K. Menner *in litt*. 2021), with the additional suggestion that '[Sumatran] birds have…red throat bleeding into breast' (Eaton *et al*. 2021). Previously, apart from a remark that the eyes of the species were 'either cream-coloured or dull red', with no geographical basis indicated for this circumstance (Tilford 2000[1]), the iris colour was consistently described and / or illustrated as red (e.g. MacKinnon 1988, MacKinnon & Phillipps 1993, Fishpool & Tobias 2005, Eaton *et al*. 2016, del Hoyo & Collar 2016, Arlott 2018). We therefore sought to assemble the evidence to determine the potential taxonomic

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[1] While this paper was in press, a revised version of the book (Tilford 2023) was published in which the iris colour of Ruby-throated Bulbul was described as 'pale orange', yet illustrated with a photograph of a bird with eyes that are clearly very pale yellow.

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(Online)

significance of this claimed distinction and any other difference that close examination of morphological and acoustic material might disclose.

Methods

Iris colour.—Photographs of *R. dispar* were collated (to October 2022) by AJB from the Macaulay Library (www.macaulaylibrary.org) (*n* = 86) and opportunistically from online trip reports (e.g. www.cloudbirders.com), and iris colour was noted when clearly visible. To minimise possible duplication, images taken at the same site on the same day were not counted unless it was explicitly mentioned that multiple individuals were involved, leaving a final sample of 55 photographs (*n* = 40 Java / Bali, *n* = 15 Sumatra). During the study of museum material (below) a note was made when iris colour was indicated on specimen labels (including females that were not measured).

Morphometrics and plumage.—One of us (NJC) examined and measured 87 specimens of male *R. dispar* at the following institutions: Naturalis Biodiversity Center, Leiden (RMNH; *n* = 41 Java, *n* = 20 Sumatra); American Museum of Natural History, New York (AMNH; *n* = 14 Sumatra); Natural History Museum, Tring (NHMUK; *n* = 5 Java, *n* = 1 Sumatra); Zoologische Staatssammlung, Munich (ZSM; *n* = 2 Java); Museo Civico di Storia Natural 'Giacomo Doria', Genoa (MSNG; *n* = 1 Sumatra); Museum für Naturkunde, Berlin (ZMB; *n* = 1 Java); Muséum national d'Histoire naturelle, Paris (MNHN; *n* = 1 Sumatra); and National Museum of Natural History, Washington DC (USNM; *n* = 1 Java). Thus our sample comprised 50 specimens from Java and 37 from Sumatra but none from Bali (material from which would naturally group with Java, as indicated in Eaton *et al*. 2021). A further 28 female specimens were measured in RMNH (*n* = 16 Java, *n* = 9 Sumatra) and NHMUK (*n* = 2 Java, *n* = 1 Sumatra). Unsexed and immature specimens were not measured. Specimens were checked for appreciable differences in plumage, and standard measurements (in mm) were taken as follows: bill from skull to tip; wing curved, from carpal to tip; tail from point of insertion to tip.

Morphometric data were normally distributed but of unequal variance, hence for each sex morphological characters were compared using Welch's unpaired t-test applying a Bonferroni correction (where the threshold for statistical significance is set at $p<0.05/n_v$). The effect size, expressed as Cohen's *d*, was calculated to investigate the strength of morphometric differences between populations, adopting the thresholds suggested by Tobias *et al*. (2010) where values >0.2, >2, >5 and >10 correspond to differences considered 'minor', 'medium', 'major' and 'exceptional' respectively.

Vocalisations.—Recordings from xeno-canto (www.xeno-canto.org) and the Macaulay Library (to October 2022) were provided on request and collated. After removing duplications and material of low quality, just five (*n* = 4 Java, *n* = 1 Sumatra) recordings of *R. dispar* song were available. Because of the small sample size, these were only visually inspected and not subject to analysis.

Results

Iris colour.—Sumatran populations of *R. dispar* exhibited consistent differences from Javan birds in iris colour. The collector J. J. Menden labelled four skins in ZMB from Indramayu, Java, as having brown eyes, and he reported a fifth with red-brown eyes to Kuroda (1933), but he appears to have been wholly cavalier ('doubtless false') in his notation of iris colour (Mees 1957). We therefore set his testimony aside, leaving specimen label data available for eight Javan and 19 Sumatran specimens. All those from Java (*n* = 5 males, *n* = 3 females) were labelled as 'pale lemon', 'pale yellow' or 'yellowish', while all

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(Online)

Figure 1. Example comparison of iris colour in Ruby-throated Bulbul *Rubigula dispar* from Java (left; © Forest Botial-Jarvis) vs. Sumatra (right; © Lars Petersson)

from Sumatra (*n* = 16 males, *n* = 3 females) were labelled as variations of red or orange and in a single case brown (which is commonly the colour of the eyes of young bulbuls [F. H. Sheldon *in litt*. 2023] including Javan populations of *R. dispar* [J. K. Menner *in litt*. 2023]).

Birds photographed on Sumatra (*n* = 15) always showed a deep orange to dark red iris, while those on Java and Bali (*n* = 40) exhibited a pale yellow to greyish iris 97.5% of the time (Fig. 1), with the exception of a single red-eyed individual (ML 109621061). This last was photographed at Bogor Botanical Gardens, West Java, a locality close to the cities of Jakarta and Bandung, where *c*.125,000 and 980,000 native songbirds respectively were estimated to be kept as pets in 2018 (Marshall *et al*. 2020). Notably, *R. dispar* was not recorded from Bogor Botanical Gardens historically (Hoogerwerf 1948, 1950, Diamond *et al*. 1987) and only appeared there after the release of 'hundreds of cagebirds' by local authorities in the 1990s / early 2000s (B. van Balen *in litt*. 2022). Consequently, we consider this individual a Sumatran bird that is either a descendant of this introduction or, perhaps more likely, a recently escaped individual from a local market.

Morphometrics.—In both sexes, Sumatran birds had longer bills and wings than Javan birds, but differences in tail length were statistically non-significant (Table 1). In males, Cohen's *d* effect sizes of 1.93, 1.07 and 0.48 were generated for bill, wing and tail length differences respectively, which classify them as 'minor' according to Tobias *et al*. (2010) thresholds (although bill length almost met the threshold for 'medium'). In females, equivalent values were 1.06, 1.87 and 0.85, thus all 'minor' differences (but with wing close to meeting the threshold for 'medium').

Plumage.—Our review of specimens suggested that the extent to which the red throat 'bleeds' onto the rest of the underparts (Eaton *et al*. 2021; see Introduction) is individually

ISSN-2513-9894
(Online)

TABLE 1

Morphometric data (in mm) of populations of Ruby-throated Bulbul *Rubigula dispar* showing mean, standard deviation, range and sample size for each character. * denotes statistical significance using a Welch's unpaired t-test applying a Bonferroni correction.

Males	**Bill**	**Wing**	**Tail**
Sumatra	**16.9 ± 0.6*** (15.6–18.1, *n* = 33)	**81 ± 3.0*** (76–92, *n* = 37)	**73 ± 2.6** (68–78, *n* = 37)
Java	**15.7 ± 0.6*** (14.6–17.1, *n* = 48)	**78 ± 1.8*** (75–83, *n* = 50)	**72 ± 3.0** (68–80, *n* = 50)
Females	**Bill**	**Wing**	**Tail**
Sumatra	**16.6 ± 0.8*** (14.9–18.2, *n* = 10)	**80 ± 1.5*** (77–82, *n* = 10)	**73 ± 2.3** (69–76, *n* = 10)
Java	**15.8 ± 0.7*** (14.1–16.7, *n* = 18)	**77 ± 1.7*** (74–80, *n* = 18)	**71 ± 2.4** (68–76, *n* = 18)

and not geographically variable. We found no consistent plumage differences between Javan and Sumatran birds.

Vocalisations.—A visual inspection of the small available sample (minimal for Sumatra) yielded no appreciable difference between islands.

Discussion

Iris colour has, in other bulbuls, been noted as a probably important reproductive signal. For example, the previous assumption that Bornean populations of Cream-vented Bulbuls *Pycnonotus simplex* were polymorphic in eye colour (red or white) was falsified when the two phenotypes were found to be only distantly related, despite nearly identical plumage (Shakya *et al*. 2019). Similarly 'Barusan Bulbul' *P. porphyreus* was recently avowed to be specifically distinct from Olive-winged Bulbul *P. plumosus* on the basis of a number of morphological differences, including a much paler iris (Rheindt *et al*. 2020, Eaton *et al*. 2021).

However, we find no plumage character that distinguishes Sumatran from Javan Ruby-throated Bulbuls, morphometric differences between them are only minor, and at present on very limited evidence no vocal differences can be detected. Furthermore, the only comparative genetic data available (Dejtaradol *et al*. 2015) are inconclusive, since their samples ostensibly from 'Jakarta' were collected from bird markets, thus could reasonably refer to either taxon. Nevertheless, we consider that Sumatran birds are sufficiently distinct from Javan birds to merit subspecific recognition.

Rubigula dispar matamerah subsp. nov.

Holotype.—Adult male, NHMUK 1888.4.1.724, collected at Sidjoendjoeng [Sijunjung], *c*.00°42'S 100°58'E, *c*.270 m, Sumatra, Indonesia, in October 1878 by Carl Bock. Bill 16.8 mm, wing 82 mm, tail 76 mm. The specimen label documents the iris colour as 'red'.

Diagnosis.—The iris of *R. d. matamerah* is basically red (varying individually between orange and crimson) instead of creamy yellow as in *P. d. dispar*. In both sexes the bill (mean males 16.9 vs. 15.7 mm, females 16.6 vs. 15.8 mm) and wing (males 81 vs. 78 mm, females 80 vs. 77 mm) are slightly longer than in the nominate.

Description of holotype.—Head black except the throat, which has loose, pale fiery-red feather tubules. Upper breast orange-yellow tinged red, shading to mustard yellow on rest of underparts. Mantle, scapulars, back, rump and uppertail-coverts dull olive green. Wing-coverts and remiges dull blackish brown broadly fringed dull yellowish green. Uppertail

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Figure 2. Holotype of *Rubigula dispar matamerah*, NHMUK 1888.4.1.724, showing the specimen label and description of iris colour (Paul F. Donald, © Natural History Museum, London)

blackish brown; undertail greyer with whitish shafts. Bill black. Legs blackish brown. Iris red, as noted on label. Illustrated in Fig. 2.

Distribution.—Judged endemic to Sumatra, Indonesia, where photographs of red-eyed individuals were collated from the northernmost (Aceh) and southernmost (Lampung) provinces of the island. Like nominate *R. d. dispar* of Java and Bali, *R. d. matamerah* appears to be confined to elevations below *c*.1,000 m.

All photographs collated from West Java were obtained at Bogor Botanical Gardens, where the species is thought to have been introduced (see above). Consequently, these images cannot eliminate the possibility that native populations elsewhere in West Java belong to *R. d. matamerah* rather than the nominate. Such a distribution (where Sumatra and West Java share one taxon and the rest of Java holds its closest relative) would not be novel, and is observed in (e.g.) *Chrysocolaptes* flamebacks and White-rumped Shama *Copsychus malabaricus*, where Sumatran taxa occur on Java west of a line that runs approximately from Pelabuhanratu Bay to Cirebon (see Mees 1996). However, the only other evidence available to us from west of this line is provided by Nicholson (1881), who reported an adult female Ruby-throated Bulbul from Mt. Karang, Banten, in westernmost Java, with straw-yellow eyes. Consequently, we conclude with reasonable certainty that *matamerah* occurs only on Sumatra.

