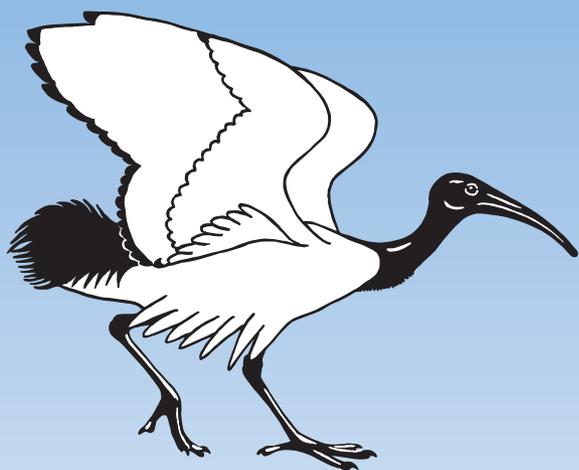


# Bulletin of the British Ornithologists' Club

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**Bulletin of the British Ornithologists' Club**

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# Bulletin of the BRITISH ORNITHOLOGISTS' CLUB

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## CLUB ANNOUNCEMENTS

### FORTHCOMING MEETINGS

The Club's next meeting, in conjunction with the Linnean Society, will be held on Thursday 6 October 2022 at 6.00pm, when Prof. Jared Diamond will talk on *What's so special about New Guinea birds?*

The meeting will be in hybrid format, both in person at the Linnean Society, Burlington House, Piccadilly, London W1J 0BF, and online via Zoom.

*Abstract.*—The tropical island of New Guinea has long played a pre-eminent role in ornithology, which caused it to be chosen as the site for the BOU's Jubilee Expedition in 1909. Part of the reason is New Guinea's many extraordinary birds, such as its birds of paradise, whose male ornamental plumages carry sexual selection to extremes; bowerbirds, whose males build the most elaborate display structures among animals; megapodes, the only birds that incubate their eggs by natural heat sources rather than by body heat; its diversity of parrots and kingfishers, orders that probably evolved in New Guinea; Greater Melampitta *Melampitta gigantea*, the only passerine known to roost underground; and its many bird groups convergent on but unrelated to the nuthatches, creepers, warblers, finches, wrens, and sunbirds of the rest of the world. Another reason is New Guinea's equatorial location combined with its high mountains, resulting in a range of habitats from tropical rainforest in the lowlands to glaciers on the highest peaks at 5,000 m. Still another reason is its simple geography: a single central cordillera with montane allospecies arranged from west to east, separating northern and southern lowlands with lowland allospecies arranged in a ring. New Guinea should not be thought of as the world's largest tropical island, but instead as Earth's smallest continent. New Guinea has proved to be ideal terrain for studying speciation, ecological segregation, and other biological phenomena. New Guineans themselves are walking encyclopedias of knowledge about their birds. The illustrated talk will explain these and other features that make New Guinea birds special. The only disadvantage to visiting New Guinea is that, thereafter, you'll find the rest of the world boring by comparison.

*Biography.*—Jared Diamond is a Pulitzer-prize-winning author of five best-selling books, translated into 43 languages, about human societies and human evolution: *Guns, germs, and steel*; *Collapse*; *Why is sex fun?*; *The third Chimpanzee*; and *The world until yesterday*. As a professor of geography at UCLA (University of California at Los Angeles), he is known for his breadth of interests, which involves research and teaching in three other fields: the biology of New Guinea birds; digestive physiology; and conservation biology. His prizes and honours include the US National Medal of Science, the Pulitzer Prize for Non-fiction, the Tyler Prize for Environmental Science, and election to the US National Academy of Sciences. He is a director of World Wildlife Fund/US. As a biological explorer, his most widely publicised finding was his rediscovery, at the top of New Guinea's remote Foja Mountains, of the long-lost Golden-fronted Bowerbird *Amblyornis flavifrons*, previously known only from four specimens found in a Paris feather shop in 1895.

Registration details will be published nearer the time on the Linnean Society website and the BOC site.

### Erratum

In *Bull. Brit. Orn. Cl.* 142: 122, in the legend to Fig. 8, the text relating to image F was incorrect. This photograph of New Caledonian Storm Petrel *Fregatta lineata* was taken off Port Stephens, New South Wales, Australia, in January 2021, by Allan Richardson, rather than off Nouméa, New Caledonia, in January 2020, by Hadoram Shirihai, as erroneously stated therein. The authors would like to apologise to the photographer concerned for any confusion that was caused.

### Friends of the BOC

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

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Sort Code: 20-45-45

Account number: 53092003

Account name: The British Ornithologists' Club

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

### 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](mailto: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](http://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](mailto: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).

# First description of the nest and eggs of Ceará Leaf-tosser *Sclerurus cearensis*, with a review of the breeding biology of genus *Sclerurus*

by Cicero Simão Lima Santos, Cecília Licarião, Weber Girão, Renata Beco & Flávio Kulaif Ubaid

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<http://zoobank.org/urn:lsid:zoobank.org:pub:2FEFC6F2-26CA-4CF6-9D7B-EC105E6D0E38>

**SUMMARY.**—*Sclerurus* is a genus of morphologically uniform, strict understorey, leaf litter specialists. We present the first description of the nest and eggs of Ceará Leaf-tosser *S. cearensis* from north-east Brazil and review breeding data for the genus. Based on three nests, the nest of *S. cearensis* was classified as cavity/with-tunnel/low cup, the type typical of the genus. The nests were excavated in banks at a mean height of  $1.48 \pm 0.22$  m above ground. Tunnels measured  $50.83 \pm 4.25$  cm and terminated in an expanded, globular chamber where a small cup of sticks harbours the two white eggs. Eggs at one nest measured  $25.7 \times 19.8$  mm and  $24.3 \times 19.6$  mm, and weighed 5.1 g and 4.5 g, respectively. Available breeding data for the genus *Sclerurus* are remarkably uniform in all aspects and match our observations of Ceará Leaf-tosser.

*Sclerurus* is a monophyletic group (Derryberry *et al.* 2011) comprising six to eight species according to different authorities (del Hoyo & Collar 2016, Billerman *et al.* 2020, Remsén *et al.* 2021), and at least 28 taxa (Winkler *et al.* 2020) of morphologically uniform, strict understorey, leaf litter specialists (Vaurie 1980). All are secretive and highly sensitive to habitat disturbance, and possess similar general behaviour and ecology (Vaurie 1980). Geographical ranges of *Sclerurus* species are dissected by the major biogeographical barriers in the Neotropics and encompass most forested environments from central Mexico to southern Brazil (d’Horta *et al.* 2012).

Ceará Leaf-tosser *Sclerurus cearensis*, until recently considered conspecific with Rufous-breasted Leaf-tosser *S. scansor*, differs in its slightly smaller size, slightly brighter back and underparts, clear white vs. dusky-scaled throat, and song (del Hoyo & Collar 2016). Genetic data support *cearensis* as an independent evolutionary lineage (d’Horta *et al.* 2011), although some authors (Billerman *et al.* 2020, Gill *et al.* 2021, Remsén *et al.* 2021) continue to treat it as a subspecies of *S. scansor*. *S. cearensis* is endemic to north-east Brazil, from southern Ceará to northern Bahia (del Hoyo & Collar 2016), and restricted to humid and dry forest habitats, with severely fragmented populations in ongoing decline due to deforestation caused by logging and agricultural expansion (Girão e Silva *et al.* 2018). It appeared (as a subspecies) in the Brazilian Red List for the first time in 2003 (MMA 2003), and is currently listed as Vulnerable (ICMBio 2018). Following recognition as a species, it was also categorised as Vulnerable on the IUCN Red List in 2016, where it remains until the present (BirdLife International 2021).

Breeding data for five of the seven *Sclerurus* species are available and are very similar (Vaurie 1980), but large knowledge gaps exist for both Short-billed Leaf-tosser *S. rufifigularis* and *S. cearensis* (del Hoyo *et al.* 2020, Remsén 2020). Generally, *Sclerurus* nests in excavated cavities in banks or steep slopes (Sick 1997, Hilty 2002), occasionally in the soil around upended tree roots (del Hoyo & Collar 2016). The only breeding data for Ceará Leaf-tosser

indicate that the species excavates burrows in banks (Girão & Albano 2008). Here, we review breeding data for the genus *Sclerurus* and present the first description of the nest and eggs of Ceará Leaf-tosser.

## Methods

**Nest description.**—This was based on three nests found at two localities in Ceará state, Brazil. One was found in the Floresta Nacional do Araripe-Apodi (FLONA Araripe), a protected area in Barbalha municipality (07°17'10"S, 39°27'49"W), southern Ceará, mainly covered by typical Cerrado formations—*carrasco*, *cerrado* and *cerradão*—with wet forest on slopes (Silva *et al.* 2018). Climate is classified as 'hot semi-arid' under the Köppen-Geiger system (Peel *et al.* 2007) and is characterised by low and highly irregular rainfall, strong insulation, high evaporation rates and mean temperatures of *c.*27°C. Relative humidity is usually low, and the few rains are concentrated in November–April. Nevertheless, rainfall is extremely scarce in some years, causing more severe droughts. Elevation varies between 760 and 970 m (960 m at the nest site).

The second (active) and third (inactive) nests were found at the village of Catolé (04°21'23.628"S, 39°01'21.66"W; 820 m), Mulungu municipality, in the Serra de Baturité, an Atlantic Forest remnant within the Caatinga biome in northern Ceará. This remnant covers 32,690 ha and forms part of the Serra de Baturité Environmental Protection Area. Considered one of the most important forested areas in north-eastern Brazil, the Serra de Baturité is the richest area of Ceará in terms of biodiversity. Part of the serra is humid even during the long dry season. Local climate is classified as tropical with dry winter (Peel *et al.* 2007). Rainfall is concentrated in November–April with a well-defined dry season across the rest of the year. Mean temperatures vary between 19 and 22°C and mean annual rainfall is 1,500 mm.

At each location we made *c.*10 hours of observation with binoculars. Nests were measured using tape (accurate to 1 mm). Eggs were measured with analogue callipers (0.05 mm accuracy) and weighed using a digital scale (0.1 g accuracy). Nest type was determined by reference to Simon & Pacheco (2005).

***Sclerurus* breeding biology review.**—We reviewed the primary and some secondary literature concerning the breeding ecology of *Sclerurus* (Goeldi 1896, Stone 1918, Todd & Carriker 1922, Pinto 1953, Herklots 1961, Skutch 1966, Monroe 1968, Skutch 1969, Wetmore 1972, Vaurie 1980, Rowley 1984, Skutch 1985, Hilty & Brown 1986, Stiles & Skutch 1989, Tostain *et al.* 1992, Haverschmidt & Mees 1994, Walters 1995, Kiff 1996, Zyskowski & Prum 1999, Denton & Blue-Smith 2000, Hilty 2002, Greeney *et al.* 2004). To update previous information, we provide a compilation of published data for each of the seven recognised species (following del Hoyo & Collar 2016).

## Results

**Nest, eggs and parental care of Ceará Leaf-tosser.**—Three nests were found. The first active nest was found on 21 December 2019 (Fig. 1) in FLONA Araripe, when an adult was seen departing a bank in wet forest. It held two pure white eggs, which measured 25.7 × 19.8 mm and 24.3 × 19.6 mm, mass 5.1 g and 4.5 g, respectively.

The second nest was found on 1 June 2020, again in a bank, in the backyard of a residence in Catolé village. The nest was near a door in the house, where there was constant movement of people, and at the top of the bank, *c.*0.5 m from the nest, there was a frequently used trail (Fig. 2). Around the nest were several ornamental plants.

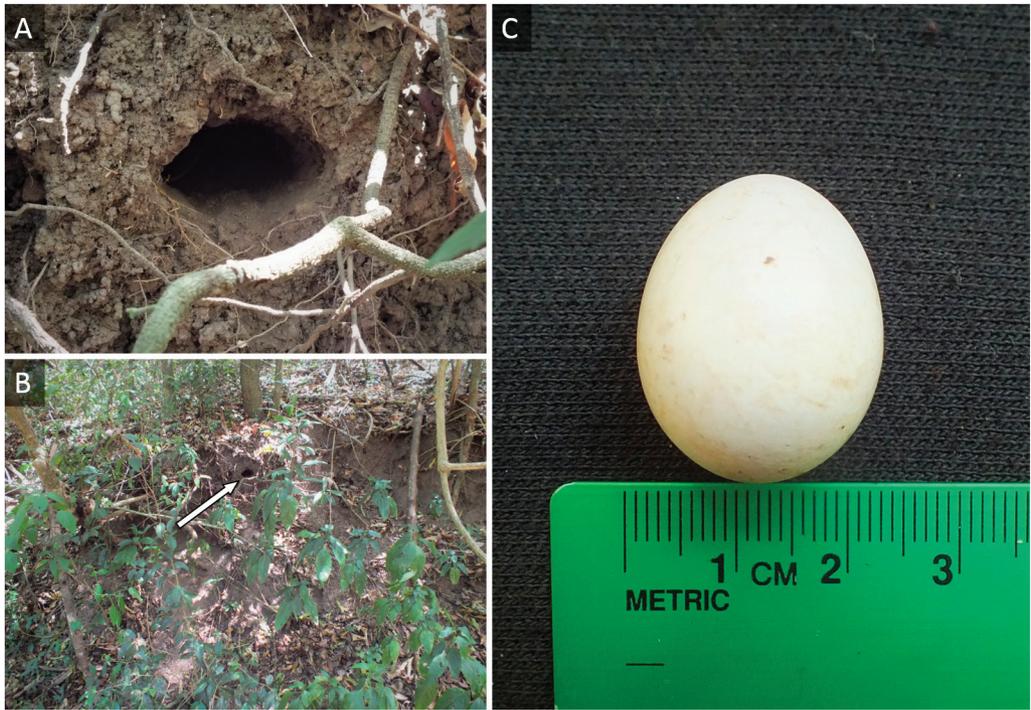


Figure 1. Nest entrance (A), location (B) and egg (C) of Ceará Leaf-tosser *Sclerurus cearensis*, FLONA Araripe, Barbalha, Ceará, Brazil, December 2019 (Cicero Santos)



Figure 2. Nest entrance (A) and partial view of the nest site (B–C) of Ceará Leaf-tosser *Sclerurus cearensis*, Catolé, Ceará, Brazil, June 2020 (Cecília Licarião)

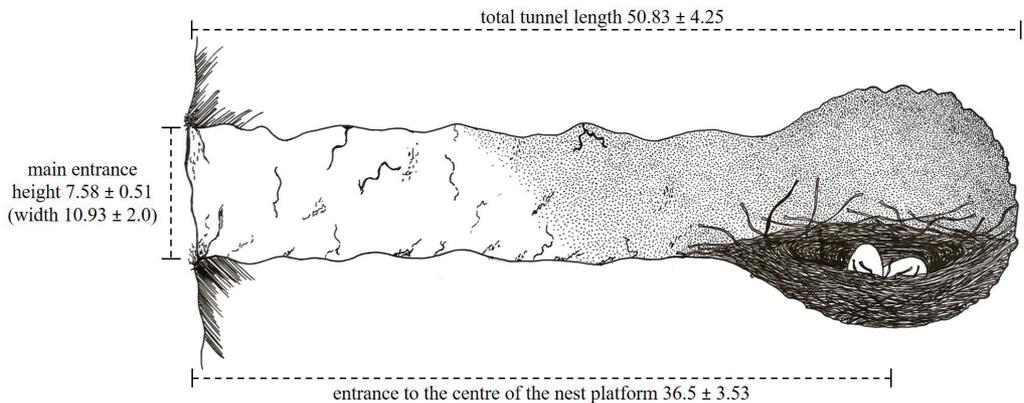


Figure 3. Schematic drawing of a Ceará Leaf-tosser *Sclerurus cearensis* nest. Mean measurements of the three nests are presented in cm  $\pm$  standard deviation.