Etymology.—'Mata merah' means 'red eye' in Bahasa Indonesia. We use the name as a noun in apposition.

Conservation.—Owing to suspected declines caused by the songbird trade *R. dispar* has been listed as Vulnerable on the IUCN Red List (BirdLife International 2022) since its acceptance as a species by BirdLife International in 2016 (del Hoyo & Collar 2016). However, Symes *et al*. (2018) postulated that trapping pressure was causing the species to decline so rapidly it merited listing as Critically Endangered, the highest IUCN category of threat. By contrast, recent studies and records have suggested that the species is not commonly kept in captivity (Marshall *et al*. 2020) and remains frequently observed and widespread in the wild (Squires *et al*. 2021, eBird 2022). As a consequence, in 2022 the species was moved from the IUCN Asian Songbird Trade Specialist Group 'Tier 1' priority list (species considered most threatened by trade for which captive breeding is considered a major management

ISSN-2513-9894
(Online)

intervention; see Collar & Wirth 2022) to the 'Tier 2' watch list (species for which population monitoring and research are recommended) (Chng & Shukhova 2022).

Such monitoring will determine whether a re-evaluation of the species on the IUCN Red List is appropriate, but for the present it is likely to remain Vulnerable (AJB). A particularly valuable dimension to the monitoring of birds in markets will be to use iris colour to track the degree of movement of birds from Sumatra to Java (and presumably but much less probably vice versa). Which of the two subspecies is contributing more to the captive populations in Indonesia will be useful to gauge. We certainly recommend that the two taxa are treated as independent conservation units and suggest that—with iris colour providing a simple and reliable means of determination—those in captive-breeding programmes (such as the small one at Prigen Ark: J. K. Menner *in litt*. 2023) are maintained as separate populations, while those seized as part of the songbird trade are released—if that is the decision of the authorities—onto the correct island to prevent admixture.

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ISSN-2513-9894 (Online)

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A critical response to Halley's (2022) 'Audubon's diary transcripts were doctored to support his false claim of personally discovering Lincoln's Sparrow *Melospiza lincolnii* (Audubon, 1834)'

by Peter B. Logan

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http://zoobank.org/urn:lsid:zoobank.org:pub:B3D52AE6-07CB-4FEE-B502-148BFD6AC61C

Summary.—In a recent article (*Bull. Brit. Orn. Cl.* 142: 329–342), Matthew Halley contended that John James Audubon (1785–1851) lied about his discovery of Lincoln's Sparrow *Melospiza lincolnii* (Audubon, 1834) during his 1833 Labrador expedition. Extracts from the naturalist's journal, published after his death in a biography prepared by his widow, Lucy (1787–1874), states that he was aboard ship 'Drawing all day' when the specimen was collected by one of his assistants. Consequently, Halley submitted that Audubon's claim in the *Ornithological biography* to having first sighted the bird was fabricated and that his granddaughter Maria R. Audubon (1843–1925) doctored her alternate version of the journal to be consistent before she destroyed the original. However, Halley overlooked critical facts, including evidence that Lucy's manuscript was compiled and edited by others; the published work contained numerous errors; and the journal entries for the previous two weeks were misdated and sometimes conjoined from multiple days, proving that her journal was not a faithful transcription of the original.

Biographers and scholars have long wrestled with the fact that John James Audubon (1785–1851), the French-American naturalist and artist responsible for *The birds of America* (1827–38), left a record of his life that was occasionally embellished or, at times, shamelessly untrue, as with his oft-repeated claim to having studied as a youth in the Paris atelier of Jacques-Louis David (1748–1825) (Logan 2016). Now and then, he was inexact in relating events, examples of which can be found in the species accounts he wrote for the *Ornithological biography* (1831–39), the five-volume textual companion to his life-sized prints.

The problem was further compounded by the efforts made after his death by his widow, Lucy B. Audubon (1787–1874), and his granddaughter Maria R. Audubon (1843–1925), to burnish his legacy with the publication of revised versions of his journals, which became the principal accounts for certain periods of his life after Maria evidently destroyed most of the originals (Logan 2016).

I am well aware of these intractable difficulties. In *Audubon: America's greatest naturalist and his voyage of discovery to Labrador* (Logan 2016), repeatedly cited by Halley (2022), I traced and evaluated all of the known sources concerning the naturalist's expedition to Labrador in summer 1833 in order to present the most reliable account for each day of the trip. Minor inconsistences between what Audubon wrote in the *Ornithological biography* and the different versions of his Labrador journal were not unusual.

Halley focused his attention on a single day of the expedition, 27 June 1833, in assessing whether Audubon personally discovered the first specimen of Lincoln's Sparrow *Melospiza lincolnii* (Audubon, 1834). He concluded that, contrary to what Audubon and Maria wrote and what has long been believed, the naturalist was not present when the bird was

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procured, pointing to the conflicting diary extract in Lucy's biography that he remained aboard his vessel 'Drawing all day' (Halley 2022: 333).

Halley's argument hinged on the assumption that this putative journal entry was transcribed by Lucy and likely reflected the content of the original holograph. However, he failed to consider the context in which Lucy's journal was prepared and edited before publication; the factual errors riddled throughout the text; and the misdating and occasional consolidation of daily entries in the weeks leading up to the bird's discovery, all of which significantly undermine his claim.

Primary sources analysed by Halley

To ascertain whether Audubon played a role in the discovery of Lincoln's Sparrow, Halley examined the following primary sources.

Audubon's own narrative of the bird's discovery, published in Vol. 2 of *Ornithological biography*. He indicated that his party 'had been in Labrador nearly three weeks'[1] when he heard the 'sweet notes' (Audubon 1834: 539) of the bird while on an excursion with the members of his party. He immediately called to his companions, and they 'followed the songster as it flitted from one bush to another to evade our pursuit' (Audubon 1834: 539). Eventually, Thomas Lincoln (1812–83) of Dennysville, Maine, was able to collect it, and Audubon found it to be a species new to him, naming it in Lincoln's honour. He returned to the vessel to begin his drawing while the others continued their search for other birds.

(2) A brief extract purportedly from Audubon's journal on 27 June asserting that he was 'Drawing all day'. This statement appeared in *The life and adventures of John James Audubon, the naturalist*, an 1868 biography heavily redacted by Robert Buchanan (1841–1901) and published under his name as editor from a manuscript Lucy had forwarded to the London publisher (Buchanan 1868: 268). A year later, the statement appeared in identical form in *The life of John James Audubon, the naturalist*, an American edition marginally revised by Lucy and identifying her as the editor (Audubon 1869: 326).

(3) A substantially longer and more detailed description of the bird's discovery largely consistent with the account by Audubon, which was included in the version of the Labrador journal published by Maria (Audubon 1897). However, she departed from Audubon's narrative by stating that the bird was discovered on 27 June, whereas Audubon was vague about the date; by noting that a Ruby-crowned Kinglet *Corthylio calendula* (Linnaeus, 1766) that was shot and lost in the underbrush during the excursion was found later the same day, while Audubon stated that it was located the 'next day' (Audubon 1834: 546); and by indicating that the naturalist remained with the shore party rather than returning to the vessel to begin drawing the sparrow.[2]

(4) Finally, the contemporaneous diary kept by Lincoln, which was donated to the Delaware Museum of Natural History (now the Delaware Museum of Nature & Science), Wilmington, by a San Francisco bookseller in 1978 and only recently relocated by Halley in a locked cabinet at the museum. Despite Halley's assertion that it 'provides support for Lucy's version' (Halley 2022: 329), it is of no probative value. Lincoln never mentioned whether Audubon was present when he shot the bird (Halley 2022).

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[1] In truth, it had been only ten days. He was evidently dating the discovery from 6 June, when his party sailed for Labrador from Eastport, Maine (Logan 2016).

[2] Halley considered these 'minor discrepancies' and speculated that 'Maria may have edited her transcript in an attempt to reconcile these minor timeline conflicts, to make her grandfather's published account seem more plausible' (Halley 2022: 335). The other possibility, which I accepted in my book, is that Maria's version of the journal for 27 June more closely adhered to the text of the original.

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Halley's rejection of Audubon's claim of discovery

After analysing the relevant sources, Halley asserted that Audubon was not present at the time Lincoln collected the specimen. He discounted Audubon's narrative and Maria's version of the journal that place him with the shore party because they conflict with Lucy's transcription, which states that Audubon stayed aboard on 27 June, 'Drawing all day' (Halley 2022: 333). He pointed out that 'on other days when Buchanan (1868) indicated that Audubon was drawing all day, the two diary transcripts are not in conflict' (Halley 2022: 334). He argued that it is unlikely Lucy miscopied that portion of the 27 June entry from either the previous or following day 'when he was evidently not drawing all day' (Halley 2022: 334).

Halley also maintained that subtle differences between the two journal entries for 28 June suggest that Maria's transcript was altered. In the version published by Lucy / Buchanan, the naturalist wrote, 'Began drawing *a new finch I discovered*, and outlined another' (Buchanan 1868: 268, Audubon 1869: 326–327; italics by Halley), whereas Maria's copy of the entry states, 'I began drawing at daylight, and finished *one of my new Finches* and outlined another' (Audubon 1897: 382, italics by Halley).

Halley contended that 'These differences are not trivial; the first includes a personal claim of discovery, whereas the second is vague about who discovered the new species' (Halley 2022: 335). In his mind, Maria, having 'doctored her transcript of Audubon's diary to bring it into alignment with his published version' (Halley 2022: 336), must have changed what Halley believed was the more reliable version of the original reflected in the Lucy / Buchanan biographies to avoid having the naturalist record 'his 'discovery' twice, in back-to-back entries' (Halley 2022: 336).

Finally, Halley formulated two, mutually exclusive hypotheses to help assess which of the two versions of the 27 June journal entry was 'the more faithful transcription' (Halley 2022: 335) by illustrating the ramifications of each. He concluded that Audubon, motivated by his narcissism, 'published a false story to bolster his authority with respect to the species' discovery, and then his granddaughter tried to cover it up' (Halley 2022: 340–341) by tracking her grandfather's published account in her version of the journal and destroying the original.

However, Halley disregarded multiple issues that plague the Lucy / Buchanan journal excerpts. When these are considered, the entry for 27 June cannot be deemed authoritative.

Lucy's manuscript was collaborative and heavily redacted prior to publication

Halley stated that 'Audubon's diaries—the most important primary sources—were first transcribed by his widow, Lucy Audubon (1787–1874), and published in extracts by Buchanan (1868)' (Halley 2022: 329). While there is evidence that Lucy prepared a transcription shortly after Audubon returned from the expedition to assist him in writing the *Ornithological biography* (Corning 1969: 1: 269)[3], there is no evidentiary support for Halley's claim that the extracts that appeared in the Lucy / Buchanan biographies decades

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[3] J. J. Audubon to V. Audubon, 24 November 1833, original MSS, John James Audubon Papers 1821–1845 (Mss.B.Au25), American Philosophical Society, Philadelphia, PA. Writing to his eldest son, Victor G. Audubon (1809–60), in London, Audubon reported that Lucy had 'transcribed, the whole of my Floridas and Labrador expeditions and arranged the whole in proper order' (Corning 1969: 1: 269) to help him write his bird biographies. The fact that both journals were in existence would have seemingly obviated the need to make an identical copy, but how she went about making the transcription and what was included is unknown because it did not survive.

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(Online)

later were transcribed by her or, even if they were, that they were not subsequently revised or edited by others prior to publication.

Lucy began collaborating on a biography of her husband with the Revd. Charles Coffin Adams (1810–88), the rector of St. Mary's Church in Manhattanville, New York, in the mid 1860s (Audubon 1869), a fact Halley failed to acknowledge. Adams rented her and a granddaughter a room in 1865, a year after Lucy was forced to sell her home following a series of financial setbacks (Harwood & Durant 1985, Spady 2020). Other biographies of the naturalist had begun to appear since Audubon's death[4], and Lucy likely hoped to improve her situation through sales of the book, while also using her intimate familiarity with his life story to cement his legacy. Lucy and Adams initially agreed to divide the royalties equally but, as the work progressed, 'Lucy grew suspicious that Adams wanted more than his 50 percent share' (Spady 2020: 156). She moved out, taking the manuscript with her (Logan 2016).

'It is not clear today how Lucy and the Rev. Mr. Adams divided the job' (Harwood & Durant 1985: 78). Buchanan, hired by the London publisher Sampson Low, Son & Marston to edit the manuscript, understood it was Adams' work, saying that it was 'prepared by a friend of Mrs. Audubon's, in New York, chiefly consisting of extracts from the diary of the great American naturalist. It needed careful revision, and was, moreover, inordinately long' (Buchanan 1868: v).[5]

Buchanan proceeded to 'cut down what was prolix and unnecessary', resulting in 'a volume equal in bulk to about one-fifth of the original manuscript' (Buchanan 1868: v). Much of the material he deleted evidently came from Audubon's journals, which Buchanan found to be 'boring' (Harwood & Durant 1985: 78).

How the manuscript was altered cannot be determined because it was never returned to Lucy (Audubon 1869). The subsequent American edition, with the exception of minor additions and edits, and the removal of objectionable comments Buchanan had made about her husband, was substantially the same as the London edition. Many mistakes of fact remained. 'Even in reference to matters she obviously had known a great deal about she made no corrections, and she misspelled names of people and places familiar to her' (Harwood & Durant 1985: 80). She even failed to correct the erroneous date for her wedding (Logan 2016).

We will never know the extent to which the excerpts published by Lucy / Buchanan or, for that matter, the version given to us by Maria, vary from the original journal. As Halley admitted, the destruction of the holograph by Maria makes 'it impossible to verify either transcription' (Halley 2022: 330).

An overlooked original journal sheds light on editing of the Labrador journal

The loss of Audubon's holographic Labrador journal does not foreclose an alternative approach in determining how and to what extent Lucy / Buchanan and Maria likely followed the text of the original.

Contrary to Halley's assertion, Maria did not destroy all the journals that she transcribed and published. Halley overlooked Audubon's most important one, documenting his historic

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[4] Among the Audubon biographies that had appeared before Lucy and Adams began their work were St John (1856), Tuckerman (1857), Smiles (1861) and Peirce (1863).

[5] Despite Buchanan's statement, scholars believe that 'Lucy made major contributions and drew, as one of her granddaughters said, 'on her own recollections and voluminous diaries' as well as on Audubon's papers (Harwood & Durant 1985: 78). Whether she was involved in transcribing the extracts of the Labrador journal that are relevant here cannot be established.

ISSN-2513-9894 (Online)

trip to England in 1826 in search of a publisher and his successful meeting in Edinburgh with William Home Lizars (1788–1859), considered Scotland's finest engraver, who agreed to produce *The birds of America* (Patterson 2011).

Lucy / Buchanan used it. Maria did too, incorporating segments in her 'European journals', the first of the three journals that made up the bulk of her two-volume book.[6] The holographic diary is now in the collection of the Field Museum in Chicago and has been transcribed and published separately by both Ford (1967, 1987) and Patterson (2011).[7]

What instantly becomes clear from a comparison of the original with those presented to the public by Lucy / Buchanan and Maria is the extent to which their versions condensed and rewrote Audubon's entries. A suitable example is presented by the extracts for 28 September 1826.

Lucy / Buchanan's version (Buchanan 1868: 108, Audubon 1869: 126):

> 'September 28. Revisited Liverpool to consult about a prospectus for my book. Stayed with Mr. Rathbone, and met there Mr. John Bohn, the London bookseller, who advised me to go to Paris and consult about cost of publication, after which I ought to go to London and compare the outlays before fixing upon any plan. Mrs. Rathbone desired me to draw the wild turkey of America the size of my thumb-nail. This she had engraved on a precious stone in the form of a seal, and presented it to me.'

Maria's version (Audubon 1897: 1: 127):

> '*Green Bank, near Liverpool, September 28*. At five this morning I left Manchester and its smoke behind me; but I left there the labors of about ten years of my life, fully one half of my collection. The ride was a wet one, heavy rain falling continuously. I was warmly welcomed by my good Liverpool friends, and though completely drenched I felt it not, so glad was I to be in Liverpool again. My being here is soon explained. I felt it best to see Dr. Traill and Mr. Roscoe, and I dined with the latter; we talked of Manchester and our friends there, and Mr. Roscoe thought well of the subscription book. From here to Green Bank, where I am literally *at home*. Mr. Rathbone and Mr. Roscoe will both aid me in the drawing up of a prospectus for my work.'

The Lucy / Buchanan version briefly summarised—in their words, not Audubon's—his lengthy account of the events of four separate days—28 September, when Audubon travelled by coach from Manchester to Liverpool (Patterson 2011); 29 September, when he met 'M^{r} Bohn [MS: Bhoon] from London, an Immense Book seller (not publisher)' (Patterson 2011: 202); 1 October, when Audubon spent the evening at Green Bank, the home outside Liverpool of Hannah Mary Rathbone I (1761–1839), the matriarch of the influential merchant family, who asked him 'if I would make a sketch of a Wild Turkey for her' (Patterson 2011: 209) so she could have a seal made for him with the engraved image; and 19 November, when he received the 'Beautifull Seal of the Wild Turkey Cock' (Patterson 2011: 302).

By comparison, Maria limited her journal to the events of September 28. While she adopted some of her grandfather's wording, she revised and summarised the rest, reducing what was an entry in excess of 900 words to 137 in hers.

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[6] The second was the Labrador journal, and the last was the 1843 Missouri River journal (Audubon 1897).

[7] In compiling The Library of America's *John James Audubon: writings & drawings*, Irmscher (1999) noted discrepancies between Ford's edition of the 1826 journal and the original. Pursuing this lead, Patterson subsequently discovered she had made a number of revisions and modifications to the text (Patterson 2011), making his edition the preferred one.

Numerous other entries follow a similar pattern. Of the two versions, Maria's edition incorporated far more of the content, although still a fraction of the original. However, she rewrote and made substantial revisions to the text, deleting Audubon's colourful but verbose descriptions or those that offended her Victorian sensibility (Harwood & Durant 1985).

Presumably, Lucy / Buchanan and Maria, respectively, took much the same approach in editing the Labrador journal, although the former included an abridged extract for each day, unlike how they had handled the 1826 extracts. In most cases, both versions contain entries that are similar enough that we can see they originated from the same source. In a few instances, Lucy / Buchanan added details that are missing from Maria's version (Logan 2016). But, without question, Maria included significantly more of the destroyed holograph than Lucy / Buchanan did.[8]

Previous entries in the Lucy / Buchanan biographies were misdated

In seeking to explain the narrative conflict in the 27 June entries, Halley has likewise ignored the fact that the editors of the Lucy / Buchanan biographies misdated the preceding journal entries and, on the day before, conjoined the events of separate days, providing a likely explanation for the disparity with Maria's edition.

From 12 through 25 June, the entries recount events that actually occurred one or two days earlier (Logan 2016: 442, note 18). The dates shown in Maria's journal were consistent with the calendar[9], with corroboration coming from a letter by one of Audubon's young companions, George C. Shattuck Jr. (1813–93)[10], and the ship's log kept by Cmdr. Henry Wolsey Bayfield (1795–1885) of the Royal Navy, who was conducting a hydrographic survey of the Labrador coastline aboard the schooner *Gulnare* and had anchored in the same harbour as Audubon's schooner, the *Ripley*, on 22 June (McKenzie 1984). Whoever prepared the Lucy / Buchanan extracts for publication failed to accurately transcribe the dates from the original journal.

While the proper timeline appears to have been restored with the extract for 26 June, the entry for that date actually included observations by Audubon that Maria indicated were from both 25 and 26 June, a compression of two days into one similar to how the 1826 journal had been edited.[11]

Halley dismissed the possibility that Lucy / Buchanan made the same mistake on 27 June, saying 'it seems unlikely that the comment ('Drawing all day') was miscopied by Lucy from the 26 June or 28 June entries, when he was evidently not drawing all day' (Halley 2022: 334). Setting aside the fact there is no evidence Lucy copied any part of the holograph for publication, Halley's assumption that Audubon was not drawing all day on 26 June is not reflected in the Lucy / Buchanan biographies (Buchanan 1868, Audubon 1869). He had to turn to Maria's journal, and there Audubon only mentioned that it had 'rained nearly

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[8] In the course of my research, I concluded that the Lucy / Buchanan version of the Labrador journal, while far less comprehensive than Maria's edition, often appeared closer to Audubon's voice, as reflected in his extant diaries and letters (Logan 2016). This suggested that they made fewer changes to the extracts they published, in marked contrast to the efforts Maria made to improve upon the holograph. However, this does not alter my opinion regarding the lack of fidelity in Lucy / Buchanan's 27 June entry to the original for the reasons expressed herein.

[9] However, the entry for 21 June was erroneously dated 22 June (Audubon 1897: 372). Whether this was Maria's error or that of the printer is unknown.

[10] G. C. Shattuck Jr. to G. C. Shattuck Sr., 22 June 1833, original MSS, George Cheyne Shattuck Papers (Ms. N-909), Box 5, Vol. 11 (June 1833), Massachusetts Historical Society, Boston, MA.

[11] Similarly, the Lucy / Buchanan extract for 21 June contains details that appear in Maria's journal on 19 and 22 June (Buchanan 1868, Audubon 1869, Audubon 1897).

all day, but we have all been on shore, to be beaten back by the rain and the mosquitoes' (Audubon 1897: 381). Bayfield confirmed that it rained all day but 'cleared for a few minutes at 4 PM' (McKenzie 1984: vol. 1: 237).

We have no information as to how long the shore excursion lasted. Given the miserable conditions, Audubon and his companions may well have retreated to the vessel after a few hours, and he spent the rest of the day drawing, as he often did during inclement weather (Logan 2016).[12] Thus, the comment 'Drawing all day' could very easily refer to his activities on 26 June, which was then erroneously incorporated in the 27 June entry.

It is equally possible that the phrase was conflated with the 28 June entry, when the weather, according to both versions of the journal, was 'rainy, foggy, dark, and cold' (Buchanan 1868: 268, Audubon 1869: 326, Audubon 1897: 382). Audubon began drawing the Lincoln's Sparrow 'at daylight' (Audubon 1897: 382) and continued until noon, when the wind shifted and created a swell that made it impossible to keep working (Buchanan 1868, Audubon 1869, Audubon 1897).