At the third nest, found by the owner of the same house, a fledgling had departed just a few days before CL arrived (1 June) at the site. This nest was in a ravine beside a dirt road in daily use by vehicles. Above the bank there was dense vegetation with 5–10 m-tall trees.

As exemplified by Fig. 3, the nest of Ceará Leaf-tosser can be classified as cavity/with-tunnel/low cup (*sensu* Simon & Pacheco 2005). Tunnels are oval in cross-section (longest on the horizontal axis) and end in a globular, expanded chamber. The cup is constructed of sticks. All three nests were excavated in earth banks  $1.48 \pm 0.22$  m above ground. Tunnel entrances were clean and not concealed, e.g., by vegetation. Nests had the following measurements: entrance width  $10.93 \pm 2.0$  cm ( $n = 3$ ), entrance height  $7.58 \pm 0.51$  cm ( $n = 3$ ), total tunnel length (from entrance to back wall of chamber)  $50.83 \pm 4.25$  cm ( $n = 3$ ), and the centre of the nest platform was  $36.5 \pm 3.53$  cm ( $n = 2$ ) from the tunnel entrance.

**Parental care.**—While we measured the first nest, the adults remained in the vicinity and one approached three times trying to enter. Adults were vigilant but permitted close approach (*c.* 5 m). When one adult was in the nest, the other always remained nearby outside, and gave an alarm call at the slightest indication of threat.

On 12 June 2020, a fledgling at the second nest made its first flight. At 07.36 h, one of the young left the nest followed by an adult. The fledgling's first flight was at a height of 1.60 m above ground. It landed 3 m from the nest, then flew again, a further 2 m. The adult gave an alarm call, flew to the nest bank, and the young flew  $>1$  m above ground in a straight line. A few minutes later, a persistent vocalisation was heard for  $>10$  minutes, then an adult was seen flying to the nest and perching at the entrance. When it noticed the observer (CL), it flew to a branch 2 m from the nest, uttered a series of calls and performed an agitated display. The very loud vocalisation of another young bird was heard close by, from the ground or a nearby branch. It called for *c.* 1 minute, then flew away. The nest's contents were checked at 09.37 h using an endoscopic camera. Only recent faeces were present.

Our observations show that the breeding season occupies at least December to June. A summary of the available breeding data for each *Sclerurus* species based on the literature is shown in Table 1. More detailed information is as follows.

#### MIDDLE AMERICAN LEAFTOSSER *Sclerurus mexicanus*

Season December–April in Costa Rica (Stiles & Skutch 1989), possibly until at least May elsewhere. A female collected in southern Mexico in April with a fully formed egg in the oviduct (Rowley 1984), and a few specimens in breeding condition in April–May in northern

TABLE 1  
Summary of available breeding information for the species of *Sclerurus*.

Species	Breeding season	Nest place	Clutch size	Incubation period (days)	Nestling period (days)	Parental care
Middle American Leaf-tosser <i>S. mexicanus</i>	December–May	in ground / between roots of fallen tree	2	unknown	unknown	unknown
Short-billed Leaf-tosser <i>S. ruficularis</i>	unknown	between upturned roots	unknown	unknown	unknown	unknown
Scaly-throated Leaf-tosser <i>S. guatemalensis</i>	August–June	in banks / between roots of fallen trees	2	21	14–15	biparental
Black-tailed Leaf-tosser <i>S. caudacutus</i>	April–June	in banks / between upturned roots	2	unknown	unknown	biparental
Grey-throated Leaf-tosser <i>S. albigularis</i>	October–June	in banks	2	unknown	unknown	unknown
Rufous-breasted Leaf-tosser <i>S. scansor</i>	August–February	in ground / between roots of fallen trees	2–3	unknown	unknown	unknown
Ceará Leaf-tosser <i>S. cearensis</i>	December–June	in banks	2	unknown	unknown	biparental

Colombia (Hilty & Brown 1986). In August in eastern Ecuador, an adult was seen carrying leaves to a hole excavated 1 m up in the soil surrounding the roots of a fallen tree (Greeney *et al.* 2004). In the extreme south-east of the same country, G. M. Kirwan (*in litt.* 2021) found an active nest in a hole in an earth bank beside a little-used trail in late December. Nest a loose cup of compound-leaf rachises and dry twigs, 10 cm in diameter (Stiles & Skutch 1989) at end of a burrow (*c.*50 cm long) in the ground or among the roots of a fallen tree (Tostain *et al.* 1992). Greeney *et al.* (2004) recorded a 4 cm tunnel opening into a cavity roughly 20 cm in diameter. Eggs first described by Rowley (1984). Clutch two, unmarked white eggs (Stiles & Skutch 1989, Tostain *et al.* 1992, Kiff 1996).

#### SHORT-BILLED LEAFTOSSER *Sclerurus ruficularis*

Said to be similar to others of genus (Hilty 2002), but nothing seems to have been published except brief reports from Suriname and French Guiana, respectively, in Haverschmidt & Mees (1994) and Greeney *et al.* (2004).

#### SCALY-THROATED LEAFTOSSER *Sclerurus guatemalensis*

Based on his work in Costa Rica, Skutch presented the first and most detailed information for this species, which digs tunnels in banks or in the mass of clay clinging to the roots of a fallen tree (Skutch 1966, 1969). Hole entrance 40 cm above the base of a bank (Monroe 1968). Unlike most congeners, tunnel curved, thus the eggs are not visible from the entrance. At the end of the tunnel, *c.*1 m long (Monroe 1968), there is a chamber and a ‘thick but shallowly cupped nest’, but the eggs rest on bare soil (Skutch 1969). Nesting starts August–September and the last young fledge in late June, a long season. All observed clutches (*n* = 4) two pure white eggs (Skutch 1966, 1985), measuring 27.4 × 21.0 mm and 27.4 × 20.6 mm (Skutch 1969). Stone (1918) described eggs of this species as ‘glossy white, smaller one very sparingly speckled with deep rich brown, larger one more heavily marked with spots and specks of olive-brown’, from near Gatún, Panama. However, the size of the eggs (24.6 × 16.2 mm and 23.3 × 15.4 mm) reported by Stone is *c.*20% smaller than those presented by Skutch (1969), and his nest description does not correspond to any *Sclerurus*. Walters’ (1995) description from Belize is also erroneous for this species: ‘[the eggs] were speckled with reddish-brown,

and dark chocolate markings. The markings were more concentrated at the broad end of the eggs. These marks were too clearly defined and regular to constitute staining'. Walters (1995) described the nest as having an oval-shaped entrance 2 cm high × 5.5 cm wide, which also does not correspond to Scaly-throated Leaf-tosser. Stone's description was discounted by Wetmore (1972) and both these descriptions were comprehensively rejected by Kiff (1996). Incubation and feeding of nestlings are apparently shared by the sexes (Skutch 1969). Incubation lasts 21 days and nestlings fledge after 14–15 days (Skutch 1969). Of the three observed nests, two were successful (Skutch 1966).

#### **BLACK-TAILED LEAFTOSSER** *Sclerurus caudacutus*

Pinto (1953) described the nest and eggs of *S. c. pallidus* from Mata do Utinga, Belém, Pará, Brazil. The nest, sited at the end of a 0.5 m-tunnel excavated in an earth bank, was a shallow cup 12–15 cm in diameter, made exclusively of dry, curved leaf petioles. Clutch was two, 26 × 20 mm, white and almost unglossed eggs, found in April 1925 (Pinto 1953). Nest in burrows in upturned roots (Greeney *et al.* 2004). Denton & Blue-Smith (2000) described two nestlings from June 1998 and measured a nest in the Tambopata Reserved Zone, Madre de Dios, Peru. The nest was a 'shallow ... cup interior 5 cm in width and 1.75 cm in height. The straight, undeviating burrow was 50 cm in length with an entrance tunnel 5 cm high and 13 cm wide. The burrow was horizontally excavated in the vertical wall of a depression'. Both adults provisioned the young (Denton & Blue-Smith 2000).

#### **GREY-THROATED LEAFTOSSER** *Sclerurus albigularis*

Nests found in May and June in Colombia (Todd & Carriker 1922). Breeds October–May, peak December–February, on Trinidad (Herklots 1961). The incubation chamber is lined with only 'a few mid ribs of leaves placed side by side'. Todd & Carriker (1922) reported that 'the nest is placed at the end of a tunnel-shaped excavation, made by the birds themselves, in a more or less perpendicular bank of earth along some small creek or road through the heavy forest...The cavity is about fifteen inches in length, the main portion being about two inches in diameter, while the nest cavity is enlarged to about twice that amount. The two ovoid, white eggs are deposited on a scant bed of dead leaves'. The curving burrow varies from c.30.5 to 46.0 cm in length.

#### **RUFOUS-BREASTED LEAFTOSSER** *Sclerurus scansor*

Nest excavated at end of a dirt bank tunnel or placed in earth caught among roots of fallen trees (del Hoyo *et al.* 2020). Eggs in August and birds in breeding condition in September and December (del Hoyo *et al.* 2020). A nest found in August 1895 in the Serra dos Órgãos, Rio de Janeiro, comprised only dry leaf-ribs (Goeldi 1896); brood patch observed in one individual in southern Brazil in February (Bugoni *et al.* 2002); clutch two pure white eggs (28 × 21 mm). The circular hole and tunnel, which made a deviation to the right, was 5 cm wide with a terminal cavity 21 cm in diameter containing the nest (Goeldi 1896).

## Discussion

Breeding data for *Sclerurus* spp. show a remarkable uniformity in all aspects and are congruent with those presented here for Ceará Leaf-tosser. All species with available data excavate their burrows in earth masses (in the ground, in river and road banks, or in the root masses of fallen trees), and build a simple cup, usually of leaf rachises, within an expanded chamber (Zyskowski & Prum 1999). Like congeners, probably both sexes of Ceará Leaf-tosser engage in all aspects of breeding. At one nest of *S. cearensis*, we observed two adults sharing incubation and nestling care. Although the birds were not marked and

sexed, Ceará Leaf-tosser probably is monogamous, like *S. guatemalensis* (Skutch 1969, Ruth & Schreck 2020).

The apparent breeding season of Ceará Leaf-tosser (December–June) coincides with that of Middle American Leaf-tosser (December–April) in Costa Rica (Stiles & Skutch 1989). Scaly-throated Leaf-tosser (Skutch 1969) and Grey-throated Leaf-tosser (Herklots 1961) nest during October–May in Costa Rica and on Trinidad, respectively, although the latter has been found with eggs as late as June in Colombia (Todd & Carriker 1922). Species with fragmentary information also nest within this period, e.g., a Black-tailed Leaf-tosser with eggs in April in northern Brazil (Pinto 1953) or nestlings in June in Peru (Remsen 2020). Rufous-breasted Leaf-tosser starts breeding earlier, with eggs in August (del Hoyo *et al.* 2020).

There is a great uniformity in nests of the genus, as its more or less rudimentary structure does not seem to vary much between species (Vaurie 1980). Some, such as Middle American, Scaly-throated and Rufous-breasted Leaf-tossers, can use large masses of soil trapped in the roots of fallen trees to build their nests (Skutch 1969, Tostain *et al.* 1992, Greeney *et al.* 2004, del Hoyo *et al.* 2020). Such sites perhaps offer an alternative in level-ground sites, where banks with exposed soil can be a scarce resource.

Burrow length varies slightly among species, but is nearly always between 0.3 and 1.0 m, with the exception a 4 cm-tunnel reported by Greeney *et al.* (2004). Tunnels are usually straight but can be curved in Scaly-throated (Skutch 1969) and Rufous-breasted Leaf-tossers (Goeldi 1896), obscuring the contents from view at the entrance. Eggs of the slightly larger sister species, Rufous-breasted Leaf-tosser are 8% greater in size than those of Ceará Leaf-tosser reported here.

Nests placed in self-excavated or adopted cavities, such as a subterranean burrow, are a feature of several other furnariid genera (Zyskowski & Prum 1999). For example, all species of *Geositta*, which is sister to *Sclerurus* (Irestedt *et al.* 2006, d’Horta *et al.* 2012), breed in cavities excavated by the birds themselves or other animals (birds or mammals) (Fraga & Narosky 1985, Silva 2015, Machado *et al.* 2017).

For those *Sclerurus* with available data, the clutch is always two eggs, with just one unconfirmed report of a Rufous-breasted Leaf-tosser nest holding three eggs (del Hoyo *et al.* 2020). Eggs are always white and unmarked, but can become soiled with mud and thus appear spotted as incubation proceeds (Skutch 1969, Kiff 1996).

There are still large gaps in our knowledge of *Sclerurus* breeding biology, e.g., for most species, information on the length of the incubation and nestling periods, breeding success and predators are still unknown (Table 1). Short-billed Leaf-tosser is the least known species, with virtually no information on its reproductive habits.

Further studies of the biology of *S. cearensis* are essential to more fully understand its seasonality, nest site preferences and clutch size. Deforestation is the main threat to the species and, consequently, its reproductive success, but other factors that can negatively impact the latter are unknown, and deserve study.

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# The colourful journey of the Eurasian Collared Dove *Streptopelia decaocto*

by Hein van Grouw

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**SUMMARY.**—In the 18th and 19th centuries the Eurasian Collared Dove *Streptopelia decaocto* was widely considered to be the wild ancestor of the domesticated Barbary Dove (domestic *S. risoria*), and even following its recognition as a species its taxonomic status was a source of confusion. Since 1900, and the species' massive geographic expansion (both naturally and by introduction) the two taxa have occasionally met. The resultant hybridisation is probably the cause of the large number of Eurasian Collared Doves with the aberrant pale colour of Barbary Doves in areas where hybridisation has occurred.

*'Besides variation in depth of colour within the normal range, very pale individuals and others that are creamy buff like S. 'risoria' occur quite frequently in Britain. There is no reason to suppose these mutants are of hybrid origin'. Goodwin (1983: 116)*

Even before the first Eurasian Collared Doves *Streptopelia decaocto* were officially recorded in the British Isles, James Fisher (1953) detailed the species' spread across Europe. Subsequently, under their own steam they have reached continental Africa and, with a little human help, they have also become common in the USA. Prior to the mid 1800s, Eurasian Collared Dove caused taxonomic confusion among ornithologists, and since 1900 it has generated interest due to its spectacular range expansion. Nowadays, many consider the species an annoyance, or at least unworthy of attention, but given its remarkable—even colourful—natural history, Eurasian Collared Dove surely deserves greater appreciation.

Frivaldszky (1838), a naturalist at the Budapest museum, was first to describe Eurasian Collared Dove taxonomically and gave it, based on legend, the species name *decaocto* (Appendix 1). Although the message the dove was supposed to pronounce—decaocto—may not be immediately obvious (try matching this two-syllable word with the three-syllable call, see Appendix 1), Eurasian Collared Dove has certainly succeeded in proclaiming it widely across the world. Its original distribution was South Asia, but by 1800 the species was already common in Central Asia, the Balkans and European Turkey (Stresemann & Nowak 1958, Nowak 1965). Since the early 20th century it has continued to expand west and south across Europe (Nowak 1965) and, around 1986, it 'jumped' from Spain to continental Africa (Robel 2000). Roughly 12 years earlier Eurasian Collared Dove was introduced in North America where it has continued to expand. It is in North America, 'the land of opportunity', where the Eurasian Collared Dove may eventually evolve into a new taxon...

## Confusing taxonomy

Although described taxonomically in 1838 by Frivaldszky based on birds from the Balkans, it took another 100 years or more before Eurasian Collared Dove became familiar in the rest of Europe. It was unknown in Western Europe until the second half of the 20th

century, thus its call sounding in the background of many films and dramas set in pre-WWII Europe is an often-unnoticed inaccuracy!

During his travels through Hungary, Johann Friederich Naumann (1780–1857) met Frivaldszky in Budapest, who showed him turtle dove skins in the museum's collection, collected in 1835 in Plovdiv, Bulgaria (formerly Philippopolis, European Turkey). Eurasian Collared Dove, then still referred to as Indian Turtle Dove *Columba risoria*, was generally considered to be the wild form of the domesticated Barbary Dove<sup>1</sup>, which was the only 'collared turtle-dove' known in Europe at the time. Naumann, however, correctly recognised the skins as different from the domestic dove and was keen to investigate further. He therefore returned to Germany with three of the skins, which he sent to M. H. C. Lichtenstein in Berlin to compare with other specimens collected in Asia and Africa. Lichtenstein, however, believed that different climates result in variety within a species, an idea introduced by C. L. Gloger in 1833 (Gloger's Rule; animals tend to be darker in warm and humid areas). Having compared Frivaldszky's birds with similar doves from elsewhere, which he considered to all be *risoria*<sup>2</sup>, Lichtenstein believed the Bulgarian doves were not significantly different and therefore not a new species (Stresemann 1953).

Based on these two rather different conclusions, Frivaldszky (1838) named the Eurasian Collared Dove *Columba risoria* var. *decaocto* (descriptions of varieties from this era can represent valid species-group names). The original description was published in Hungarian, and, as the journal was rather obscure, Frivaldszky's name *decaocto* for Eurasian Collared Dove was long overlooked. As Naumann had encouraged him to describe the species, and also produced its accompanying plate (Fig. 1), Frivaldszky gifted him a specimen (Figs. 2–3).

Brian Houghton Hodgson (1801–94), Britain's diplomatic representative in Nepal between 1820 and 1843, amassed a large collection of birds and mammals. When he returned to England in 1843, he donated this collection, including c.2,200 bird skins, to the British Museum, and it still is one of the most important of its kind from the Himalayan region. His collection was augmented by drawings commissioned from native artists depicting each species, each drawing numbered and cross-referenced to a specimen label attached to the leg or neck of the skin (Fig. 4). Nearly the complete set of drawings was donated to the museum with the specimens (Gray 1844). Hodgson's intentions in compiling this visual catalogue are unclear. He may have planned to use them for a publication about the birds of Nepal, although there appears to be no direct evidence for this.

Among the Nepalese birds in Hodgson's collection are several specimens of Eurasian Collared Dove, which he labelled no. 107 in line with the species' numbered drawing (Fig. 5). He had also sent to the museum a list of the species he had collected, which was published in *The zoological miscellany* (Hodgson 1844). Therein, Hodgson referred to the species as *Columba douraca* (presumably from its Hindi name, 'Dhor fakhta'<sup>3</sup>). The name *douraca* was never published formally by Hodgson and is not mentioned on the drawing, so

<sup>1</sup> Barbary Dove is the domestic form of African Collared Dove *Streptopelia risoria*. Until the late 1800s, however, many ornithologists considered Eurasian Collared Dove, which they called *Columba* (*Streptopelia*) *risoria*, to be the wild ancestor of Barbary Dove (van Grouw 2018).

<sup>2</sup> The different specimens Lichtenstein used in his comparison, and whose differences he believed were the result of climate, belonged to five different species (Stresemann 1953); African Collared Dove, Barbary Dove, Vinaceous Dove *S. vinacea*, Ringed Dove *S. capicola*, Mourning Collared Dove *S. decipiens* and Eurasian Collared Dove.

<sup>3</sup> Newman (1906) assumed that Hodgson's name *douraca* was founded on a bird from a place called Dhourakha, which he presumed was in Nepal, but admitted that he could not find it on a map.



Figure 1. Depiction by J. F. Naumann of Eurasian Collared Dove *Streptopelia decaocto* to accompany the species' type description by Frivaldszky in 1838 (Hein van Grouw, © Natural History Museum, London)



Figure 2. Type specimen of *Streptopelia decaocto*, collected in 1835 in Plovdiv, Bulgaria by Carl Hinke, in the Naumann Museum, Köthen (© Naumann Museum, Köthen)



Figure 3. Watercolour by J. F. Naumann of the type of *Streptopelia decaocto*, previously published only in the Naumann Museum guidebook (© Naumann Museum, Köthen)

is a *nomen nudum*<sup>4</sup>. Nevertheless, it was accepted by many authorities as the species name of Eurasian Collared Dove (Fig. 6), e.g., Schlegel (1873), Stejneger (1887) and Salvadori (1893). These, and many other contemporary authors, no longer considered the species to be the wild ancestor of the domestic Barbary Dove.

However, Othmar Reiser, an Austrian ornithologist and curator at the National Museum of Bosnia and Herzegovina in Sarajevo, discovered Frivaldszky's work and realised that the specific name *decaocto* antedates Hodgson's *douraca*. He published that the correct name for Eurasian Collared Dove is *decaocto*, firstly in German (1894), and later, via Dresser (1903) in English. After Hodgson more workers had named the species, but all of these names are junior synonyms of *decaocto* (see Appendix 2).

As mentioned, Eurasian Collared Dove was long known mainly by the name *risoria*, and later *douraca*, from India. Indian birds are generally smaller and darker than those

<sup>4</sup> *Nomen nudum* ('naked name') is a nomen that seems to be a correct scientific name, and may originally have been intended to be one, but which has not (yet) been published with an adequate description of the taxon involved and therefore cannot be accepted under the *International code of zoological nomenclature*.

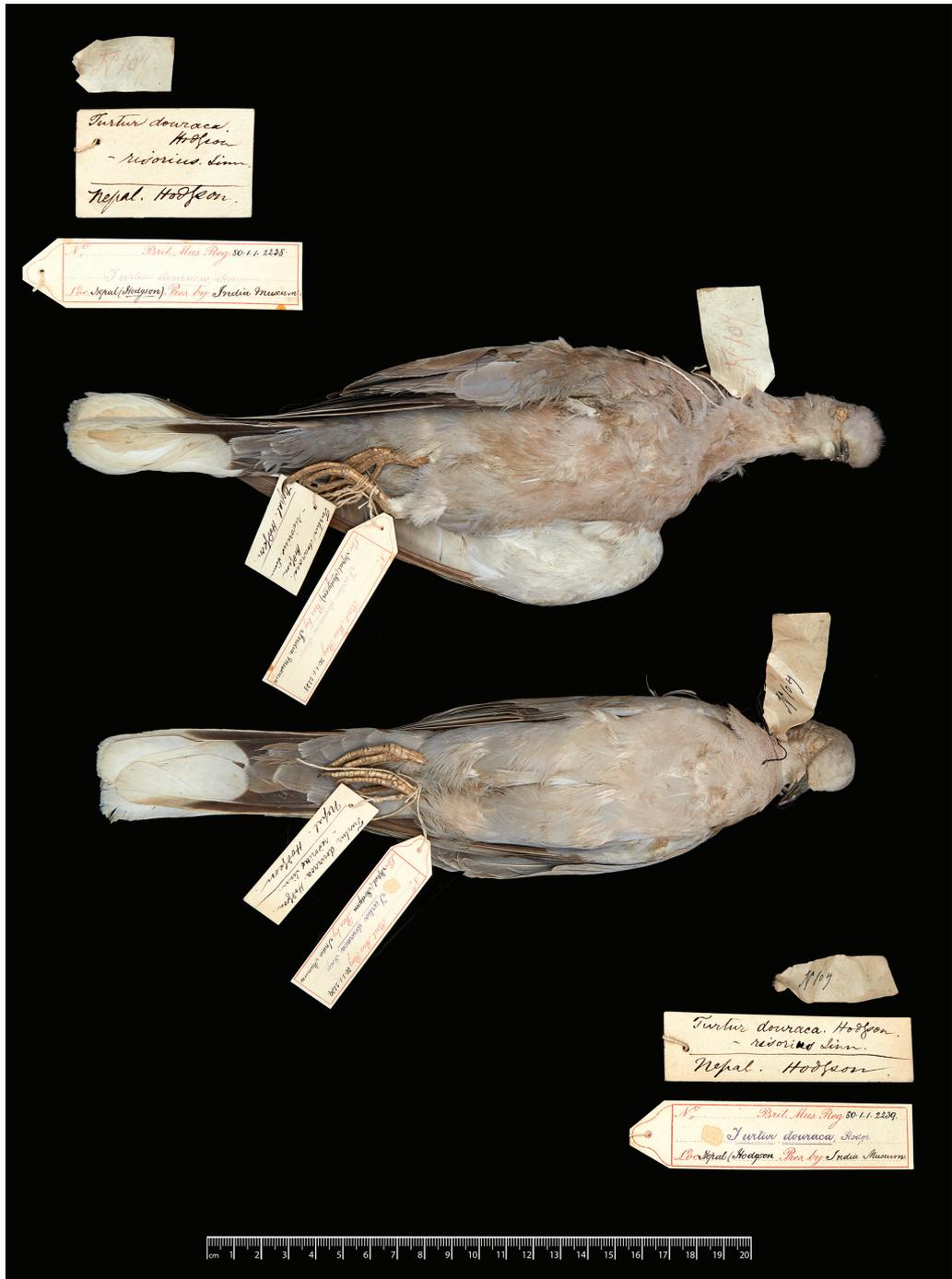


Figure 4. Eurasian Collared Dove *Streptopelia decaocto* specimens collected by Hodgson in Nepal, and which he called *Columba douraca*. His collection was augmented by a set of drawings depicting each species, commissioned from native artists, numbered and cross-referenced to a label attached to the specimens. The drawing of *Columba douraca* is no. 107. Specimens NHMUK 1880.1.1.2238 and NHMUK 1880.1.1.2239, Natural History Museum, Tring (© Aimee McArdle, Natural History Museum, London)



Figure 5. Drawing no. 107; Hodgson's *Columba douraca* from Nepal (© Natural History Museum, London)



Figure 6. Despite the specific name *douraca* never being published by Hodgson, it was nevertheless accepted by many ornithologists as the name for Eurasian Collared Dove and specimens were labelled accordingly, including this Eurasian Collared Dove collected in the 1820s in Japan by P. F. von Siebold, in the Naturalis Biodiversity Center, Leiden, RMNH.AVES.258559 (© Naturalis Biodiversity Center, Leiden)

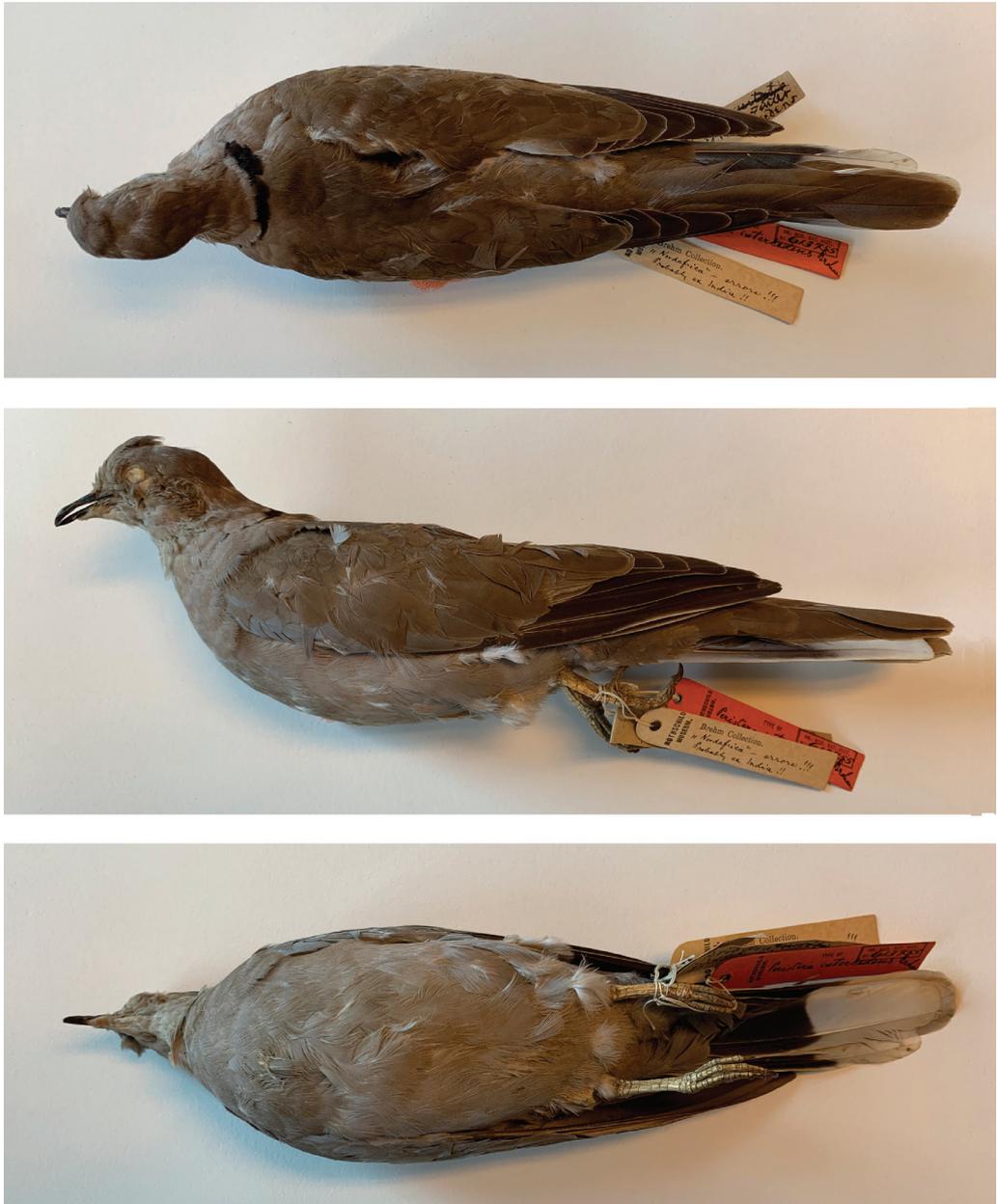


Figure 7. Type specimen of *Peristera intercedens*, AMNH 613755; Brehm (1855) incorrectly thought it came from Africa but, based on its dark colour and small size, it almost certainly was collected in southern India or Sri Lanka (© American Museum of Natural History, New York)

in the Balkans and Central Asia. Newman (1906) therefore suggested recognising them as different subspecies: the larger and paler birds, after Frivaldszky's Balkan doves, *S. d. decaocto*, and the darker smaller birds from India as *S. d. douraca*, after Hodgson's doves from Nepal. This, however, was never accepted. In fact, if there had been the need to distinguish these two, Brehm's name *intercedens* is the earliest available name for Indian birds. Based on a Eurasian Collared Dove specimen from his own collection (Fig. 7), Brehm



Figure 8. Eurasian Collared Dove *Streptopelia decaocto xanthocyclus*, Bagan, Myanmar, 15 November 2013 (© Otto Samwald)

(1855) named the species *Peristera intercedens*, the Middle Laughing Dove<sup>5</sup>. From where and whom he obtained the specimen are unknown, but Brehm assumed incorrectly that it was from North Africa. Based on its small size and dark colour the specimen was almost certainly from (southern) India or Sri Lanka.