At this northern latitude, dawn occurred around 03.00 h on 17 June (Audubon 1897, although it is misdated 19 June[13] in Buchanan 1868 and Audubon 1869), and three days later, Audubon indicated there was 'scarcely any darkness now' (Audubon 1897: 371, misdated 22 June in Buchanan 1868: 258 and Audubon 1869: 315). To Audubon, the hours he spent on his illustration on 28 June might well have qualified as a day's worth of drawing since the crew of the *Ripley* soon began preparations to sail with the changing winds (Logan 2016).

Halley noted that in two other instances, 4 July and 7 July, both versions of the journal are in agreement that Audubon was drawing all day (Halley 2022). However, he made no effort to explain how consistency between the journals on these dates offers a window into the conflict between the 27 June entries. Halley also failed to acknowledge that, according to Maria's journal, Audubon spent time ashore on both 4 July ('After dinner John and I went on shore to release a *Uria grylle*[14] that we had confined in the fissure of a rock': Audubon 1897: 389) and 7 July ('When fatigued with drawing I went on shore for exercise, and saw many pretty flowers…': Audubon 1897: 391).

Halley's hypotheses testing fails to validate his conclusion

To help determine which of the versions of the 27 June journal entry is likely 'the more faithful transcription' (Halley 2022: 335), Halley formulated two mutually exclusive hypotheses, based on the presumption that each of the extracts is authoritative. He then separately sought to negate each hypothesis by elucidating the corresponding implications of that presumption, ultimately concluding that the Lucy / Buchanan extract is closer to the original. However, when assessed with evidence Halley has overlooked or ignored, his analysis falls apart.

He posited that if Maria's putative journal entry was truer to the original, then Lucy would have had to (1) replace 'Audubon's exciting passage about the discovery of *M. lincolnii*, the first new species discovered on the Labrador expedition, with the uneventful phrase 'Drawing all day,' in the 27 June entry,' which 'requires not only an omission, but an addition, to the diary text' (Halley 2022: 335); and (2) change 'I began drawing at daylight,

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[12] According to the Lucy / Buchanan extracts and / or Maria's journal, Audubon was at his drawing table on the *Ripley* during inclement weather on 28 June; 8, 9, 10, 16, 17, 19, 27 and 29 July; and 1 and 4 August. In the *Ornithological biography*, Audubon also described working on his illustration of a pair of Labrador Falcons on 7 August: '…it rained for hours, and the water fell on my paper and colours all the while from the rigging of the Ripley' (Audubon 1834: 554).

[13] This was the first of the two separate entries dated 19 June in the Lucy / Buchanan biographies.

[14] Black Guillemot *Cepphus grylle* (Linnaeus, 1758).

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and finished one of my new Finches and outlined another' found in Maria's journal on 28 June (Audubon 1897: 382), to 'Began drawing a new finch I discovered, and outlined another' (Buchanan 1868: 268, Audubon 1869: 326–327) in the Lucy / Buchanan's version (Halley 2022: 335). In his opinion, Lucy would have had no motive to do so, lending validity to her version of the journal.

With respect to the first point, Halley wholly disregarded the substance of the editorial note in the Lucy / Buchanan biographies immediately preceding the 27 June entry (Halley 2022: 333, fig. 2). The editors, identified by the pronoun 'we', announced that they had omitted the portions of the journal 'taken up with an account of the birds, and nests, and eggs found here, and matters related to ornithology', which the naturalist had used to write his *Ornithological biography*, and 'used only that part of the records which has a more general interest' (Buchanan 1868: 268, Audubon 1869: 326).

Thus, even if Lucy 'was aware of the importance of her late husband's new discoveries, to the success of his books, and that including diary entries relevant to those discoveries would make her own book more successful' (Halley 2022: 335), as Halley imagined, the discovery of Lincoln's Sparrow was omitted for editorial reasons.[15] Likewise, there is no mention in the Lucy / Buchanan extracts of Audubon's discovery and collection of another new species, Boreal Chickadee *Poecile hudsonicus* (J. R. Forster, 1772), on 18 July (Buchanan 1868, Audubon 1869). In both cases, those accounts are included in the *Ornithological biography* (Audubon 1834), as they are in Maria's journal.

As for Halley's second point, once the tale of the sparrow's discovery was deleted from the manuscript, a reference to Audubon's role in finding the bird in the following day's entry on 28 June, as he was working on his drawing, was to be entirely expected. We cannot know if Lucy had anything to do with it before the manuscript was sent to England, but contrary to Halley's assessment, she certainly had a motive to include this detail.

Moreover, given the destruction of the original journal, it is impossible to know how, if at all, the 28 June entry in either journal was revised. We know that both versions of the journal were heavily edited. Thus, comparing the extracts for 28 June, as Halley does by parsing the disparate ways they are expressed and surmising what the motives of the editors may have been, is pure conjecture.

Halley's failure to negate this hypothesis effectively establishes that Maria's version is more likely to be truer to the original. Consequently, there is no need to consider the alternative hypothesis, which presumes the authenticity of the Lucy / Buchanan extract.

Additional commentary

The remainder of Halley's paper focuses on an examination of Lincoln's diary and the contemporary custom among 19th-century ornithologists and their hired collectors as to who had the right to claim the discovery of a new species. Neither is on point.

Lincoln's diary does not provide support for the Lucy / Buchanan version of the journal, despite Halley's claim to the contrary. Lincoln never addressed the issue of Audubon's role in discovering Lincoln's Sparrow. He left his diary blank from 20 through 30 June, as Halley conceded. When he returned to its pages on 1 July, he did not mention that he had procured the specimen, even though Audubon had already been at work on the drawing for two days (Buchanan 1868, Audubon 1869, Audubon 1897, Halley 2022). The only thing he had to say about their recent excursions while anchored among the Esquimaux Islands, was that '[t]here were but few birds breeding there and [those] so shy that it was almost impossible

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[15] The placement of the editorial note right before the 27 June entry strongly suggests that Audubon's handwritten entry for that date consisted of ornithological details.

to get at them' (Halley 2022: 337). This appears to be entirely consistent with the description by Lincoln's son, Dr Arthur T. Lincoln (1856–1926), of his father having been 'extremely modest about his own attainments' (Townsend 1924: 239).

According to Halley, Lincoln's sole reference to the bird was on 4 July, and then his only comment was that 'Mr. A. finished a drawing of a new finch which I [shot] at Esquimaux Islands. There are several rare and [beautiful] plants peculiar to the country represented upon [it]' (Halley 2022: 338). Even then, Lincoln did not acknowledge that he had collected the three plants Audubon used as a background, a fact included in Maria's journal but missing from the Lucy / Buchanan extract.

With nothing in Lincoln's diary to support his thesis, Halley then speculated that Lincoln's 'half-hearted attempt to destroy the pages containing his expedition diary suggests he may have been aware they contained passages that cast doubt on Audubon's (1834) published account' (Halley 2022: 336). However, Halley failed to identify a single passage from the diary that contradicts Audubon's narrative.

Other extant accounts of the expedition by members of Audubon's party also do not address whether Audubon discovered the sparrow.[16] Joseph Coolidge (1815–1901) was the subject of an 1896 profile in the *San Francisco Call*, a daily newspaper, in which he related previously unpublished tales about the expedition and was not averse to criticising the naturalist as 'a free drinker' (Logan 2016: 432). He never mentioned whether Audubon was with the shore party. Nor did William Ingalls (1813–1903), who corresponded with and was interviewed in person shortly before his death by Ruthven Deane (1851–1934), a fellow of the American Ornithologists' Union and well-known Audubon scholar (Deane 1910, Osgood 1935).

Halley maintained that Ingalls 'took issue with his personal narratives and plainly stated that Audubon rarely left the boat during the expedition' (Halley 2022: 333), referencing a vague statement in a letter Ingalls wrote to Deane in 1902, almost 70 years later ('Mr. Audubon being almost all the time aboard at work did not have so good a knowledge of the *moss* of which he speaks, as we boys did…': Deane 1910: 45). Ingalls provided no specifics as to Audubon's activities on 27 June. He was merely saying that the young men who accompanied the naturalist spent more time ashore than Audubon did, no surprise given that their only responsibilities were 'to explore, to gather information, to hunt and to bring ourselves and *new species of birds*, home at night' (Deane 1910: 45).

Both versions of the journal reflect that Audubon remained aboard the schooner when the weather was bad or he had birds to draw. However, on other days, especially when the weather was nice, as it was after clearing early on 27 June, he frequently went ashore over the course of the expedition (Logan 2016).[17]

It also bears noting that Audubon was the only member of the expedition who knew the birds of eastern North America well enough to have recognised the song of the Lincoln's Sparrow as that of a possible new species. Had he been absent from the excursion party on 27 June and not exhorted his young colleagues to collect it, one can reasonably question whether they would have prevailed.

With respect to Audubon's financial arrangement with his young companions, Halley asserted that during the 19th century, 'it was generally assumed that a scientist's obligation

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[16] Audubon's youngest son, John W. Audubon (1812–62), did not leave an account of the trip as far as we know (Logan 2016). A contemporaneous journal that George C. Shattuck Jr. kept during the expedition is believed to have been lost or destroyed (Townsend 1918).

[17] According to Maria's journal, Audubon spent some portion of the day ashore in Labrador on 17, 22, 23, 27 and 29 June; 2, 3, 5, 6, 7, 14, 17, 18, 19, 20, 21, 22, 23, 24, 26, 28, 29, 30 and 31 July; and 3 August (Audubon 1897), belying Halley's claim that he 'rarely left the boat' (Halley 2022: 333).

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to the collector, with respect to acknowledging their role in the discovery of a new species, was discharged' by being 'paid directly' or 'otherwise financially indebted (e.g., for travel costs) to the ornithologists who published their discoveries' (Halley 2022: 338). Audubon, however, did not compensate Lincoln or the others for their services; indeed, he asked them to reimburse him for the cost of their food during the voyage, amounting to around $35 each (about $1,129 in 2021 dollars: Webster 2022).[18] Thus, Halley argued that Audubon's purportedly false narrative about discovering Lincoln's Sparrow cannot be justified by his role as the publishing scientist.

The comparison Halley seeks to draw is inapposite. The young men who accompanied Audubon and his son John to Labrador were eager volunteers pursuing their own passions and purpose, not hired collectors expecting to be paid. Lincoln was one 'who ever since his childhood [had] manifested a decided preference for ornithological pursuits' (Audubon 1834: 437). The opportunity to spend the summer chasing birds alongside the famous naturalist must have been an appealing proposition. George Shattuck Jr., who had just finished his classes at the Medical School of Maine when a letter from his father arrived in early May with Audubon's invitation, replied with the reasons he wanted to go:

> 'With such a man as Mr Audubon under what great advantages shall I prosecute the study of natural history, of comparative anatomy. And are not these worth acquiring of themselves, are they not worth acquiring, as bearing upon the profession I am to pursue. Can I ever study them under so great advantages. Then I expect great benefit to my bodily health, from the bodily exertions I shall be compelled to make, and from the exposure to the open air. You see then the objects which I expect to gain'.[19]

In addition, Audubon financed the lion's share of the expedition, roughly $2,000 ($64,500 in 2021 dollars: Webster 2022).[20] Lincoln's reimbursement for his food was a trifling sum in comparison. Even if Audubon was bound by the customary practice Halley described, Lincoln would have been financially indebted to him for a portion of the travel costs, discharging any obligation to recognise Lincoln's role as the bird's collector. Nevertheless, Audubon not only acknowledged Lincoln as the one who procured the specimen but named the species after him.