Currently all populations in Europe and Asia, except Myanmar (see below), are considered *decaocto*. The difference in size is often explained by Bergmann's Rule (Keve-Kleiner 1943, Nowak 1975), an ecogeographical rule which states that within a broadly distributed taxonomic group, populations in colder environments are larger than those in warmer regions. Although originally formulated in the context of species within a genus, it has often been recast in terms of populations of a species, as may be the case for Eurasian Collared Dove. Doves from South India and Sri Lanka are indeed smallest, but also generally darkest in colour, which, however, cannot be explained by Bergmann's Rule, but rather by Gloger's Rule.

The doves in Myanmar, however, are more distinctive and easily recognised from those in Europe and elsewhere in Asia. Besides being slightly darker overall, they have a distinctive yellow orbital ring instead of greyish white (Fig. 8). Although Oates (1883: 293) already mentioned this characteristic ('eyelids and skin of face yellow'), prior to the early 20th century no one else had drawn attention to the fact that Burmese birds differed in this respect from Indian ones. It was Newman (1906) who fully recognised this difference, based on a live bird in London Zoological Gardens, which he described as a new subspecies, *xanthocyclus*, for its yellow orbital ring. In fact, in October 1896 the zoo had received three individuals, presumably from the Minbu and Mague districts of upper Burma. One, a male,

<sup>5</sup> In many languages, including German, Barbary Dove is called 'Laughing Dove' (Lachtaube) for the typical laughing call it makes when excited (in contrast, Laughing Dove *Streptopelia senegalensis* does not give a laughing call at all!). In the past, similar-looking species with a black neck-ring were often also referred to as 'laughing dove'. Brehm (1855) distinguished six different 'species' of 'Lachtaube', including domestic Barbary Dove, African Collared Dove, Eurasian Collared Dove, Vinaceous Dove *S. vinacea*, Red-eyed Dove *S. semitorquata* and Dusky Turtle Dove *S. lugens*.

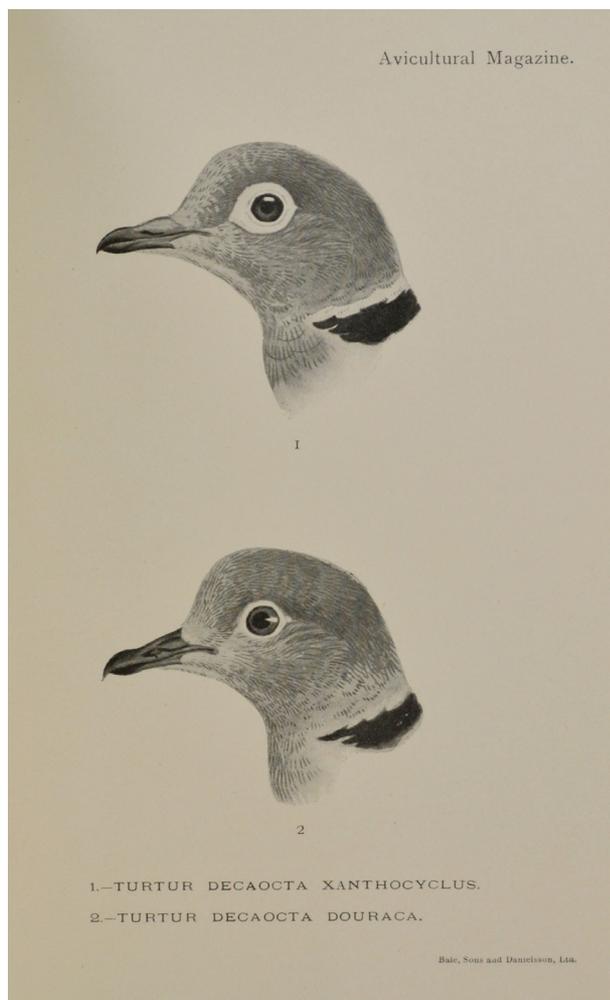


Figure 9. Illustration in Newman (1906) captioned 'Fig 1. Head of *Turtur decaocto xanthocyclus*, from the original sketch of the living bird [whereabouts of the original sketch unknown]. Fig. 2. Head of *Turtur decaocto douraca*, traced from the Indian drawing in Hodgson's MSS. Birds of India, Vol. V., pl. 82, type of *Turtur douraca*' (Hein van Grouw, © Natural History Museum, London)

lived almost ten years in the zoo but when, around 1904, Newman's attention was drawn to this dove, the other two had already died. Unfortunately, despite Newman's request, the dove's skin was not retained as, apparently, the cadaver was heavily damaged by rats post-mortem (Newman 1906), so the type specimen of *xanthocyclus* no longer exists (Fig. 9).

Currently only two subspecies of Eurasian Collared Dove are recognised—*decaocto* and *xanthocyclus*—and birds introduced to the Americas are of the nominate race.

### Global spread—a brief overview

The original range of Eurasian Collared Dove is assumed to have been arid areas in South Asia (Stresemann & Nowak 1958, Nowak 1965). Precisely when the species started spreading into the Balkans and European Turkey is unknown, but by 1800 it was already common there (Stresemann & Nowak 1958, Nowak 1965).

In those areas of the Balkans formerly under Turkish control (i.e. part of the Ottoman Empire), e.g., parts of Bulgaria, Serbia, Albania and Herzegovina, Eurasian Collared Dove flourished in the towns and cities because it was protected mainly by the Muslim population (Matvejev 1950). They encouraged the species by providing nest sites around their houses

(Naumann 1837, McGregor 1906), and in certain areas the punishment for killing a dove was a fortnight in prison (Reiser 1939). However, once the Turks were forced to cede their occupation of the Balkans in 1878, a large part of the Muslim population left, thus Eurasian Collared Dove lost its protector, its numbers diminished rapidly and in certain areas disappeared completely (Reiser 1894, 1939, Pichler 1906). After 1900 it made a slow recovery and by 1930 had regained its former distribution in the Balkans. Thereafter, the species appeared unstoppable and continued its expansion; in a relatively short period the rest of Europe was colonised. This spread was documented in detail by Fisher (1953), Stresemann & Nowak (1958) and Nowak (1965, 1991). As Turkey is considered the type locality of Eurasian Collared Dove, and the colonisation proceeded via Turkey into the rest of Europe, in many countries the common name refers to this (e.g., Dutch: Turkse Tortelduif, German: Türkentaube, French: Tourterelle Turque, Danish: Tyrkerduen, Swedish: Turkduva, Spanish: Tórtola Turca, Portuguese: Rola-turca). The first bird in England was recorded in summer 1952 at Manton, Lincolnshire (May & Fisher 1953), where it remained until at least 1958, but never found a mate (Hudson 1965). Close by, however, in Yorkshire, a bird dealer was known to have sold Eurasian Collared Doves imported from India between 1947 and 1951. Although no escapes were recorded, the Lincolnshire bird could have been one of the imported individuals, so it was never accepted as the first British record. Three years later, however, there was no doubt about the pair that turned up in Cromer, Norfolk, making 1955 the date of the first official record in Britain (Hudson 1965).

The species was first recorded in captivity in the USA around 1900, when 24 individuals were in the property of Charles Otis Whitman (1842–1910), Professor of Zoology at the University of Chicago. They were imported from Japan to be used in his studies on behaviour, inheritance and hybridisation in pigeons. Whitman called them the 'Japanese Ring-dove' *S. douraca* (Whitman 1919). But their fate after Whitman died in 1910 is unknown.

In all probability the origin of the Eurasian Collared Dove in America was the aviary of a bird breeder in Nassau, New Providence in the northern Bahamas. In fact, the origin was the Netherlands, which is where he obtained his birds in the early 1970s, although he thought they were Barbary Doves! In late 1974 several escaped, influencing the breeder's decision to release the remainder, and it is believed that in all 50 individuals were liberated (Smith 1987). Given the species' 'urge' to expand, and probably also due to the warm climate, they thrived and in less than ten years all the islands to the west were colonised. Probably by the late 1970s but certainly in the early 1980s, Eurasian Collared Doves were present at several places in Florida and, consistent with the usual westward direction of this species' expansion, surely arrived from the Bahamas. At the time several populations of feral Barbary Doves were flourishing in south-east Florida, so the new arrival remained unnoticed for a while, making the precise year of arrival unknown (Smith & Kale 1986).

Probably after the first doves reached Florida hybridisation with the feral Barbary Doves occurred. However, Eurasian Collared Doves, and probably their hybrids too, continued their march across the continent. Currently, the species can be found in nearly every North American state, in parts of Canada and Mexico, as well as Central America.

## Colour aberrations

Compared to its close relative, the domestic form of African Collared Dove *Streptopelia risoria* (Barbary Dove), remarkably few colour aberrations are known in Eurasian Collared Dove. One, however, is rather common and occurs throughout the species' range. It is often referred to as buff, blond or leucistic, but is a form of Ino and is the same mutation

as occurs in Barbary Dove<sup>6</sup> (van Grouw 2018). The Ino mutation is a variation of the gene SLC45A2 (pers. obs.; Appendix 3), which codes for a protein in the melanin cells and regulates melanin synthesis (Domyan *et al.* 2014). Several mutations of this gene, located on the sex-chromosome in birds, have been recorded in many different bird species (Appendix 3). The Ino mutation in Barbary and Eurasian Collared Doves causes incomplete melanin synthesis; the quantity of melanin granules is unchanged but the granules are lighter in colour, resulting in the overall plumage being paler, and the usually blackish and greyish parts more brownish. Due to the high concentration of melanin in the neck-ring, the change in colour in this feature is invisible to the naked eye. Although Goodwin (1973, 1983) believed the mutation occurred naturally in the species and not as a result of hybridisation with Barbary Dove, some facts could suggest otherwise. For example, the Canary Islands already had an established population of feral Ino-coloured Barbary Doves before the Eurasian species arrived around 1989, colonising all islands in the archipelago within ten years (Garcia-del-Rey 2015). Barbary Dove still breeds locally on all islands except El Hierro (Bowler 2018) but numbers have declined, presumably due to being outcompeted by the larger and more aggressive Eurasian Collared Dove. The two species did hybridise on the islands (pers. obs.), which suggests a role for inter-species hybridisation in generating this colour aberration in Eurasian Collared Dove. The number of pale-coloured (Ino) Eurasian Collared Doves on the Canaries is certainly very high (Figs. 10–13).

Ino individuals recorded in countries with no established feral Barbary Dove populations (Figs. 14–16) may indeed be the result of recurrent mutation or ancestral variation in the Eurasian species. For example, an Ino-coloured fledgling found in the Netherlands, rescued and kept in captivity, aside from its colour, showed no morphological or behavioural signs of recent hybridisation (see footnote 6). However, it cannot be ruled out that the trait originated from an early hybridisation event with Barbary Dove. Knowingly or unknowingly, hybrids are bred in captivity and, when escaped or released, can survive well in the wild and interbreed with pure Eurasian Collared Doves. It is known that around 1950 Eurasian Collared Doves were imported from India into Britain by dealers (Hudson 1965), and little imagination is needed to predict that at least some of those procured by aviculturists were mated with Barbary Doves to produce hybrids. Some may have escaped or been released. The fact is Ino Eurasian Collared Doves have been observed over the last 70 years in Britain (Goodwin 1973; Fig. 17).

Barbary Doves escaping captivity in spring or summer in western Europe often survive for months or even longer, and can interbreed with the Eurasian species. Just one

<sup>6</sup> I conducted unpublished research into behaviour, vocalisations and colour inheritance in Barbary Dove, Eurasian Collared Dove and their hybrids for >15 years (1990–2006). One bird was a female Eurasian Collared Dove with a colour similar to Ino in Barbary Dove. Found as fledgling in the wild, other than colour the individual possessed all of the morphological and behavioural characteristics of Eurasian Collared Dove (e.g. size, mass, eye colour, tail markings and call, which are all different from Barbary Dove). The female was crossed with an Ino male Barbary Dove. All of the offspring, of both sexes, were Ino-coloured. Also, further crosses (first-generation hybrids [F1] together and F1 with both parents) produced only Ino-coloured offspring. Whether the mutation of this female Eurasian Collared Dove originated from earlier hybridisation with Ino Barbary Dove or occurred spontaneously is unclear but, based on the breeding results, it appears to be the same as Ino in Barbary Dove. In crosses and back-crosses with normal-coloured Eurasian Collared Doves, colour inheritance of this Ino Eurasian Collared Dove matched Ino in Barbary Dove (in accordance with the gene being located on the Z-chromosome; among bird breeders referred to as ‘sex-linked inheritance’). In another experiment, Ino Barbary Doves (both sexes) were crossed with normal-coloured Eurasian Collared Doves, and the offspring (both sexes) successively back-crossed with Eurasian Collared Doves. Depending on which species was the male and female parent in the initial cross, after 3–5 generations of back-crossing, the Ino offspring were, in all characteristics other than colour, indistinguishable from Eurasian Collared Dove. Ino-coloured doves were identical to the Ino-coloured female Eurasian Collared Dove found as a fledgling in the wild. The normal-coloured offspring could not be distinguished from normal Eurasian Collared Doves.



Figure 10. Ino Eurasian Collared Dove *Streptopelia decaocto*, female, La Gomera, Canary Islands, March 2010; old and heavily bleached plumage (© Alois van Mingeroet)



Figure 11. Ino Eurasian Collared Dove *Streptopelia decaocto*, male, La Gomera, Canary Islands, March 2012; old and heavily bleached plumage (© Alois van Mingeroet)



Figure 12. Ino Eurasian Collared Dove *Streptopelia decaocto*, female, La Gomera, Canary Islands, April 2013; old and heavily bleached plumage (© Alois van Mingeroet)



Figure 13. Ino Eurasian Collared Dove *Streptopelia decaocto*, female, Lanzarote, Canary Islands, February 2018; old and heavily bleached plumage (© Nico van Wijk)



Figure 14. Ino Eurasian Collared Dove *Streptopelia decaocto*, female, Jodhpur, Rajasthan, India, March 2013; old and heavily bleached plumage (© Pranjal J. Saikia)



Figure 15. Ino Eurasian Collared Dove *Streptopelia decaocto*, female, Tórshavn, Faroe Islands, 28 May 2020; old and heavily bleached plumage. The species is rare on the islands with just ten breeding pairs (Jens-Kjeld Jensen *in litt.* 2020), so if this female and any subsequent male offspring breed, then the mutation could become established, just as leucistic Common Ravens *Corvus corax* did in the past (van Grouw 2014) (© Marita Gulckett)



Figure 16. Ino Eurasian Collared Dove *Streptopelia decaocto*, female, Enkhuizen, Noord Holland, the Netherlands, May 2011; old plumage bleached but fresh tertials show the colour caused by the Ino mutation prior to bleaching (© Jacob Jorritsma)



Figure 17. Ino Eurasian Collared Dove *Streptopelia decaocto*, juvenile, Ely, Cambridgeshire, England, April 2021; juvenile plumage still unbleached (© Ian Barton)

hybrid dove carrying the Ino mutation in its genome can introduce the mutation into the population. The gene which harbours the Ino mutation is located on the Z-chromosome (one of the sex-chromosomes). The sex-chromosome carrying the mutation will be passed from one generation to the next, while other characteristics of Barbary Dove become more 'diluted' in each generation, thus the third generation is morphologically identical to a pure Eurasian Collared Dove (see footnote 6). Depending on which species was the male and female parent of the first interspecific hybrid, to the human ear the call will be indistinguishable from Eurasian Collared Dove within five generations (see footnote 6).

In birds, males have two Z-chromosomes and females just one, so only males can possess two different alleles of any gene on the Z-chromosome. These males are heterozygous (i.e. possess two different alleles) for a mutation on the Z-chromosome. The allele for normal (wild) colour is dominant over Ino. Therefore, an Ino offspring is possible from a pair of normal-coloured Eurasian Collared Doves only if the male is heterozygous for the mutation. Ino offspring, however, are always female (van Grouw 2018). Ino males can only be the product of a female with the mutation paired to a heterozygous male. Ino Eurasian Collared Dove females have been recorded breeding but, as the mutation is still very rare in Europe, the chance of pairing with a heterozygous male is tiny. On the Canaries, where the number of Ino-coloured doves is much higher, Ino males are recorded (Fig. 11).

Although the origin of the Ino mutation in European doves is not always certain, in North America there seems little doubt it came from Barbary Dove, rather than recurrent mutation. As already stated, the first birds on the Bahamas escaped from an aviculturist who believed that his Eurasian Collared Doves were Barbary Doves (Smith 1987), so one can assume that at least some of the escapees were hybrids. The fact that throughout the species' current range in North America, from Mexico to Canada, aberrant-coloured Eurasian Collared Doves are recorded rather frequently (Contreras Balderas *et al.* 2011, Rodríguez-Ruíz *et al.* 2017, Hampton 2018), confirms the suggestion that among the founder population at least some carried interspecific genes.

In fact, in North America two different mutations are regularly encountered in Eurasian Collared Dove (Fig. 18), both of which are common in Barbary Dove. One is the aforementioned fawn-coloured Ino mutation (Fig. 19) but the other is a form of leucism, causing white plumage mixed with normal-coloured feathers (Fig. 20). It is a rather odd member of the group of mutations classified as leucism. In leucism white feathers are the result of the congenital and heritable absence of melanin-producing cells from some or all of the skin where they would normally provide the growing feather with melanin. The white pattern in normal leucism occurs already in juvenile plumage and the amount and pattern of white feathering does not change with age. In the form of leucism in Eurasian Collared Dove, however, juvenile plumage is rather different from adult plumage in which the final, static, mix of white and coloured feathers occurs. Instead, juvenile plumage is a mix of white and coloured barbs giving an overall 'grizzled' appearance (Figs. 21–22). Each juvenile feather is replaced by either a fully white or an entirely normal-coloured feather in adult plumage. This form of leucism is rare in birds but occurs in Barbary Dove. In fact, it is the only leucistic mutation present in this species in America, is rather popular among breeders, and is therefore commonly available. The origin of the same mutation in Eurasian Collared Dove in the USA does not therefore appear to be a mystery.

One mutation that certainly occurred in the Eurasian species is Brown (for details of this mutation in birds, see van Grouw 2021) as that mutation is not yet present in Barbary Dove. Brown is probably the commonest mutation in birds in general but remarkably is absent in certain species. It is also one of the first to occur in species bred in captivity and is common in Canary *Serinus canaria*, Budgerigar *Melopsittacus undulatus*, Zebra Finch



Figure 18. Eurasian Collared Doves *Streptopelia decaocto* showing different mutations (three Ino and one leucistic), Chandler, Arizona, USA, November 2015 (© Theo van Wallene)



Figure 19. Ino Eurasian Collared Dove *Streptopelia decaocto*, Chandler, Arizona, USA, November 2015 (© Theo van Wallene)



Figure 20. Leucistic Eurasian Collared Doves *Streptopelia decaocto*. (Top) Chandler, Arizona, USA, December 2015; different bird from that in Fig. 21 (© Theo van Wallene); (below) British Columbia, Canada, October 2014 (© John Gordon)



Figure 21. Leucistic Barbary Dove in full juvenile plumage; the entire feathering is an intermix of white and coloured barbs giving it a 'grizzled' appearance; each feather will be replaced by either a fully white or a normal-coloured feather in adult plumage (Hein van Grouw)



Figure 22. Leucistic Eurasian Collared Dove *Streptopelia decaocto* in partly juvenile plumage, Chandler, Arizona, USA, November 2015; all large wing feathers (primaries, secondaries and tertials) juvenile and still 'grizzled' due to the mix of white and coloured barbs, whereas in adult plumage these feathers are either all white or fully coloured (© Theo van Wallene)

*Taeniopygia castanotis*, many European finches (e.g. Common Chaffinch *Fringilla coelebs*, Eurasian Greenfinch *Chloris chloris*, European Goldfinch *Carduelis carduelis*), Japanese Quail *Coturnix japonica*, Muscovy Duck *Cairina moschata*, domestic duck *Anas platyrhynchos* and domestic pigeon *Columba livia*, to name a few. In chickens, which have been domesticated for millennia, the mutation occurred only as recently as 1994 (Carefoot 1996). In Barbary Dove it is unknown, yet. It is also rare in Eurasian Collared Dove, and I am aware of only a few cases.

Brown is, like Ino, caused by a single recessive genetic mutation on the Z-chromosome, and therefore mainly females with this mutation are encountered in the wild. The mutation also causes incomplete melanin synthesis but, in this case, only eumelanin is affected and remains dark brown instead of becoming black. Pheomelanin is unaffected and therefore a brown Eurasian Collared Dove is more reddish brown than an Ino (Fig. 23). However,



Figure 23. Brown Eurasian Collared Dove *Streptopelia decaocto*, NHMUK 1889.2.2.1516, collected in 1872 in Raipur, India; due to the mutation, incomplete oxidised melanin pigment is very light sensitive and bleaches rapidly, so old plumage can be nearly white, especially parts exposed continuously to sunlight, like the tips of the primaries and central tail feathers. Unlike Ino, in which both eumelanin and pheomelanin are incompletely oxidised, in Brown eumelanin alone is affected and pheomelanin is normal, so the plumage of a Brown Eurasian Collared Dove is more reddish brown than an Ino (© Aimee McArdle, Natural History Museum, London)



Figure 24. Brown female Eurasian Collared Dove *Streptopelia decaocto*, Herk-de-Stad, Belgium, August 2013, with old and strongly bleached plumage (© Jan Ruymen)

incompletely synthesised eumelanin caused by the mutation Brown is very light sensitive and bleaches rapidly in sunlight (Fig. 24). Within a couple of months, fresh, but aberrant, Brown plumage can become nearly white, making correct identification challenging.

### Impact of hybridisation

Hybridisation between wild species and their domestic counterparts—feral or free-ranging—is widely considered to threaten biodiversity. Interbreeding may result in the introgression of different alleles, shaped by artificial selection, into wild populations, with potential negative consequences, such as loss of genetic diversity, disruption of adaptation to local conditions or, ultimately, extinction (Rhymer *et al.* 1996, Allendorf *et al.* 2001, Randi 2008). Based on the many papers published on the subject, such concerns appear to be expressed mainly for iconic species like Wolf *Canis lupus* or Wildcat *Felis silvestris*, and species of economic interest such as Red Junglefowl *Gallus gallus*. Such hybridisation should be of equal concern for wild populations of, e.g. Rock Dove *Columba livia* and Mallard *Anas platyrhynchos*, but they do not seem to be on the radar of conservationists. The same applies to Greylag Goose *Anser anser* and its domestic counterpart, where interbreeding may even introduce alleles of another species into wild Greylags. There are two distinct domestic goose lineages, stemming from Greylag Goose and Swan Goose *Anser cygnoides* (Crawford 1990). Only a few original breeds still derive solely from one ancestral species, and most domestic geese are a mix of the two. Any feral ‘farmyard goose’ interbreeding with wild Greylags will contribute non-specific genes to the population. Even after many generations the influence of Swan Goose on Greylags can be seen in individuals with a visibly darker hindneck. At a molecular level the influence remains much longer, even forever. Its potential impact—negative or positive—on future Greylag populations is unknown (see Heikkinen *et al.* 2020).

Comparably, many Eurasian Collared Doves show evidence of traits of Barbary Dove in their genome, especially in areas where both species occur or occurred, for example in the Canaries and the USA. Based on the frequency of Ino individuals in other European populations, one can assume that Barbary Dove genes are more widespread than initially assumed. Due to the species' expansion this spread is not unexpected (Currat *et al.* 2008, Quilodran *et al.* 2020).

## Discussion

The North American population of Eurasian Collared Doves as a whole can be assumed to be impure. Because many of the founders were probably hybrids (see above), and the first doves to reach mainland Florida interbred with the local feral Barbary Doves (Smith 1987), this assumption seems likely. Further, the high frequency of colour aberrations commonly present in Barbary Dove that also occurs in the American population of Eurasian Collared Doves underlines the suggestion that the founder birds were impure.

Heritable colour morphs can have positive effects in the right habitat, whether they occur naturally in a population or through interbreeding. Coloration *per se* may not directly influence survival, but there is apparently a link between plumage colour and behavioural and physiological characteristics (e.g. greater resistance to stress, more aggression, and different metabolism) associated with survival. Thus, in some cases, colour morphs may behave differently due to their respective physiological properties and eventually, due to differences in behaviour / habitat choice, they may evolve into distinct taxa (van Grouw 2017). As many subspecies of birds in arid areas are often remarkably light coloured, the pale-coloured Ino Eurasian Collared Doves may do well in North American deserts and eventually evolve into a distinct taxon. Indeed, as the genome of all Eurasian Collared Doves in America probably includes some Barbary Dove genes, one may already consider them something other than *S. decacoto*. Over time, when the 'species' becomes well established in North America with several different colour morphs, they may warrant their own taxonomic status. Currently the genus *Streptopelia* includes 17 species (Dickinson & Remsen 2013). The North American Collared Dove might make number 18—deca-octo!

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### Appendix 1: How Eurasian Collared Dove got its name

According to an old legend from the Balkans, Eurasian Collared Dove was created by Zeus, god of sky and thunder, to fulfil the prayers of a poor maid. Paid only 18 pieces a year, she prayed to the gods for it to be made known how miserably she was rewarded for her labours by her hard-hearted mistress. Thereupon, Zeus created this dove to proclaim a voluble *deca-octo* [eighteen], which it still does. This story was told to Imre Frivaldszky (1799–1870) by Carl Hinke, who collected the first specimens for the Hungarian Natural History Museum in Budapest (Naumann 1837, Stresemann 1953). Based on this legend, Frivaldszky named the species *decaocto*. In different versions of the same tale Zeus transformed himself or the girl into a dove to proclaim ‘eighteen’ all over the world to shame the tight-fisted mistress.

Another folklore tale, from Asia Minor, which could be the basis of the dove’s name concerns a Roman soldier who took pity on Jesus on his way to Calvary (Stephanides 1957). The soldier wanted to give Jesus some milk but the milkmaid demanded 18 coins. He had only 17 and the seller refused to reduce her price, so when Christ was crucified, because of her meanness she was turned into a dove and condemned to repeat *deca-octo*, eighteen, for the rest of time, to punish and shame her. She would regain her human shape only if she consented to say *deca-epta*, seventeen. In some Balkan countries it was added that if the milkmaid, out of obstinacy, says *deka-enmaea*, nineteen, the world will end!

The message the dove was supposed to give—*deca-octo*—may not be immediately clear as this two-syllable word does not ‘fit’ the three-syllable call—*koo-KOO-kook*. However, in several Balkan languages the word eighteen is also a three-syllable word, e.g., *tiz-en-nyolc* (Hungarian) and *opt-spre-zece* (Romanian).

### Appendix 2: All the same

Eurasian Collared Doves from the Balkans through Central Asia (‘Turkestan’) to Korea and Japan are generally larger and paler than Indian birds. Because of this, Hume (1874) described the doves from Yarkand (in the modern Chinese autonomous province of Xinjiang) as a species and stated, ‘The Kashgar Ring Dove [Kashgar, in Yarkand; one of the westernmost cities of China] is certainly distinct from the Indian *risorius*’. The specimen he used was collected by Ferdinand Stoliczka in Kashgar on 5 February 1874 (Sharpe 1891) and Hume (1874) therefore named it *Turtur stoliczkae* (Figs. 25–26). For many years *stoliczkae* was often recognised as a subspecies of Eurasian Collared Dove (e.g. Roonwal 1940, Goodwin 1983) based on supposed differences from the nominate, but these are now considered insignificant. Frivaldszky (1838) based his name *decaocto* on doves in the Balkans, so *stoliczkae* of Hume, who evidently was unfamiliar with Frivaldszky’s work, is a junior synonym of *decaocto*. The same is true for *torquata* Bogdanow, 1881, from Turkestan, *zarudnyi* Serebrovski, 1927 (Fig. 27), from eastern Iran, and *koreensis* Buturlin, 1934, from Korea, which are all considered junior synonyms of *decaocto*.