As a final note, if Audubon's narcissism drove him to fabricate his narrative so he could claim to have first discovered Lincoln's Sparrow, as Halley claimed, it makes little sense that Audubon subsequently acknowledged in his species account that upon his return to New York, he found that specimens of the bird were already lying in the collection of William Cooper (1798–1864), partially diminishing the significance of his discovery (Audubon 1834).

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[18] Halley estimated that the $35, adjusted for inflation, would be 'approximately $1,700 today' (Halley 2022: 338). He does not cite a reference for his inflation conversion, but the second source I consulted also places the figure substantially lower, at $1,106 (Friedman 2022). In both cases, I converted the 1833 cost to 2021 dollars, the inflation rate of 2022 having yet to be determined when Halley's article was published.

[19] George C. Shattuck Jr. to George C. Shattuck Sr., 5 May 1833, original MSS, George Cheyne Shattuck Papers (Ms. N-909), Box 5, Vol. 11 (1–13 May 1833), Massachusetts Historical Society, Boston, MA.

[20] Halley noted that there is a disparity in the estimated cost of the Labrador expedition, with Audubon informing his eldest son, Victor G. Audubon, in a post-expedition letter that it was 'about $2,000' (Corning 1969, 1: 243), while Maria reported it was 'approximately $1,500' (Audubon 1897: 346). I am inclined to accept Audubon's figure given the fact his letter was written shortly after he returned, and he had no reason to misrepresent the amount to his son.

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Other errors in Halley's paper

Halley's paper contains multiple factual errors that must be noted, to ensure they are not perpetuated by future scholars. Halley erroneously declared that 'Maria admitted destroying the original diaries in her possession (only one, from 1820–21, is now extant, see Corning 1929)' (Halley 2022: 330).[21] In fact, Maria confessed only to the destruction of Audubon's journal of 1822–24, which covered a period when the family was suffering 'extreme poverty' (Arthur 1937: 243). The 1826 journal, which comprised a portion of her European journals, survived, as did fragments of the Missouri River journal (Patterson 2016). However, to advance his claim that she destroyed them all, Halley altered the quoted portion of Maria's letter with the purported admission ('I burned [them] myself in 1895…I had copied from [them] all I ever meant to give to the public… (Arthur 1937: 243)' (Halley 2022: 330) by substituting 'them' for 'it', a troubling departure from scholarly norms.

This is not to suggest that Maria didn't destroy the Labrador journal and possibly others, as I and other scholars widely believe. However, I know of no explicit admission by her to having done so.

Halley also added error-ridden bracketed material to a quote from the *Ornithological biography*. According to Halley, 'in late August 1832, when Lincoln 'offered to lead [Audubon] to those retired woods [at Point Lepreau, Quebec] where the Spruce Partridges are found' (Audubon 1834: 437), he was also asked to contribute to the expenses' (Halley 2022: 340). The excursion to which Audubon was referring was actually made in the vicinity of 'the delightful little village' of Dennysville, Maine, where the Audubon family had been invited to stay with the Lincoln family, as is clear from Audubon's narrative (Audubon 1834: 437).[22] Audubon's trip to Point Lepreau, New Brunswick (not Quebec), occurred in May 1833 (Logan 2016).

In a similar vein, Halley misrepresented my views, writing that 'biographers have generally assumed that Maria destroyed the diaries because 'there were aspects of Audubon's private musings [she] did not wish to share with the public' (Logan 2016: xv)' (Halley 2022: 330). The full sentence in my biography, which includes a prefatory clause Halley omitted ('In view of the repressed cultural attitudes that prevailed at the time': Logan 2016: xv), indicates that this was among the reasons I believed she chose to revise her grandfather's journals, not in regard to her decision to destroy them.

In the legend to his fig. 1, Halley stated that 'Audubon's text account of 'Lincoln's Finch / *Fringilla Lincolnii*' (Audubon '1834': 539) was not published until 'after 1 January 1835' despite its preface being dated '1st December 1834' (Stone 1906: 303)' (Halley 2022: 331). Halley's reliance on an unsourced statement by Witmer Stone (1866–1939) in an early 20th-century article ('The preface is dated December 1 but it is quite likely that it did not appear until after January 1, 1835'; Stone 1906: 303), long before Audubon's correspondence became generally accessible to scholars[23], is misplaced. In fact, Audubon announced in

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[21] The referenced 1820–21 diary, known as the Mississippi River journal, was reportedly not in Maria's possession when she transcribed the other journals for her book (Deane 1904). It is now in the collection of the Ernst Mayr Library of the Museum of Comparative Zoology at Harvard University, Spec. Coll. MCZ F117.

[22] Audubon wrote that with Lincoln as a guide, they 'set out on the 27th of August, my two sons accompanying us' (Audubon 1834: 437). They searched 'the whole day…yet not a single Grous did we find…' (Audubon 1834: 437). Upon their 'return towards sunset, as we were crossing a meadow belonging to [Lincoln's] father, not more than a quarter of a mile from the village', they learned from 'people employed in making hay' that 'about half an hour after our departure they had seen a fine covey' (Audubon 1834: 437–438).

[23] The *letters of John James Audubon, 1826–1840*, edited by Howard Corning, was first published in a two-volume edition of 225 copies in 1930.

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a letter on 10 December 1834 to his close friend the Revd. John Bachman (1790–1874) of Charleston, South Carolina, that the second volume of the *Ornithological biography* 'is out!' (Corning 1969: 55).[24] He promised to send 'a few English copies' from Liverpool the following week (Corning 1969: 2: 56).

Halley also erred in stating that Audubon's vessel 'departed on 29 June' (Halley 2022: 338) from its anchorage near the Esquimaux Islands, where the sparrow was collected. The *Ripley* actually left harbour on 28 June (Buchanan 1868, Audubon 1869, Audubon 1897, McKenzie 1984).

Further, Halley's contention that Audubon's assistants 'were members of wealthy families' (Halley 2022: 338) is true only for three of the four young men who signed on for the expedition. The fourth, Joe Coolidge, was the 18-year-old son of the captain of the US Revenue Cutter *Swiftsure*, assigned to the Passamaquoddy Customs District in Eastport, Maine (Logan 2016), hardly a man of means.[25]

Finally, Halley stated that 'On 31 May 1833, immediately after listing the members of his expedition party (including Lincoln) in a letter to his eldest son, Victor Gifford Audubon (1809–60), Audubon wrote (my italics): '*we* pay three hundred and fifty Dollars per month for the entire use of the Vessel with men &c. but have to supply ourselves with provisions' (Corning 1969: 231)' (Halley 2022: 338–339). While the letter was dated 31 May, its contents and his correspondence to Lucy make clear that it was written on 20 or 21 May. It was post-dated because Audubon planned to mail it to Lucy for transmittal to Victor in London shortly before he expected to sail for Labrador on 1 June. As a consequence, only Lincoln, Shattuck, and his son John were identified in the letter as members of the expedition. Ingalls and Coolidge would join the group later that month. Additionally, by 22 May, Audubon had altered his arrangement with the owners of the *Ripley*, with them agreeing to supply the provisions for each of the members of his party at $3 per week (Logan 2016). Audubon had certainly hoped to have his assistants reimburse him for the pro rata cost of their food (Logan 2016). But, contrary to Halley's assumption, there is some doubt they all did. In the Lucy / Buchanan journal, Audubon wrote with obvious rancour at the end of the voyage that 'I was not very well pleased that nearly the whole burden of the Labrador voyage was put on my shoulders, or rather taken out of my poor purse; but I was silent, and no one knew my thoughts on that subject' (Buchanan 1868: 309, Audubon 1869: 375).[26]

Conclusion

Halley's revisionist claim that Audubon fabricated his account of the discovery of Lincoln's Sparrow requires more than conjectural proof of its validity. However, he has overlooked or ignored critical facts that refute his argument. When all the evidence is considered, the brief extract in Lucy / Buchanan's heavily redacted version of the Labrador journal that Audubon was 'Drawing all day' on 27 June, upon which Halley principally relied, does not stand up to scrutiny as an authoritative source. At the same time, the other two primary sources, *Ornithological biography* and Maria's rewritten journal, suffer from their own reliability issues and cannot be entirely trusted, as serious

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[24] J. J. Audubon to J. Bachman, 10 December 1834. Original MSS in the John James Audubon Papers (bMS Am1482), letter 68, Houghton Library, Harvard University, Cambridge, MA. The correct publication date was also referenced in Logan (2016) and Logan & Sidor (2021).

[25] In July 1836, Congress increased the salary of Revenue Cutter captains to $1,200 annually (Anon. 2022). This would equate to approximately $35,000 in 2021 dollars (Webster 2022).

[26] This comment does not appear in Maria's edition of the journal. She apparently felt her grandfather's resentment at not being reimbursed for some of the costs, as he had expected, placed him in a negative light.

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scholars and biographers have known for decades. To his credit, Halley has highlighted this point, even as he has fallen short in his effort to discredit Audubon's narrative of the bird's discovery.

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On the name *Struthio australis* Gurney Sr, 1868, and its type specimens

by Robert P. Prŷs-Jones & Judith White

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Summary.—The name *Struthio australis* Gurney Sr, 1868, was based on three captive birds that arrived at the Zoological Society of London in November 1861. A skeleton of one of these is shown to survive in the bird collection of the Natural History Museum, but whether the other two syntypes still exist is doubtful.

In the *Catalogue of the birds in the British Museum* under the heading *Struthio australis*, Salvadori (1895: 576) referred to the specimen designated *g* as a 'Type of species', this being the skeleton of a bird from South Africa that had been purchased by the then British Museum (BM), now Natural History Museum (NHMUK), from the Zoological Society, which itself had acquired it from Sir George Grey. Seventy years later, however, in her catalogue of NHMUK non-passerine type specimens, Warren (1966: 26) wrote that 'The type material, including the skeleton listed as type by Salvadori…, cannot be traced with certainty.' However, our investigation suggests that Warren (1966) was mistaken regarding Salvadori's listed type.

The name *Struthio australis* was first applied to the South African Ostrich by Gurney (1868). In doing so, he pointed out that although Sclater (1862a) had defined plumage differences between the South African Ostrich, of which the Zoological Society of London had obtained three live specimens from Sir George Grey (1812–98) on 1 November 1861, and the North African Ostrich *S. camelus*, he had failed to provide a name for the southern form. In fact, shortly thereafter Sclater (1862b) provided a name for two (a male and a female) of these birds in a separate paper, but only by means of the bald statement 'Var. *meridionalis*' and without reference to his prior description of their distinguishing characteristics. Use of 'Var.' would not of itself debar subsequent use of *meridionalis* in a subspecific context (ICZN 1999, Art. 45.6.4), but the name given by Sclater (1862b), lacking any associated description, was a *nomen nudum*, and was seemingly not used in later publications (*cf*. Salvadori 1895: 575); instead, *australis*, based on the three specimens mentioned above, has been the accepted scientific designation for the South African Ostrich since it was published.

Sir George Grey was Governor of Cape Colony and High Commissioner for South Africa from 1854 until 1861. As well as being a colonial administrator, he was an enthusiastic naturalist who collected a wide array of plants and animals, both living and dead, some of which he passed to museums, zoos and botanical gardens in Britain, and he became a member of the Zoological Society of London (Spearman 2000). Notably, Grey had a keen interest in ostriches, playing a key role in their domestication in South Africa and thereby laying the foundation for the ostrich farming industry there (Rees & Rees 1898). From at least 1858, Grey was presenting live animals to the Zoological Society (Scherren 1905), and in summer 1859 these included two young ostriches from South Africa, which unfortunately died before they were old enough to be compared to the North African Ostriches already living there (Sclater 1862a). Subsequently, in 1861 he contributed 'two valuable collections of animals' to the Zoological Society, which were brought back to Britain by a Mr James Benstead, 'a collector employed by the Society' (Scherren 1905: 130). The second of these

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collections, handed over in November, included the three living South African Ostriches referred to above (Sclater 1862a).

Unfortunately, the BM's *Catalogue of birds*, where Salvadori (1895) listed the *australis* type, does not include registration numbers, unique to each specimen. However, both its General Register and Aves Skeleton Register record a still extant specimen 1862.12.22.3, purchased from the Zoological Society and registered as being the skeleton of a *Struthio*, which from its assigned number must have been acquired in or somewhat before December 1862. Although the Zoological Society had taken possession of three living South African Ostriches on 1 November 1861, only two can still have been alive at the end of 1861, i.e. those listed by Sclater (1862b: 71), whose volume included '… only the Vertebrated animals living in the Gardens on the 31st of December last' (Sclater 1862b: iii). By the end of 1862, apparently all had died, as they are not mentioned in the equivalent volume by Sclater (1863: 86). Therefore certainly at least one of the original three 'Var. *meridionalis*' mentioned by Sclater (1862a) was already dead in good time to become what is now NHMUK 1862.12.22.3.

At that time, the BM was also still noting acquisitions of bird skeletons, though no longer bird skins, soon after their arrival in the museum in its Vellum Catalogue series, which recorded each specimen by species rather than by its arrival batch (Knox & Walters 1992). The entry for specimen 1862.12.22.3 there, as Skel. Vell. Cat. 356f, i.e. as the sixth specimen on the page created for *Struthio camelus* skeletal material, greatly strengthens the case for it belonging to the *australis* type series, as it additionally refers to it as 'variety Struthio meridionalis Sclater'. This was seemingly done to distinguish the specimen as the first of this variety knowingly to be acquired by the BM, and indeed the apparently original BM label attached to the specimen also states '*Struthio meridionalis*'. Its scientific interest was therefore both realised and highlighted at acquisition by the BM.

There thus appears little doubt that the skeleton registered as NHMUK 1862.12.22.3, which is also Skel. Vell. Cat. 356*f* and matches the locality and acquisition details of specimen *g* in Salvadori (1895), is one of the original type series of the name *Struthio australis* Gurney Sr, 1868, although ironically it now obviously lacks any of the distinguishing plumage features used to define the taxon. The whereabouts, or indeed continued existence, of the other two types is unclear, as is the precise part of southern Africa from which they all originated.

In this context, it may be noted that Vincent (1949: 148) restricted the type locality of *Struthio camelus australis* to 'Naarip Plain, near Walvis Bay, S. W. Africa', and this seems to have been accepted by most authorities subsequently (e.g. Clancey 1965, 1980, Hockey *et al*. 2005). However, the grounds which Vincent provided for doing this are less than compelling, as they relate to comments on *S. c. australis* in Andersson (1872), by both his editor Gurney and Andersson himself, that do not appear to be directly linked to the type series. Although the collector Andersson was at Walvis Bay in late August 1861 and apparently on his way to Cape Town (Dean *et al*. 2006), it remains to be established definitively from whom and from where Grey and Benstead acquired the type series of *Struthio australis*.

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First record of Campina Thrush *Turdus arthuri* for Bolivia

by Joseph A. Tobias

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Summary.—An adult thrush trapped in a mist-net near Guayaramerin, dpto. Beni, Bolivia, in April 2005, was initially identified as Black-billed Thrush *Turdus ignobilis* although several subtle plumage features appeared to differ from the expected race *T. i. debilis*. These features match those of Campina Thrush *T. arthuri*, a cryptic species subsequently split from Black-billed Thrush based on molecular evidence, and now known to occur widely in shrubby thickets and stunted *campina* forest across much of Amazonia. This record extends the known distribution of *T. arthuri* south-west from the nearest known localities in Amazonas and Rondônia, Brazil. *T. arthuri* is presumably resident in north-west dpto. Beni in suitable habitat, and potentially occurs elsewhere in Bolivia from Pando to eastern Santa Cruz in similar *campina*-like habitats associated with weathered outcrops of the Brazilian Shield.

During field surveys of dpto. Beni in 2003–05 (Tobias & Seddon 2007), I visited a range of habitats close to the main highway from Riberalta to Guayaramerin, an area put on the ornithological map by the late Sjoerd Meyer, who rediscovered Masked Antpitta *Hylopezus auricularis* in swampy forest by the río Beni on the outskirts of Riberalta in 1994 (Meyer 1998). Meyer also surveyed the road to the Brazil border from Riberalta, finding some scarce grassland species, including Rufous-sided Pygmy Tyrant *Euscarthmus rufomarginatus*, in *campo* at San Lorenzo de Pampa. Subsequent visitors to the area focused on these localities—in easy reach of Riberalta—but tended not to venture further towards Guayaramerin where different habitats appear.

Approaching Guayaramerin on this road, I noticed a small area of dense stunted forest, similar to habitats known in Brazil as *campina*. I spent two mornings in April 2005, and another three mornings in October 2005, mist-netting and making sound-recordings at the most accessible patch of habitat, *c.*16 km from Guayaramerin at 10°55.027’S, 65°26.805’W (referred to as Guayaramerin site B in Tobias & Seddon 2007). During these visits, I made the first documented records for Bolivia of Green-tailed Goldenthroat *Polytmus theresiae*, Pale-bellied Mourner *Rhytipterna immunda* and Ruby-topaz Hummingbird *Chrysolampis mosquitus*, as well as the first records of Black Manakin *Xenopipo atronitens* and Red-shouldered Tanager *Tachyphonus phoenicius* for dpto. Beni (Tobias & Seddon 2007).

During my second visit, on 25 April 2005, I trapped an adult *Turdus* sp. with a black bill in shrubby vegetation with dwarf trees (canopy height 1–5 m) interspersed with rough grassland. This was the lowest-stature vegetation at the site, and supported a relatively small number of bird species, including Green-tailed Goldenthroat, Red-shouldered Tanager and White-fringed Antwren *Formicivora grisea rufiventris*. In the same habitat, I had recently trapped 2–3 Creamy-bellied Thrushes *Turdus amaurochalinus*, migrants or non-breeding visitors from a breeding range further south, easily identified by their pale yellowish bills. The bird with the black bill was slightly unfamiliar in overall pattern (Fig. 1), so I considered all possible options. It was clearly not a Hauxwell’s Thrush *T. hauxwelli*, which has a browner bill and more rufous plumage, and is generally restricted to the lower storey of tall humid forest. Bill colour also eliminated Unicoloured Thrush *T. haplochrous*,

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Figure 1. Adult Campina Thrush *Turdus arthuri*, near Guayaramerin, dpto. Beni, Bolivia, October 2005 (Joseph A. Tobias)

a mysterious Bolivian endemic that I had searched for unsuccessfully on several occasions in dpto. Beni. The individual appeared most similar to Black-billed Thrush *T. ignobilis*, which is common nearby in forest edge, overgrown clearings and gardens. Nonetheless, the stunted vegetation where it was mist-netted seemed anomalous, lacking the usual array of species found alongside Black-billed Thrush. I was also struck by the plumage tones and head pattern, leading me to wonder whether it might be a different subspecies than I was used to.

I was unable to determine the subspecies based on available literature, so the images remained labelled simply as *T. ignobilis* for 15 years. In 2020, I finally had time during the Covid-19 pandemic to transfer my records to eBird, and started to work on a checklist for 'site B' from notebooks and images (https://ebird.org/checklist/S66602837). When I uploaded the images of *T. ignobilis* as media files, I was again surprised at the bird's unfamiliar appearance. By this time, Black-billed Thrush had undergone recent taxonomic revision with some populations split as Campina Thrush *T. arthuri* (Cerqueira *et al*. 2016). Given that the habitat I surveyed in 2005 was structurally very similar to types of Brazilian *campina*, it seemed likely that the thrush I trapped was *T. arthuri* and comparison of plumage features confirms this. The key features that separate this individual from *T. ignobilis* are the darker face with dusky or slaty feathering around the eyes, well-defined streaking or flecking evenly spaced on the pale throat, and the cold grey head, wings and underparts (Fig. 1). In comparison, the local race of Black-billed Thrush *T. ignobilis debilis* has slightly warmer 'mousey-brown' plumage, a less dusky face (Figs. 2–3), and the throat is either largely unstreaked in the centre or a more uniform smudgy brown, similar to the rest of the underparts (Figs. 2–4).

Although cryptic and unremarkable in plumage, *T. arthuri* has a very distinctive jay-like call. I did not notice this in the field and made no recordings that can be ascribed to

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Figure 2. Black-billed Thrush *Turdus ignobilis debilis*, Los Amigos Research Station (CICRA), Madre de Dios, Peru; the lower throat of this subspecies is often white and unstreaked (Joseph A. Tobias)

Figure 3. Black-billed Thrush *Turdus ignobilis debilis*, Amazonia Lodge, Madre de Dios, Peru (Joseph A. Tobias)

Figure 4. Black-billed Thrush *Turdus ignobilis*, Anorí, Antioquia, Colombia; this individual illustrates the characteristics of subspecies *ignobilis* and *goodfellowi*, which have darker throats, lacking white, creating a much more uniform impression to the underparts (Joseph A. Tobias)

the taxon. Intriguingly, *T. arthuri* appears to sing only rarely, if ever, and there are as yet no confirmed recordings for this species of the complex songs known in all closely related taxa.

Biogeographical considerations.—Previous records of *T. arthuri* are from southern Venezuela, Guyana, Suriname, and Amazonian Brazil south-west as far as Rondônia (Cerqueira *et al*. 2016). My record from near Guayaramerin extends the range another 250 km to the south-west, into Bolivia. The presence of *T. arthuri* in Bolivia makes biogeographic sense because *campina* specialist birds are generally distributed widely albeit very patchily over the Brazilian Shield, which here extends narrowly over the upper rio Madeira into Bolivia (Moskovits *et al*. 2003). Several species, including Citron-bellied Attila *Attila citriniventris*, *Rhytipterna immunda*, *Tachyphonus phoenicius* and *Xenopipo atronitens*, have similar patchy distributions across weathered formations of the Brazilian Shield, with a few records into easternmost Bolivia.

Further field work may reveal that the range of *T. arthuri* extends further south into eastern dpto. Santa Cruz given that other stunted forest species (e.g., *Tachyphonus phoenicius*, *Xenopipo atronitens*) occur in Noel Kempff Mercado National Park (Killeen & Schulenberg 1998). However, *T. ignobilis* was not recorded during intensive field work—including mist-netting—in and around this protected area (Killeen & Schulenberg 1998), suggesting that *T. arthuri* must be rare and local if it does indeed occur there. The species may also occur in dpto. Pando, where patches of similar habitat are widely scattered and poorly surveyed.

The stunted forests of dpto. Beni are not referred to locally as 'campina' and they appear to grow on different substrates to most Brazilian *campinas*. The ground at 'site B' was sandy in a few patches, but mainly covered in loose iron-rich volcanogenic deposits, suggesting a different geological history (Tobias & Seddon 2007). Despite this difference,

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the vegetation structure was reminiscent of *campina* growing on poorly drained, weathered clays or ancient rock outcrops more widely in South America. This retrospective record from Guayaramerin confirms that *T. arthuri* is widespread in a variety of different 'stunted forest' types or shrubby thickets across the Guiana and Brazilian Shields, being replaced on younger, more fertile, sedimentary soils in much of western Amazonia by *T. ignobilis debilis*.