### Appendix 3: Ino explained

The term ‘Ino’ (from the Greek or Latin *Ine* = ‘belonging to’ or ‘like’) is used in European aviculture for the pale form (sex-linked imperfect albinism) of captive birds such as finches and parrots. Although Ino mutations can be categorised as a form of albinism, they are not albino and many are far from white. The causes of Ino are variations in a gene called SLC45A2 which codes for the protein ‘solute carrier family 45 member 2’ in melanin cells. Although the precise function of SLC45A2 is unknown, it probably transports molecules necessary for normal melanin synthesis (Domyan *et al.* 2014). Several different mutations (alleles)



Figure 25. Type specimen of *Turtur stoliczkae*, ZSI 26534, National Zoological Collections of the Zoological Survey of India, Indian Museum, Kolkata, named by Hume (1874) for Ferdinand Stoliczka who collected it on 5 February 1874 in Yarkand. For more than 100 years *stoliczkae* was recognised as a subspecies of Eurasian Collared Dove but is now considered a junior synonym of *decaocto* (© Zoological Survey of India , Kolkata)



Figure 26. Pl. 14 of Hume's *Turtur stoliczkae* in Sharpe (1891) (Hein van Grouw, © Natural History Museum, London)

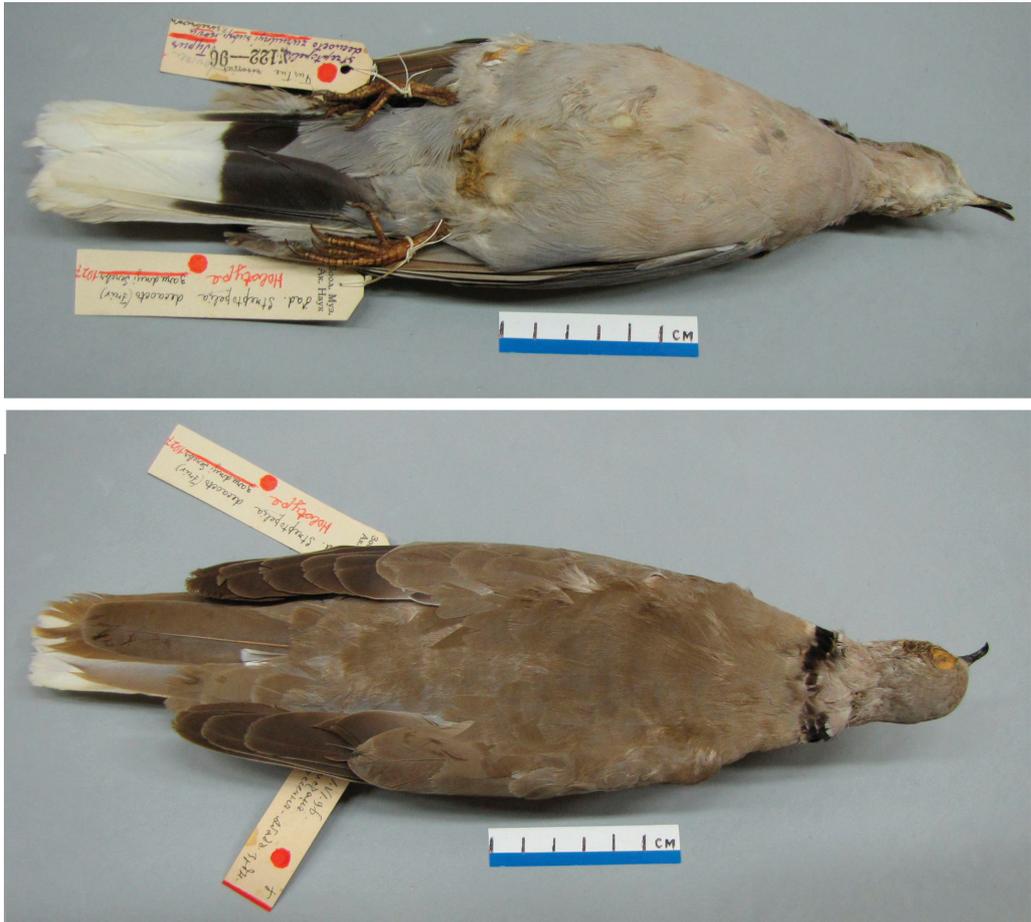


Figure 27. Type specimen of *Streptopelia decaocto zarudnyi*, collected in east Iran on 13 June 1896 by N. Zarudny, ZIN 32107/122-96, Zoological Museum of the Zoological Institute, Russian Academy of Sciences, St Petersburg; the name *zarudnyi* is now a junior synonym of *decaocto* (© ZIN, St Petersburg)

of the SLC45A2 gene, which is located on the Z-chromosome in birds, are known in different species (Gunnarsson *et al.* 2007). These mutations have different effects on the final melanin pigmentation. In some, hardly any melanin is produced, resulting in near-white plumage, whilst in others the plumage is only slightly paler than normal.

The near-white form is often called sex-linked imperfect albinism (Gunnarsson *et al.* 2007) due to its inheritance, and because the plumage is nearly white. In medical science it is known as Oculocutaneous Albinism type 4 (Lamoreux *et al.* 2010). For the darker (less pale) forms, many different names are employed, frequently based on those used in aviculture. I term all mutations of the SLC45A2 gene, Ino.

A common and widespread phenotype in the domestic pigeon, also resulting from a mutation of the SLC45A2 gene, is 'dilution' (Domyan *et al.* 2014, Domyan & Shapiro 2017). Breeding (hybridising) tests conducted by myself and others (Cole & Hollander 1950) have indicated that Ino in Barbary Dove (often also called 'blond' or 'fawn'), and Dilution in the domestic pigeon, are genetically essentially the same, and therefore it can be assumed Ino in Barbary Dove is also the result of variation in the SLC45A2 gene.

# The status and distribution of three species of *Sternula* terns on the eastern coast of Africa and in the western Indian Ocean, with two species new for Mozambique

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**SUMMARY.**—The status of three *Sternula* terns in southern and eastern Africa and the Indian Ocean is updated based on observations in Mozambique during October 2009–August 2021. Damara Tern *S. balaenarum* and Saunders’s Tern *S. saundersi*, both new to Mozambique, were found at the San Sebastian Peninsula in August 2018 and have been recorded regularly since. Damara Tern arrived in May, numbers were lower June–July, with a peak of 100+ in August–October. Breeding plumage was assumed by late October and all departed in early November; those aged were all adults. Observations of ringed birds suggested they originated from colonies in South Africa. Numbers of Damara Tern reached the Key Biodiversity Area designation threshold population for the site in 2020. These are the first records of large numbers of Damara Tern in the Indian Ocean, whilst timings suggest the species is partly transient at the site and may also occur further north. Saunders’s Tern was recorded at San Sebastian in all months except March and April, with 5–80 regularly present, and peak numbers perhaps in October–December. Birds were observed in a range of plumages in all months, from non-breeding, transitional to full breeding. Courtship feeding was observed in September–November suggesting at least some attempt to breed locally, although disturbance is high. Birds in non-breeding plumage may stem from Northern Hemisphere breeding localities. Little Tern *S. albifrons* was a numerous migrant in southern Mozambique in October–May, peaking in April when large numbers were observed during pelagic trips to the continental shelf edge, and at onshore roost sites including San Sebastian. Smaller numbers fed in coastal lagoons and freshwater lakes. Three Little Terns had been colour-ringed in Israel.

Allport (2018) reported significant records of selected tern and gull species from Mozambique for the period October 2010–August 2017. *Sternula* terns were not covered in that paper but the first records of Damara Tern *Sternula balaenarum* and Saunders’s Tern *S. saundersi* in Mozambique along with an update on the status of Little Tern *S. albifrons* are reported herein. The findings provide new insights into the distributions of *Sternula* in eastern Africa and the Indian Ocean which we detail below, with comments on identification and areas for future study.

Observations were made across the range of sites outlined in Allport (2018) plus data from 24 trips to the San Sebastian Peninsula, April 2018–August 2021, in the Santuário Bravio de Vilanculos (22°07'46"S, 35°32'37"E, known as ‘the Sanctuary’) including visits to Ilha Linene sandbanks by boat (see Appendix 1 for dates and observer details). Many of the observers were visiting to see the newly discovered birds reported herein and timings were inconsistent across tides and time of day.

Damara and Saunders’s Terns are monotypic, but Little Tern has at least five subspecies (Gochfeld *et al.* 2020a) of which the nominate occurs widely in eastern and southern Africa.

The East Asian and Australasian race *sinensis* (sometimes treated as a separate species, Eastern Little Tern, the limits of which are still to be defined; Cramp 1985, Higgins & Davies 1996) is a potential visitor to the western Indian Ocean (Urban *et al.* 1986).

Saunders's Tern was treated as a species by Vaurie (1965) and Voous (1973), and all modern taxonomies have followed this (IOC 2020). There has, however, been no comprehensive taxonomic review and no DNA analysis of the Little / Saunders's Tern group to date (J. M. Collinson *in litt.* 2019).

#### **DAMARA TERN** *Sternula balaenarum*

Nests colonially on beaches of Angola, Namibia and South Africa, south and east to the Indian Ocean at Algoa Bay, Eastern Cape, where the largest colony in South Africa increased to 45 pairs in 2018/19 (Martin 2019). It breeds in the austral summer with peak laying in late October–December at most colonies (Hockey *et al.* 2005, Whittington *et al.* 2015, Martin 2019). Nearly all leave southern Africa for non-breeding grounds on the West Africa coast. Departure starts in April, with birds moving north and coalescing into larger flocks in northern Namibia. From there, they migrate to the Gulf of Guinea, sparingly reaching as far west as Ghana to Senegal (Wallace 1973, Urban *et al.* 1986, Borrow & Demey 2001, Hockey *et al.* 2005, Braby 2010). Oceanic upwellings off the West African coast peak in September coinciding with the species' presence in the region (Hockey *et al.* 2005).

Damara Tern is considered absent from the Indian Ocean, after Feare & Bourne (1978) demonstrated that accounts of hundreds in Seychelles (Mountford 1971, Penny 1974) were erroneous. More recently there has been three records on the coast of KwaZulu-Natal, in September–October 2013 (KwaZulu-Natal Rare Birds Database; D. Cyrus *in litt.* 2019). The species occurs only in coastal waters with no records at freshwater sites (Hockey *et al.* 2005).

Damara Tern can be identified from other *Sternula* in breeding plumage by its full dark brown cap and nape (appearing black in the field) and uniform grey upperparts, paler than, and without the contrasting paler rump and tail of, adult Little Tern. When not in wing moult, adults show less contrast between the inner and outer primaries than other *Sternula* but can do so when in primary moult (Hockey *et al.* 2005). The bill is black at all ages (with a pale yellowish base to the mandible visible at close range) and, whilst not longer than other *Sternula* (Hockey *et al.* 2005), it appears noticeably slimmer, narrower-tipped and more pointed than sibling species. Non-breeding plumage is not well studied but in Eastern Cape, adults lose their brown cap in April–May, with the lores, forehead and mid-crown white, and grey mottling in the dark brown hindcrown; the breeding head pattern is reassumed in August–September. Adult primary moult probably commences at the end of breeding and has been noted as halfway complete in July (Hockey *et al.* 2005) but is otherwise little known (M. Boorman *in litt.* 2021).

**Recent records in Mozambique.**—On 6 August 2018 GA & DG visited the tidal roost at Chichuene, colloquially known as 'Rattray's Point', on the ocean beach of the San Sebastian Peninsula, east of Ilha Linene in the Sanctuary (22°07'46.2''S 35°32'37.9''E) where c.1,500 terns were seen and photographed. Some of the images involved c.30 small terns in non-breeding plumage with a grizzled hindcrown, finely tapered all-black bill and uniform pale upperwings showing less contrast in the outer primaries than is usual in Little and Saunders's Terns (Fig. 1). GA suspected they were Damara Terns but was not very familiar with the species and a record involving so many so far outside its known range seemed improbable. After consulting the late A. J. Tree, the record was considered tentative despite the documentation. However, on 28 September 2018 at the same location DG photographed one of six in more advanced breeding plumage with an all-black crown, confirming the identification (Fig. 2). None was recorded during the next visit on 31 December 2018.



Figure 1. Damara Tern *Sterna balaenarum* (above) and Saunders's Tern *S. saundersi* (below; this individual identified from other images), Rattray's Point, San Sebastian Peninsula, Mozambique, 6 August 2018; note fine-tipped all-dark bill, grizzled crown, forehead and above eye, and relatively pale outer primaries of Damara Tern (Gary Allport)



Figure 2. Damara Tern *Sternula balaenarum*, Rattray's Point, San Sebastian Peninsula, Mozambique, 28 September 2018; diagnostic all-dark cap and nape in breeding plumage (David Gilroy)



Figure 3. Part of a flock of Damara Terns *Sternula balaenarum*, including one Saunders's Tern *S. saundersi* and four *Sternula* spp., San Sebastian, Mozambique, 30 October 2019 (Niall Perrins)

On 2 September 2019 CR found 29 Damara Terns in breeding plumage at Rattray's Point, and DG observed 17+ there on 15 September. With increasing observer interest, larger numbers were found, all loafing on the same area of sandbanks, including 75 on 18 September and a max. 100+ on 24–28 October. Numbers then quickly declined to single figures by mid November. In 2020 none was seen in two visits in February, but 15–25 were recorded in May–July. In 2021 none was seen in January, but 80 in May and 106 in August (Appendix 1).

This suggests a decline in numbers at the site from late October and absence from mid November to May (Table 1), consistent with attendance at breeding colonies further south. There is a suggestion of greater numbers on arrival in May (one count of 80), then a continuous presence until peak counts in late August and October. However, data are still meagre and numbers at the one known accessible site in the San Sebastian / Bazaruto area are likely to vary with local conditions.

A single was photographed with a metal ring on its left leg in August 2018, and two ringed birds were seen on 18 September 2019, one with a metal ring on the left leg and a white flag on the right. Details are unclear but it is almost certain that the latter individual was marked at Algoa Bay, South Africa, as a breeding adult on 3 December 2008, making it at least 13 years old at the time (P. Whittington *in litt.* to M. Boorman 2020 and *in litt.* to CR 2021).

The finding of this threatened bird on the Indian Ocean coastline >1,500 km north of all previous records was unexpected. The birds at San Sebastian seem most likely to originate from breeding colonies in the Eastern Cape, South Africa, where recent shifts east in some seabird populations have occurred, possibly due to climate-driven changes in relative

abundance of fish in coastal waters (Blamey *et al.* 2015). Occurrence in Mozambique may be a quite recent phenomenon reflecting a local shift in breeding but a significant change for post-breeding migration, affording more direct access to the Indian Ocean. Indeed, a direct link from the Algoa Bay colony to the Mozambique non-breeders has already been speculated (Martin 2019).

The birds at San Sebastian may involve individuals present throughout the non-breeding season, as well as others on passage to as yet unknown wintering grounds further north. Our limited data show peaks in May and August–October suggesting stop-over and possibly congregating northbound migrants (as in Namibia; Braby 2010), and return to colonies in late October–November. Were these birds to travel as far north as they do in West Africa (*c.*07°N) then the Somali coast would be within range. Observers in eastern Africa should consider this species in the identification of any *Sternula* observed (see below). Further ringing studies of Damara Terns will be attempted at San Sebastian in the near future.

**Global conservation importance.**—Recent advances in the recognition of sites of global importance for biodiversity conservation have led to the development of the Key Biodiversity Areas programme (KBAs; IUCN 2016). This builds on the Important Bird & Biodiversity Areas (IBA) programme of BirdLife International, to identify sites important for all biodiversity using a new global standard (IUCN 2016). This new methodology has been applied by the Ministry of Land & Environment in Mozambique supported by a working group facilitated by the Wildlife Conservation Society, with ornithological input by national institutions and BirdLife International (GA). The first inventory of Mozambique IBAs (Parker 2001) identified the Bazaruto Archipelago as an IBA, the southern limit of which abuts the northern border of the Sanctuary.

The global population of Damara Tern is estimated at 9,000 birds but is decreasing and the species is considered globally Vulnerable by BirdLife International (Braby *et al.* 1992,

TABLE 1

Counts of *Sternula* terns at Rattray's Point, Santuário Bravio de Vilanculos, San Sebastian Peninsula, Vilanculos District, Mozambique, 2018–21. Site visits were of 1–4 days duration and maxima were taken when there was a range of counts during a site visit. Count data are grouped by month across years and presented in ascending order; zeros indicate that the observers confidently assessed genuine absence (see full data in Appendix 1).

Month	Count visits	Little Tern	Saunders's Tern	Damara Tern
January	2	26	30	0
February	2	206, 1,200	11, 15	0, 0
March	1	230	0	0
April	1	25		
May	2	0, 1	4, 15	40, 80
June	1	0	25	25
July	1	1	20	20
August	3	0, 1, 10	4, 5, 6	29, 80, 106
September	3	1, 200	0, 4, 15	6+, 29, 75
October	4	0, 70, 140	10, 15, 80	0, 2, 50+, 100+
November	3	5, 26, 60	0, 1, 2	0, 8, 11
December	1	70	26	0
Total 24				

Braby 2011, Crawford *et al.* 2018, BirdLife International 2020) and regionally as Critically Endangered (Taylor *et al.* 2015).

The KBA threshold for a site holding a species categorised as Vulnerable is >1% of the global population, which in Damara Tern equates to 90 birds. Counts at the Sanctuary exceeded this in October 2019 and August 2021 (Table 1, Appendix 1), thus the site qualified and is included along with the national park as a single KBA 'Grande Bazaruto' (<https://wcs-global.maps.arcgis.com/apps/Shortlist/index.html?appid=2b6445c402514b81a0ed327b081ea12c>). Bazaruto National Park might also be expected to hold Damara Terns.