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Non-breeding season records of warblers in the *Phylloscopus reguloides* lineage from Thailand and Myanmar

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Summary.—A total of 20 individual *Phylloscopus* warblers in the 'Blyth's Leaf Warbler *P. reguloides* lineage', caught for ringing in the non-breeding season in Thailand and Myanmar, were resolved via mtDNA assay as *P. reguloides* (seven individuals), Claudia's Leaf Warbler *P. claudiae* (12) and Hartert's Leaf Warbler *P. goodsoni* (one). As expected, *P. claudiae* proved to be the most widely distributed. The occurrence of four *P. claudiae* on an island in the Thai Gulf, alongside large numbers of typically Sundaic wintering species on northbound migration during late March–early April, indicates that its non-breeding season range probably extends further south than previously recognised, into that subregion.

The *Phylloscopus* warblers formerly united as Blyth's Leaf Warbler *Phylloscopus reguloides* (*sensu lato*) have recently been shown by molecular analysis to represent three distinct lineages. *P. reguloides* is sister to the lineage comprising Claudia's Leaf Warbler *P. claudiae* and Hartert's Leaf Warbler *P. goodsoni* (Olsson *et al*. 2005, Alström *et al*. 2018). This arrangement is further supported by analyses of vocalisations (Päckert *et al*. 2009). Plumage differences among the three taxa are slight, however, all possessing a pale median crown-stripe, two wingbars and narrow white edges to the inner margins of the two or three outermost rectrices. *P. claudiae* and *P. goodsoni* differ from each other chiefly in the degree of yellow suffusion on their face and underparts, although this is difficult to judge under field conditions.

Monotypic *P. claudiae* is the most northerly distributed and widespread, its breeding range lying mostly north of the Changjiang (Yangtze) River in Gansu, Sichuan and Shaanxi, north to Hebei, in China (Cheng 1987, Dickinson & Christidis 2014). The distribution of *P. goodsoni* is more southerly, with nominate *goodsoni* in Guangxi and Guangdong, and *P. g. fokiensis* further north in Fujian, Jiangsu, Hubei and Shaanxi where it almost meets *P. claudiae* (Päckert *et al*. 2009, Dickinson & Christidis 2014). Four races of *P. reguloides* are distributed in the Himalayas from Kashmir in the west, east to north-west Vietnam and elsewhere in northern continental South-East Asia, including the montane outlier of the Langbian Plateau (Dickinson & Christidis 2014). In Thailand, breeding of *P. reguloides* [*assamensis*] was first proven on Thailand's highest mountain, Doi Inthanon, 2,565 m (Alström & Olsson 1994), and it is also apparently resident on a few other 2,000 m-plus peaks in Thailand, including Doi Pha Hom Pok (2,285 m), and probably Doi Chiang Dao, Chiang Mai Province (2,175 m), and in the west on the ornithologically little-known peak of Doi Kajela, 2,152 m, Tak Province (16º10'N, 99º02'E) based on the evidence of birds singing during April (PDR pers. obs.). Further, *P. reguloides assamensis* 'probably breeds throughout the mountains of

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Burma, and has been recorded from Mt. Victoria, North East Burma, the Shan States and Karenni' (Smythies 1986).

The winter distributions of these taxa are imperfectly known, owing to their morphological similarity. Relatively few of the specimens in museums have been subjected to DNA assay. *P. reguloides* (*sensu stricto*) is presumed to be either resident or a short-distance or elevational migrant throughout its range (e.g., Ali & Ripley 1983). The co-occurrence of *P. claudiae*, wintering alongside *P. reguloides* in parts of South-East Asia, had long been recognised, based on the slightly longer, more pointed wing of the relatively long-distance migrant *claudiae* compared to *reguloides.* Nonetheless, although Deignan (1945) acknowledged Ticehurst's (1938) identification of ten March-collected individuals from the Doi Inthanon summit (Doi Ang Ka) as *P. reguloides assamensis*, his subsequent Thailand checklist (Deignan 1963) omitted these, and unaccountably only listed *P.* [*reguloides*] *claudiae* therein: from Thailand's northern plateau (Chiang Rai, Chiang Mai and Lamphun Provinces) and the extreme north of the north-eastern plateau (Loei Province). Wintering birds presumed to be *P. claudiae* have since been found much more widely in Thailand: at lower elevations in the north-east, especially in Khao Yai National Park; in the south-eastern provinces, in the western forest complex, around Bangkok (on passage), and in the north of the peninsula south to *c.*12ºN (Lekagul & Round 1991, Treesucon & Limparungpatthanakij 2018). However, the possibility that some of these birds might have included *P. goodsoni*, the winter distribution of which is poorly known, cannot be eliminated owing to the morphological similarity of the two.

The picture is further complicated by nomenclatural confusion, as nominate *P. g. goodsoni* was formerly placed as a subspecies of Sulphur-breasted Leaf Warbler *P. ricketti*, whilst *P. g. fokiensis* was subsumed under *P. reguloides* (Watson *et al*. 1986). There are relatively few unequivocal records remote from the Chinese breeding range of either, although *P. g. goodsoni* is known to winter on Hainan and *P. g. fokiensis* may be widespread in northern continental South-East Asia (Dickinson & Christidis 2014). The two *P. goodsoni* subspecies are thought to overwinter in roughly equal proportions in Hong Kong, where *P. claudiae* is, as yet, unrecorded (Carey & Pang in prep.).

Three individuals collected in Phongsali province, northern Laos, in March 2005, one from montane elevation (>1,000 m) and two from steep, submontane land, were determined by mtDNA assay as *P. goodsoni* (Fuchs *et al*. 2007). Although the subspecies was not determined, the specimens are deposited in Muséum national d'Histoire naturelle, Paris, and are available for scrutiny. Subsequently, a long-staying bird photographed in a Bangkok city park during 17 January to 11 February 2015 (Robson 2015, Bird Conservation Society of Thailand, unpubl.) was considered to be a nominate *P. g. goodsoni*, whilst two heard singing at. *c.*1,200 m elevation, Khao Yai National Park, on 21 February 2021 were considered to be *P. goodsoni* ssp. (Bird Conservation Society of Thailand 2021, Roddis & Loseby 2021). Sound recordings archived on Xeno-canto indicate the non-breeding presence of *P. goodsoni* in non-montane elevations of both central Myanmar (A. Lastukhin & V. Sotnikov) and Cambodia (F. Lambert; www.xeno-canto.org).

We were primarily concerned to identify the winter ranges and relative abundance of *P. claudiae* and *P. goodsoni* ssp. in Thailand and Myanmar among '*P. reguloides* lineage birds' that were captured and released during ringing activities.

Methods

We collected feathers for DNA assay from a total of 23 *P. reguloides* (*sensu lato*) mist-netted and ringed at five discrete localities (Table 1): Doi Chiang Dao and Doi Lang (the north-east ridge of Doi Pha Hom Pok), both montane, at elevations of 1,450 m and 1,900 m

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TABLE 1
Locations where *Phylloscopus* spp. were sampled

Location	**Coordinates**	**Elevation (m)**
Indawgyi Lake, Kachin State, Myanmar	25°06′N, 96°17′E and 25°14′N, 96°22′E	180 m
Doi Lang, Mae Ai District, Thailand	20°06′57″N, 99°07′44″E	1,900 m
Khun Huai Mae Kok Substation, Doi Chiang Dao Wildlife Sanctuary, Chiang Mai Province, Thailand	19°22′27″N, 98°50′05″E	1,450 m
Khao Yai National Park headquarters area, Nakhon Nayok Province, Thailand	14°24′58″N, 101°22′43″E	750 m
Ko Man Nai (Man Nai Island), Rayong Province, Thailand	12°36′44″N, 101° 41′18″E	sea level

respectively, in Chiang Mai Province; Khao Yai National Park, Nakhon Nayok Province (*c*.750 m, where exclusively winter visitors); the island of Ko Man Nai, Rayong Province (four individuals, all apparently on northbound spring migration during March–April); and Indawgyi Wildlife Sanctuary, Kachin State, northern Myanmar (three apparently wintering birds in lowland secondary forest at *c*.180 m elevation; Table 1). All were measured and weighed and basic wing formula (position of the tip of the second outermost primary, p2, numbered ascendantly, in relation to the tips of the inner primaries) was noted for most. All individuals are referred to in subsequent text by ring number.

Laboratory protocols.—We extracted DNA from feather samples using NucleoSpin tissue kit (Macherey-Nagel), with 0.1% Dithiothreitol (DTT) added to increase the DNA yield (Olsson *et al*. 2005). Partial cytochrome-*b* (Cyt b) mitochondrial gene was amplified using primers: L14841 (5′-AAAAAGCTTCCATCCAACATCTCAGCATGATGAAA-3′) and H15547 (5′-AATAGGAAGTATCATTCGGGTTTGATG-3′; Helbig *et al*. 1995). We performed Polymerase Chain Reaction (PCR) using AccuStart II GelTrack PCR SuperMix (Quanta BioSciences) with concentration of ingredients suggested by the manufacturer. The PCR reactions were performed using an Eppendorf Mastercycler gradient thermocycler under the following conditions: 94°C for three minutes followed by five cycles at 94°C for 30 seconds, 48°C for 30 seconds, 72°C for one minute, then 30 cycles at 94°C for 30 seconds, 51°C for 30 seconds, 72°C for one minute and a final 72°C for five minutes (Saitoh *et al*. 2015). The PCR products were visualised with 1.5% agarose gel electrophoresis and purified using NucleoSpin Gel and PCR Clean-up (Macherey-Nagel). The products were sent for sequence analyses using Applied Biosystems BigDye Terminator v3.1 Cycle Sequencing Kit protocol.

Genetic analyses.—Sequences of collected samples were deposited in GenBank (Table 2) and aligned with sequences of recognised *P. reguloides* (AY656231, AY656233, AY656238, and EU851077–EU851079), *P. claudiae* (EU851083 and MH079258), *P. goodsoni* (AY656225, EU851081, and the three individuals referred to by Fuchs *et al*. 2007) using ClustalW in MEGA7 v. 7.0.21 (Kumar *et al*. 2016). Yellow-vented Warbler *P. cantator* (AY606157) and *P. ricketti* (AY606172) served as outgroups. We used Kakusan4 (Tanabe 2007) to select the best-fit evolutionary model under the Akaike Information Criterion (AIC; Akaike 1974) and Bayesian Information Criterion (BIC; Schwarz 1978) for Maximum Likelihood (ML) and Bayesian Inference (BI) approaches, respectively. The selected model for the ML was GTR Gamma and for BI was HYK85 Gamma. The ML trees were constructed using RAxML v8.2.12 (Stamatakis 2014) on CIPRES Science Gateway V3.3 (Miller *et al*. 2010) with 1,000 bootstrapping iterations. We considered bootstrap values higher than 70% as significant support. The BI trees were performed in MrBayes v3.2.6 (Huelsenbeck & Ronquist 2001) under a Metropolis-coupled, Markov chain Monte Carlo (MC-MCMC) approach, started from random tree, run twice in parallel with a four-chain analysis for

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five million generations. The trees were sampled every 100 generations and 25% of these were discarded as 'burn-in'. We then evaluated stationarity by checking Effective Sample Size (ESS > 200) using Tracer v1.7.1 (Rambaut *et al*. 2018). We considered 95% posterior probabilities or higher from the remaining trees as significant support. The ML and BI trees were visualised and edited in FigTree v1.4.3 (Rambaut 2009).