#### LITTLE TERN *S. albifrons* / SAUNDERS'S TERN *S. saundersi*

These are phenotypically and, to a lesser extent, ecologically similar, temperate- to tropical-breeding terns. They range from locally resident to long-distance migrants in the region (Urban *et al.* 1986).

**Identification.**—The diagnostic characters of Saunders's Tern have been the subject of debate and there is inconsistency in the ornithological literature, but most authors agree (e.g., Cramp 1985, Chandler & Wilds 1994, Olsen & Larsson 1995a,b, Sinclair & Ryan 2010, Gochfeld *et al.* 2020b) that a small suite of characters can be used to distinguish adult Saunders's Tern in breeding plumage from Little Tern (Table 2). These characters are given for breeding-plumaged birds in Afrotropical field guides (e.g., Stevenson & Fanshawe 2002, Sinclair & Ryan 2010).

There has been much discussion in the literature concerning the separation of Little and Saunders's Terns in non-breeding plumages but no consistent characters have emerged (Cramp 1985, Olsen & Larsson 1995a,b). The status of Saunders's Tern, especially in the non-breeding season, is thus tentatively reported in the region's major ornithological works.

A recent detailed analysis based on birds of known identity in the Persian Gulf by Mullarney & Campbell (2022) has advanced the identification criteria of Little and Saunders's Terns. They stressed the importance of inner wing pattern in breeding and non-breeding plumages, finding that fresh-plumaged Little Terns show a relatively darker upperside to the inner wing with a clear white trailing edge to the secondaries; in Saunders's Tern this is consistently paler, often near-white, with less contrast. There is also evidence to suggest that non-breeding head pattern differs, with Saunders's having a narrower dark line through the eye and more white on the rear crown. The status overview of the two species below is as reported in the current literature but this will require significant revision in light of Mullarney & Campbell (2022).

**Breeding ranges.**—*S. a. albifrons* is a Palearctic–Afrotropical migrant, breeding from coastal north-west Europe through the Mediterranean (Cramp 1985, Habib 2016a) and the Middle East to islands in the Persian Gulf and northern Red Sea (Cramp 1985, Hollom *et al.* 1988). Inland, it breeds widely in Russia east of *c.*28°E and south of *c.*57°N, Central Asia to Afghanistan and, further south-east, the Indus Basin in India (Vaurie 1965, Rasmussen & Anderton 2012). Nesting of *S. a. albifrons* on Diego Garcia, Chagos Archipelago in the central Indian Ocean reported by Carr (2005; based on Bruner 1995 and Symens 1999) represented a significant southward extension of this taxon's breeding range. However, subsequently Carr (2011, 2015) suggested that these breeding birds may be Saunders's Terns, although this remains unclear.

Little Tern is typically a coastal and colonial breeder in north-west Europe and the Mediterranean, but also nests inland on lakes and broad rivers mostly in the Middle East and in its mainland Asian range (Cramp 1985).

Saunders's Tern breeds in small colonies on coasts of the Red Sea, north to at least Yanbu in Saudi Arabia (Boland & Alsuhaybany 2020, Almalki 2021), Eritrea (Semere *et al.*

TABLE 2  
 Characters to distinguish breeding plumage adult Saunders's Terns *Sternula saundersi* from Little Tern *S. albifrons* (see text for sources).

Saunders's Tern	Little Tern
White patch on forehead smaller and squarer, ending before leading edge of eye	White patch on forehead more triangular and extends as supercilium above the eye
Black outer primaries with faint grey bloom, forming a clear block of usually three, sometimes more, feathers in outer wing	Normally one or two black outer primaries
Moult of second series of primaries arrested at p7 (hence three outer primaries dark)	Moult arrested at p8 or p9
Paler pearl-grey on upperside, especially mantle, with less contrast to rump and tail	Darker lead-grey back, usually with contrasting paler rump
Olive or brown feet, yellow only on rear tarsus and soles	Yellow or yellowish-orange feet and legs
Preference for saltwater	Found widely in both fresh- and saltwater habitats

2008) and south to Socotra (Porter & Suleiman 2014) and southern Somalia (Ash & Miskell 1983, Urban *et al.* 1986), east on coasts of Oman and the Persian Gulf (Hollom *et al.* 1988) to north-west India and northern Sri Lanka (Rasmussen & Anderton 2012, Panagoda *et al.* 2020). It has not hitherto been clear if it is locally resident in the Red Sea and Persian Gulf, but using new identification characters Mullarney & Campbell (2022) found Saunders's Tern to be absent from this region in September–March.

There have been recent breeding records in Sinai, Egypt (Habib 2014, 2016a,b) but birds showing intermediate characters between *saundersi* and *albifrons* have been found in the northern Red Sea, casting doubt on the status in this region (Y. Perlman *in litt.* 2019). The presence of Saunders's Tern in Sinai is, however, clear (O. Campbell *in litt.* 2021).

It was reported as a 'numerous resident throughout the Maldives' by Ash & Shafeeg (1994) but no specimens in (diagnostic) breeding plumage were located by Rasmussen & Anderton (2012) and the only report of breeding, from North Malé Atoll in March–April (Phillips & Sims 1958), lacks details. There are recent anecdotal reports of breeding at Huvadhoo Atoll (in the south) but these lack confirmation (Shafeeg 1993, Anderson 2007, Anderson & Shimal 2020; C. Anderson *in litt.* 2021). A small number of 'Little Terns' nesting on Diego Garcia (Bruner 1995, Symens 1999, McGowan *et al.* 2008) were implied to be Saunders's Terns by Carr (2015). A single adult Saunders's Tern photographed on Diego Garcia in May 2005 was present in the likely breeding season and was reported at the time as the first record for the territory (Carr 2005: 39). This is potentially the species' southernmost breeding locality.

The breeding ranges of Little and Saunders's Tern reportedly overlap in the northern Red Sea, Persian Gulf and coastal Sri Lanka (Cramp 1985). In the Red Sea and Persian Gulf, the two select different nesting habitats: Saunders's is coastal whilst Little Tern breeds on inland freshwater bodies (Jennings 2010; O. Campbell *in litt.* 2021). Recent work by Panagoda *et al.* (2020) appears to be the first to document syntopic breeding of these species in mixed colonies (estimates of 560 pairs of Saunders's and 115 pairs of Little Terns *S. a. sinensis*; S. Seneviratne *in litt.* 2021) in north-west Sri Lanka. They found Saunders's differed

from Little Tern in smaller clutch and nest size, and nested at higher densities. Previously reported differences between the two species in egg coloration were confirmed (Wait 1931, Baker 1935, Urban *et al.* 1986). There was no difference in courtship displays but also no observations of mixed pairs. This study supported the separation of these two species but further work where *S. saundersi* and *S. a. albifrons* breed in sympatry would help to examine species limits more fully.

The breeding season is earlier in the western part of the range of Saunders's Tern. In the Red Sea nesting is reportedly in February–late April (Newton 2006) or late March–June (Jennings 2010), with egg-laying dates from the end of February to early June on the Farasan Islands, in the southern Red Sea (Almalki 2021). In the Persian Gulf breeders arrive in late February–March and begin breeding immediately, with fledging by mid May, departure commencing June–early July, the majority gone by late August and a few records to October (Mullarney & Campbell 2022; O. Campbell *in litt.* 2021). In Sri Lanka the season is later with birds on eggs and with chicks in May–June, and the season reportedly lasting until September (Panagoda *et al.* 2020; S. Seneviratne *in litt.* 2021). North (1945) reported Saunders's Terns breeding at Brava, Somaliland (now Barawa, Somalia) in August but it is unclear at what stage these birds were.

**Non-breeding ranges.**—All populations of *S. a. albifrons* migrate south in the boreal winter (Cramp 1985) to western, eastern and southern Africa (Urban *et al.* 1986); it is reported to be absent from North Africa at this season (Hollom *et al.* 1988).

In southern Africa, Little Tern is uncommon in the Western and Eastern Cape but is locally common on lagoons and shores of the Indian Ocean coast from central KwaZulu-Natal north through Mozambique (Clancey 1982, 1996, Hockey *et al.* 2005). Southern African birds are thought to breed in western Europe or the Mediterranean (Cramp 1985), although given the mainly easterly distribution in the region, Central Asian origin has been considered likely (Hockey *et al.* 2005). A lack of inland records suggests birds travel south along the coast but there are few published records to support this (Urban *et al.* 1988). There are no confirmed / published records of Little Tern in Madagascar (Safford & Hawkins 2013) but Mullarney & Campbell (2022) found those non-breeders identifiable to species (photographs on eBird) to be Little Terns. This species initially arrives in southern Africa in August, with peak counts in October–March, but small numbers reportedly occur year-round (Hockey *et al.* 2005).

Nominate *albifrons* also migrates through Afghanistan and Pakistan to the Indian Ocean and winters on the west coast of India south to Mumbai. It may be a regular winter visitor to the Maldives (Phillips 1963, Ash & Shafeeg 1994) but no details have been published (Rasmussen & Anderton 2012). There are, however, five recent sightings of birds in breeding plumage in February–April by observers aware of the identification issues (Anderson 2007; C. Anderson *in litt.* 2021). Little Tern is not thought to occur further south in the central Indian Ocean as all Seychelles records have been carefully assessed and nearly all those positively identified are Saunders's (four records of Little Tern; Skerrett & Disley 2011, Safford & Hawkins 2013, Skerrett *et al.* 2017). Mullarney & Campbell (2022) found one further record of Little Tern in Seychelles (November 2004; <https://ebird.org/checklist/S76069671>) but all other records involved *S. saundersi*. Specimens and sightings of birds with dark primary shafts, previously identified as Saunders's Terns, in western Thailand and Peninsular Malaysia (Sibley & Monroe 1990, Chandler & Wilds 1994) were re-identified by Wells (1999) as *S. a. albifrons* (this taxon's easternmost records). Wells (1999) suggested these birds presumably originate from the Asian breeding range.

Eastern *S. a. sinensis* may occur regularly in Africa in the non-breeding season but the only evidence involves a bird ringed as a chick in Java, Indonesia, recovered in Ghana

(Cramp 1985, Urban *et al.* 1986). This taxon breeds in Sri Lanka (Rasmussen & Anderton 2012) but was found not to occur in the Seychelles by Feare & Bourne (1978), and there is only one record in the Chagos Archipelago (Carr 2005), suggesting it does not regularly reach west of the central Indian Ocean.

Saunders's Tern is thought to winter in the southern Red Sea, Somalia and Socotra where it was reported to be resident by Urban *et al.* (1986), but published accounts are non-committal or lack details (Ash & Miskell 1983, Porter & Suleiman 2014). It was reported to be seasonally present in coastal Kenya and Tanzania (Britton 1980, Urban *et al.* 1986), however Mullarney & Campbell (2022) by reviewing photographs on eBird found that non-breeders from Saudi Arabia, Yemen, Socotra, Oman, Kenya and Tanzania were all Little Terns, thereby significantly altering our understanding of the non-breeding range of both species. In Madagascar, Saunders's Tern has been reported on the west coast south to at least Toliara, in November–March, with some to May and one in July (Safford & Hawkins 2013). Mullarney & Campbell (2022) again found eBird images to be mainly Little Terns but at least one Saunders's Tern was photographed at Nosy Ve.

The full extent of the winter range of Saunders's Tern is unclear, due to identification difficulties, but in the central Indian Ocean it likely involves substantial numbers in the Maldives (Anderson & Shimal 2020; C. Anderson *in litt.* 2021). A careful review of records in Seychelles concluded that it is present September–April with observations in all months except June (Feare & Bourne 1978, Skerrett & Disley 2011, Safford & Hawkins 2013). The largest number is 1,800 at St François Atoll (March 2007), with up to 800 at Aldabra (October) and 200–300 on Bird Island in September–April, with max. 380 in December (Safford & Hawkins 2013). Numbers on St François consistently exceed IBA thresholds (Adam *et al.* 2009). Mullarney & Campbell (2020) confirmed these identifications from a small sample of images, finding Saunders's Terns at Bird and Farquhar Islands and Aldabra. Small numbers have been seen in Comoros, Mauritius and Rodrigues (Safford & Hawkins 2013). It has also been recorded on the west coast of India in winter including the Laccadives (Rasmussen & Anderton 2012, Aju *et al.* 2021) but status in Sri Lanka is unclear. Saunders & Salvin (1896) reported three immature specimens collected by E. W. Oates in 'lower Pegu, Burma' (presumably the Gulf of Martaban near the town of Bago, Myanmar); their identity requires confirmation. There are recent confirmed records on Cocos (Keeling) Island where it has been regularly reported since 2006 (two records accepted by the Birds Australia Rarities Committee; Carter & McAllan 2007, Jackett *et al.* 2020) with up to 15 apparently present November–March (eBird records annual 2010–21). This appears to be the south-eastern limit of non-breeders, as there are no records in Indonesia or continental Australia.

Saunders's Tern was first reported in southern Africa by Saunders & Salvin (1896) based on three specimens from Durban Bay (see Appendix 2) and it was admitted to the southern African list accordingly. Two of these specimens were re-examined by Clancey (1982) and were considered to be *S. a. albifrons*; on which basis he retrospectively substantiated his prior removal of *S. saundersi* from the regional list (Clancey 1980). As part of the present study two of these specimens were examined by GA at the Natural History Museum, Tring, and found to be non-breeding *S. a. albifrons* (using identification criteria in Mullarney & Campbell 2020). Photographs of the third specimen, at Naturalis Biodiversity Center, Leiden, revealed it to be a nominate Little Tern. These findings uphold Clancey's (1980) decision to exclude *S. saundersi* from the southern African list.

Saunders's Tern occurs solely in marine habitats and is rare, possibly unknown, inland, although it has been reported to forage in saline ponds and salt pans (Safford & Hawkins 2013; for reasons given above, the latter may have been Little Terns).



Figure 4. Little Terns *Sternula a. albifrons* were common on pelagic trips off southern Mozambique, October–April, but infrequent and occurred in small numbers onshore except at a small number of undisturbed roost sites, or in bad weather. Maputo Bay, Mozambique, 23 February 2016 (Callan Cohen)

**Recent records in Mozambique.**—In nine years of observations in southern Mozambique Little / Saunders’s Terns were recorded in every month (2010–19; GA pers. obs.), but positive identifications were determined only for birds in breeding plumage. There were a small number of positively identified Little Terns in late September and more as they attained breeding plumage in February–April. No field observations of birds in the period October–January were considered identifiable to species and they were treated as Little / Saunders’s but all photographs were re-examined in light of Mullarney & Campbell (2020) and all those identifiable were Little. The majority of non-breeding plumage birds were probably Little rather than Saunders’s Terns. Where subspecific identification was possible, all were *S. a. albifrons* and *sinensis* was not suspected.