Results

The samples from 20 individuals were successfully amplified but in three further individuals, from Khao Yai, the sequences were unrecoverable, apparently due to contamination. The final alignments from collected samples and downloaded sequences revealed 670 bp (130 variable sites and 115 parsimony informative sites). As ML and BI approaches provided similar topology, only the BI tree is shown (Fig. 1).

Of these 20 birds, seven were resolved as *P. reguloides* with high statistical support (100% bootstrap value and 100% posterior probability; Table 2). The clade of *P. reguloides* was further divided into two subclades. Our three Myanmar individuals, A34517, A34516 and A34567, caught in lowlands of Indawgyi Wildlife Sanctuary, were closely related to birds from montane elevations elsewhere in the same country (AY656231 and EU851078 from Mt. Victoria (Natmataung National Park), and from Nepal (AY656238 and EU851077) with 100% bootstrap and posterior probability. The relationship of the same three to additional Myanmar birds from Mt. Victoria (AY656233 and EU851079) received lower statistical support (70% bootstrap and <90% posterior probability, Fig. 1). Four northern Thai montane-trapped birds, 1A03637 (Doi Lang), 1A23428, 1A23030 and 1A01942 (Doi Chiang Dao, Table 2) were more closely related to *P. reguloides* from Yunnan, China (EU851079) and northern Tonkin, Vietnam (AY656233) with high statistical support (100% bootstrap value and 100% posterior probability). Another Doi Chiang Dao bird, 1A01944, clustered with *P. goodsoni* from Jiangxi (EU851081) and Guangdong, China (AY656225) and with three Fuchs *et al*. (2007) *P. goodsoni* from northern Laos, OP90367, OP90368 and OP90369 (100% bootstrap value and 100% posterior probability; Fig. 1).

A further 12 individuals (two from Doi Chiang Dao, 1A01729 and 1A01730, six from Khao Yai, 1A03127, 1A03104, 1A03137, 1A03138, 1A03177 and 1A03200, and four from Man Nai Island, A35381, A35387, A35388 and A34420) nested with *P. claudiae* from Gansu (EU851083) and Shaanxi, China (MH079258), with 100% bootstrap value and posterior probability; Fig. 1, Table 2).

Six of the seven *P. reguloides* were tentatively identified as that taxon before release based on wing formula (p2 falling between p9 and the tips of the secondaries, Table 2). Seven of the 12 *P. claudiae* were likewise correctly attributed to taxon on the basis of their longer p2 (= p7, one individual; = p8, four individuals; and = p8/9, two individuals; primaries numbered ascendantly). A further *P. claudiae* could not be reliably assigned on wing formula (p2 = 9/10), and wing formula was not noted for the four remaining birds (Table 2). While *P. goodsoni* could not be excluded for any of these *claudiae* based on wing formula, the relative weakness of any yellow suffusion on the supercilium and throat observed at time of capture was then judged to more likely indicate *P. claudiae*. Neither plumage details nor wing formula were specifically noted for the single *P. goodsoni* that was sampled.

Discussion

Although *P. reguloides* (*sensu stricto*) is known as an elevational migrant that winters in the Himalayan foothills and plains of northern India (Ali & Ripley 1983, Rasmussen &

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TABLE 2

Biometrics, wing formula, body mass, ring numbers and accession numbers of sampled *Phylloscopus* (wp = wing point; nr = not recorded). Primaries are numbered ascendantly.

Ring no	**Date**	**Location**	**mtDNA determination**	**wing**	**tail**	**bill**	**tarsus**	**wp**	**p2**	**mass (g)**	**GenBank no.**
A34516	29 Jan 18	Indawgyi,	*reguloides*	61	44	13.5	18.2	p5 (p4)	=p10	7.3	MT921120
A34517	29 Jan 18	Indawgyi,	*reguloides*	62	46	12.8	19.0	p5 (p4)	=p10	7.0	MT921122
A34567	06 Feb 18	Indawgyi,	*reguloides*	57	43	12.5	17.7	p4=p5	=p9/ss	nr	MT921121
1A03637	28 Mar 08	Doi Lang	*reguloides*	56	42	12.0	13.9	p4=p5	=ss	7.3	MT921119
1A01942	3 Dec 09	Doi Chiang Dao	*reguloides*	61	47	13.0	17.8	nr	nr	7.6	OP381448
1A23030	24 Jan 15	Doi Chiang Dao	*reguloides*	58	45	13.5	18.2	p4=p5	=p9	10.1	MT921131
1A23428	16 Dec 15	Doi Chiang Dao	*reguloides*	61.5	47	13.7	19.9	p4=p5	=10/ss	7.2	MT921123
1A01944	3 Dec 09	Doi Chiang Dao	*goodsoni*	60	46	13.7	16.8	nr	nr	7.4	MT921116
1A01729	30 Jan 09	Doi Chiang Dao	*claudiae*	63	47	13.6	nr	nr	nr	8.1	MT921118
1A01730	30 Jan 09	Doi Chiang Dao	*claudiae*	61.5	46	13.5	17.4	nr	nr	7.5	MT921117
1A03104	19 Nov 06	Khao Yai	*claudiae*	62	46	nr	nr	nr	nr	7.3	MT921130
1A03127	28 Oct 07	Khao Yai	*claudiae*	61	46	nr	nr	p4=p5	=p7	7.0	MT921129
1A03137	10 Nov 07	Khao Yai	*claudiae*	61	45	nr	nr	p4=p5	=p8	7.3	MT921128
1A03138	11 Nov 07	Khao Yai	*claudiae*	62	43	nr	nr	p4=p5	=p9/10	7.6	MT921127
1A03177	20 Jan 08	Khao Yai	*claudiae*	60	45	nr	nr	p4=p5	=p8	7.2	MT921126
1A03200	5 Mar 08	Khao Yai	*claudiae*	58	44	nr	nr	nr	nr		MT921125
A35381	19 Mar 21	Ko Man Nai	*claudiae*	62	45	13.0	16.7	p4	=p8	8.3	MZ404594
A35387	20 Mar 21	Ko Man Nai	*claudiae*	57	41	12.3	16.8	p4 (p5)	=p8/p9	7.4	MZ404595
A35388	20 Mar 21	Ko Man Nai	*claudiae*	61	44	13.9	17.6	p5 (p4)	=p8/p9	6.8	MZ404596
A35420	6 Apr 21	Ko Man Nai	*claudiae*	60	42	14.3	16.5	p4	=p8	9.3	MZ404597

Anderton 2005) our three Indawgyi individuals may be the first confirmed records from comparable lowland elevations in Myanmar or South-East Asia.

P. claudiae was confirmed, as expected, to be a widespread winter visitor in forested habitats of both lowland and montane elevations in Thailand. While the *P. claudiae* from Doi Chiang Dao and Khao Yai were apparently over-wintering birds, four others from the island of Ko Man Nai during late March–early April were almost certainly northbound passage migrants. The island, which lies 5.5 km off the eastern Thai coast, is a noted hotspot for migration during March to May (Round *et al*. 2015, Round & Dymond 2022). Almost all migrants caught on the island during those months were judged to be Sundaic winterers, probably making landfall following a *c*.600 km sea-crossing from Pattani Province, southern Thailand, which is *c*.600 km due south, on the extreme northern edge of the Peninsular Malayan bulge. Our captures might suggest, therefore, that small numbers of *P. claudiae* winter, as yet undetected, in the Sunda subregion, perhaps alongside the relatively common wintering Eastern Crowned Leaf Warbler *P. coronatus*.

The status of *P. goodsoni* remains to be further elucidated, however. Judged on the few Thai and other South-East Asian records, it is either scarce or overlooked, and is possibly

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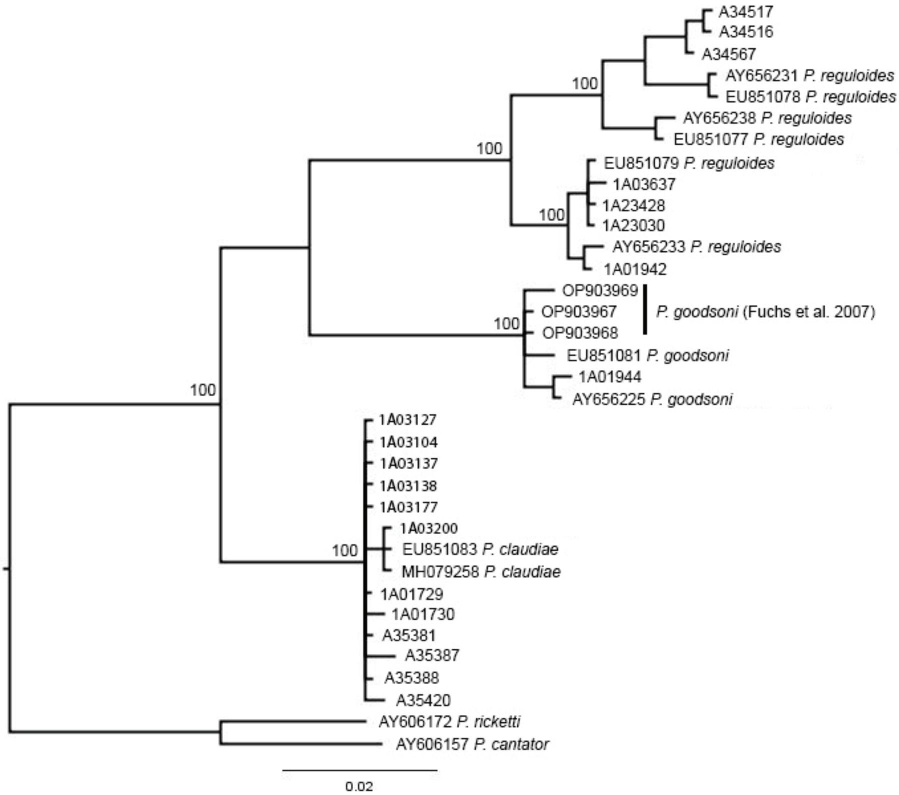

Figure 1. Bayesian Inference phylogenetic tree based on partial Cyt-*b* (B) gene of collected samples and those downloaded from GenBank, with Sulphur-breasted Warbler *P. ricketti* and Yellow-vented Warbler *P. cantator* serving as outgroups. Numbers on each node represent posterior probabilities. (All samples collected in this study are represented by ring numbers with either A or 1A preceding the five-digit number.)

more frequent in the east of the region. Separation of *P. goodsoni* and *P. claudiae* in field observations is problematical, and their similarity extends to behavioural traits. Nuthatch-like clambering on tree trunks and larger branches is frequently observed in birds identified both as *P. claudiae* (Treesucon & Limparungpatthanakij 2018) and *P. goodsoni* (Carey & Pang in prep.) but so far may not have been recorded in *P. reguloides*. Further sampling, whether by mist-netting and examination in the hand, or from sound-recordings of winter-singing birds, across a range of habitats and elevations in mainland South-East Asia, may improve our knowledge of the non-breeding season distribution and status of *P. claudiae* and *P. goodsoni* alongside *P. reguloides*.

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