Little Tern is thus a numerous migrant in southern Mozambique in October–May. They arrived in late September in small numbers and were observed in groups of up to 200 on pelagic trips from Maputo. Despite significant numbers offshore in this period only a few in non-breeding plumage (1–30) were found on beaches or feeding over lagoons and salt pans, usually with other terns but sometimes resting onshore in groups during stormy weather (Fig. 4). Largest numbers were seen from pelagic trips off Maputo in March–April. Tight flocks of up to 300 were observed, presumably on passage over the continental shelf edge, which sometimes paused to join other terns feeding over shoals of Yellowfin Tuna *Thunnus albacares*. The max. count was of 1,000 Little Terns on 25 April 2013 and the latest seasonal records were 140 on 22 May and ten on 30 June. There were six records of Little / Saunders’s Terns in non-breeding plumage (presumably second-calendar-year birds) during June–September, all on coastal beaches and lagoons. The offshore sightings broadly match reports by Lambert (2005) who recorded 50–200 Little / Saunders’s Terns per day offshore from Zavora to Bazaruto in March–April 1987–89.

Observations at San Sebastian showed a similar annual pattern with small numbers in August, then up to 200 in non-breeding plumage during the austral summer followed by a period when breeding-plumaged Little Terns, presumably on passage, were present in larger numbers (max. 1,200 on 11 February 2020; Table 1, Appendix 1). Little Tern has also been reported from the islands of adjacent Bazaruto National Park (Downs & Wirminghaus 1997) with January counts of 90 in 1996 (Kohler & Kohler 1996, Dodman & Taylor 1996), 1,515 in 1997 (Dodman *et al.* 1997) and 831 in 1998 (Dodman *et al.* 1999).

A few Little Terns were seen at inland rain-fed freshwater lagoons in the Sanctuary at San Sebastian and, further south 10–140 birds (max. on 23 May 2015) were seen in December–May on inland freshwater bodies at Lagoa Xingute, Maputo Special Reserve (26°30′28.3″S, 32°48′43.5″E).

Three Little Terns were seen at the Sanctuary bearing white Darvic rings with two-letter codes. Unfortunately, none was legible in the field, but they were almost certainly marked

in Israel (Y. Kiat *in litt.* 2019). This observation supports the hypothesis that Little Terns in Mozambique originate from the eastern European breeding range (Hockey *et al.* 2005).

In summary, the overall pattern of occurrence of Little Tern in southern Mozambique is of coastal passage in September–November with fewer during November–early March and then stronger passage in April. This suggests that most Little Terns in this part of the Indian Ocean spend the boreal winter further south than Mozambique, but it is also possible that there are more substantial numbers offshore at this time.

On 6 August 2018 GA & DG visited the tern and wader roost at Rattray's Point, San Sebastian. A *Sternula* in breeding plumage was found that showed features including reduced square-cut white frons, pale grey mantle and contrastingly dark outer primaries (Fig. 5). GA suspected this to be a Saunders's Tern but as the photographs were not of high quality, none showed the bird in flight and just a singleton was involved—in consultation with the late A. J. Tree—the record was then considered tentative.

However, on 2 September 2019, CR visited the site again and, among several thousand terns, saw a group of four *Sternula* with the features of Saunders's Tern (Fig. 6) confirming the identity of the individual seen in 2018. These birds were in full breeding dress and engaged in courtship-feeding. There were further sightings on 15 September (DG) and 15 were found on 18 September in loose groups of up to six, including four courtship-feeding, probably the same as on 2 September (CR, J. R. Nicolau *et al.*). The species was seen by several observers during 4 October–17 November 2019, including up to 20 in breeding plumage and possibly as many as 60 in non-breeding plumage (Appendix 1).

Saunders's Terns were seen in small numbers (2–30) during nearly all subsequent visits, with records in all months except March and April (Table 1, Appendix 1) and birds in breeding plumage peaked at up to 20 in September–November. Photographs of the birds were checked and the identifications confirmed using the criteria of Mullarney & Campbell (2022). In addition, three birds in transitional plumage and two in non-breeding plumage were identified from photographs taken on 6 August 2018 and at least 26 Saunders's Terns in transitional and full non-breeding plumage on 31 December 2018 (Fig. 7).

Based on Little Terns (Cramp 1985), the behaviours observed in September 2019 were interpreted as at least one pair in courtship with a male carrying fish, 'parading', and a female adopting a receptive 'hunched' posture (Fig. 6A) followed, after presentation of the fish, by 'erect-posture' by both birds (Fig. 6B). This type of courtship-feeding is thought to establish and maintain pair bonds and is normally a pre-requisite to successful copulation, but the behavioural sequence observed in Little Terns prior to copulation is different from courtship-feeding (Cramp 1985) and we did not observe attempted copulation by Saunders's Terns.



Figure 5. Saunders's Tern *Sternula saundersi*, Rattray's Point, San Sebastian Peninsula, Mozambique, 6 August 2018; first record for Mozambique and southern Africa. Note square-cut white forehead not extending above eye, at least three dark outer primaries and contrastingly pale, pearly-washed mantle (vs. blue lead-grey in Little Tern) and dull-coloured legs (Gary Allport)



Figure 6. Courtship-feeding by Saunders's Terns *Sternula saundersi*, San Sebastian Peninsula, Mozambique, 2 September 2019. A. (top) male (left) 'parading', carrying food while female (right) adopts receptive hunched posture. B. (lower) both birds in 'erect posture' after fish presented, with head up and carpal bars free from body in male; note Damara Tern *S. balaenarum* in foreground (Christine Read)



Figure 7. Part of a group of at least 26 Saunders's Terns *Sternula saundersi*, Rattray's Point, San Sebastian Peninsula, Mozambique, 31 December 2018; non-breeding birds identified using criteria developed by Mullarney & Campbell (2022) for separation from Little Tern *S. albifrons*. The head pattern shows a narrow black line behind the eye with a pure white rear crown and lacks a white 'notch' or hint of eyestripe above the eye, the mantle is pale grey and wings tricoloured, with white secondaries and a contrasting dark carpal bar (Christine Read)

Of particular note, in October 2019, were birds in non-breeding plumage moulting their outer primaries (Fig. 8). There was also at least one that appeared to be in late post-juvenile moult which was seen begging from birds in adult breeding plumage at this time (T. Hardaker *in litt.* 2021). Moult in *Sternula* is complex (Chandler & Wilds 1994, Olsen & Larsson 1995b, Cherubini *et al.* 1996) and is not well understood in Saunders's Tern, but the late stage of primary moult fits what might be expected for breeders in the Red Sea or Persian Gulf that had commenced primary moult post-breeding. However, the plumage of the breeding-plumaged adults and accompanying juveniles does not match the Red Sea nesting regime. It is notionally possible that the juvenile(s) originated from a colony further east, where the season stretches to September, but juveniles in the Persian Gulf show more abraded plumage by July (see Mullarney & Campbell 2022).

It was noted that the Saunders's Terns did not associate with Little Terns and possibly preferred drier areas of sand for roosting and gathering than Little Terns (E. Marais *in litt.* 2021).

Saunders's Tern is new to Mozambique and a re-addition to the southern African list (T. Hardaker *in litt.* 2019) following its removal by Clancey (1980). Unlike the surprise discovery of Damara Tern, this finding was not unexpected since the migratory range was thought to extend south along the coast of Kenya and Tanzania to latitudes in Madagascar similar to San Sebastian. However, as indicated above, Mullarney & Campbell (2022) suggested that the species has a smaller more oceanic non-breeding range and is probably much less numerous than previously thought (perhaps even warranting a review of its conservation status). This is particularly true in the western Indian Ocean where the species seems to be generally absent or at least greatly outnumbered by Little Tern, and it is possibly mostly limited to Seychelles, the Maldives and other oceanic atolls. Its occurrence in Mozambique may therefore be at the limits of the non-breeding range of birds from the main breeding colonies in the Red Sea and Persian Gulf.

Our evidence suggests that Saunders's Terns in Mozambique may not, or perhaps not only, derive from known breeding populations to the north. We recorded the species in breeding plumage in May–December when courtship-feeding was seen, and well-grown juveniles were begging at adults in September–November coinciding with the non-breeding season for northern breeders, so at least some could form part of a more local (Southern Hemisphere) breeding population. However, some in non-breeding plumage were in primary moult, matching the schedule of the northern breeding population (Figs. 7–8) so it



Figure 8. Five Saunders's Terns *Sternula saundersi*, Rattray's Point, San Sebastian Peninsula, Mozambique, 5 October 2019. One adult in breeding plumage (second from right) and three (left and far right) in non-breeding plumage show advanced primary moult. The bird in the centre is a first-calendar-year bird nearly completing post-juvenile body moult, but still with a brownish tinge to median coverts, possibly with some darker markings on mantle, fresh uniform primaries and a shorter, less deeply forked tail. Note contrasting pale secondaries of non-breeders, a feature not shown to same degree by non-breeding Little Terns *S. albigrons* (Mullarney & Campbell 2022) (Trevor Hardaker)

is possible that both migrants from the north and breeders from as yet unknown southern breeding colonies are involved. Saunders's Tern is considered a breeding resident in the southern Red Sea, Somalia and Socotra (although the presence of birds in the non-breeding season in these areas now warrants review given new identification criteria) and it may also breed south of the equator on the Chagos (albeit apparently on a northern timetable). It is noteworthy that Roseate Terns *Sterna dougallii* have also been recorded in breeding plumage and displaying at San Sebastian and other coastal sites nearby (Allport 2018; GA, DG & CR pers. obs. 2019): their breeding sites are unknown. There are, however, no modern records of terns breeding in coastal southern Mozambique and the San Sebastian area is probably too disturbed by people and natural and feral predators for terns to breed successfully without active management. Surveys of the new Grande Bazaruto KBA are needed with particular attention to potential tern breeding areas.

## Identification issues

The recent advance in identification of Little and Saunders's Terns (Mullarney & Campbell 2022) is already enabling a better understanding of the non-breeding distributions of these species in the Indian Ocean region. Further research is, however, still needed on field characters and regional distributions (see Mullarney & Campbell 2022).

The findings reported here suggest that Damara Tern may occur in the Indian Ocean, conceivably even as far north as Somalia, in April–September, presenting a new identification challenge in the Indian Ocean. Little Terns should be present in small numbers in the region at this time, but these may be second-calendar-year birds in faded, non-breeding plumage, and probably in active moult. Damara Tern is in non-breeding plumage until at least early September and whilst notionally straightforward to separate from Little / Saunders's Terns by the uniform pearl-grey upperparts, fine-tipped black bill and shorter-legged appearance at rest (pers. obs.), these characters are only diagnostic with good views and in direct comparison. A uniform outer wing and lack of contrasting darker outer primaries is a good feature in freshly moulted Damara Terns, but care is needed as birds in post-breeding primary moult can develop a very similar outer wing pattern to Little / Saunders's Terns, since their older outer primaries darken with age and contrast with the growing inner feathers (Fig. 9). Damara Tern tends to have a dusky, ill-defined carpal bar in fresh non-breeding plumage (Hockey *et al.* 2005) but this fades to leave a more uniform overall tone to the upperwing (pers. obs.). Clear white primary shafts and pale legs are additional features in good views. As yet, there is no good illustration of Damara Tern in non-breeding plumage, the most accurate being in Borrow & Demey (2014).



Figure 9. Damara Tern *Sternula balaenarum*, San Sebastian Peninsula, Mozambique, 9 May 2021. An adult in non-breeding plumage illustrating the dark primary wedge that can be shown in advanced primary moult. The otherwise monotone upperwing, with an ill-defined carpal bar, separates it from Little *S. albifrons* and Saunders's Terns *S. saundersi* in similar plumages; note also pale primary shafts (Niall Perrins)

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**Appendix 1:** Counts of *Sterna* terns at Rattray's Point, Santuário Bravio de Vilanculos, San Sebastian Peninsula, Vilanculos District, Mozambique, 2018–2021, by ourselves and others. Numbers are maxima from multi-day counts and zeros denote confidently assessed genuine absences. eBird checklists accessible at <https://ebird.org/checklist/xxxx>.

Observers	Date	Little Tern	Saunders's Tern	Damara Tern	<i>Sterna</i> sp.(p).	eBird checklist
CR	1 April 2018	25				
GA & DG	6 August 2018	0	5	29		S47777348
DG	28 September 2018	200	0	6+		
CR <i>et al.</i>	31 December 2018	70	26	0	200+	
CR	2 January 2019	26				
CR & DG	9 March 2019	230	0	0		

CR <i>et al.</i>	2 September 2019		4	29		
J. Nicolau, CR <i>et al.</i>	17–21 September 2019		15	75	25	
T. Hardaker <i>et al.</i>	4–7 October 2019	0	80	2		
E. Marais <i>et al.</i>	23 October 2019	70	14–15	0		S60860584; S60905294
CR <i>et al.</i>	24–28 October 2019			100+	14	
N. Perrins <i>et al.</i>	28–31 October 2019	120–140	10	50+		S65417443; S65417442
O. Hamerlynck	30 October–3 November 2019	5	2	11		S61218967
P. Scholtz	14–17 November 2019	60	0	8	70+	
CR	30 November 2019	26	1	0		
E. Marais & A. McLean	11 February 2020	1,200	15	0		S65020517
E. Marais	29 February 2020	206	11	0		S65394214
DG	8 June 2020	0	25	25		
DG	18 July 2020	1	10–20	15–20		
DG	1 January 2021		25–30	0		
CR & N. Perrins	10–14 May 2021	0	12–15	80		S88193201; S88587216
E. Marais	25–28 May 2021	1	4	40		S90788718
E. Marais	1 August 2021	1	6	106		S92617736
J. Hogg	4 August 2021	4–10	4	80	50	S92902659

**Appendix 2:** Putative specimens of Saunders's Tern *Sternula saundersi* from southern Africa reported by Saunders & Salvin (1896).

Saunders's Tern was considered to occur in the Indian Ocean as far south as South Africa (e.g., by Vaurie 1965) based on three specimens collected in Durban Bay (Saunders & Salvin 1896). Clancey (1982) reported his own attempts to trace and check these specimens, as a result of which he retrospectively justified his prior decision to remove *saundersi* from the southern African list (Clancey 1980).

Saunders & Salvin (1896) mentioned three specimens of *saundersi* from 'Natal' (Table 3): one collected by Verreaux in the early 19th century at the Rijksmuseum Natuurlijke Historie, Leiden (now Naturalis Biodiversity Center), and two in what is now the Natural History Museum, Tring, *ex* Shelley collection. Saunders was mindful of the significance of these records: 'It is certainly remarkable that *saundersi* should go down to Natal (Durban Bay) but after careful examination of the specimens I can come to no other conclusion'. Since the focus of Saunders & Salvin (1896) was the specimens in England it might be inferred that he only examined these two. Clancey (1982) contacted both museums and G. F. Mees (*in litt.*) reported the specimen had by then been catalogued as *S. a. albifrons* which his examination confirmed, but gave no details of the identification. Mees was also of the view that Saunders had not examined the Leiden specimen. The other two birds in Tring were searched for by D. W. Snow at Clancey's request. He was only able to locate one among the *S. albifrons* skins in 1981. The specimen details were not given by Clancey (1982) but D. W. Snow (*in litt.*) reported that 'on the criterion of the three outer primaries it agrees with *albifrons* rather than *saundersi*'. Having received reports on two of the three specimens Clancey (1982) concluded 'the contention that *S. a. saundersi* reaches South Africa rests entirely on incorrectly determined specimens'.

On a visit to NHMUK in December 2019, GA located two specimens among the Little Tern skins, both *ex* Shelley collection and dated 19 March 1878 from Durban Bay. The Shelley Museum label shows them as '*Sterna balaenarum*', i.e. Damara Terns, but this was crossed out on one label, and other labels, presumably added later and bearing the name 'E Mus. Howard Saunders', are both labelled '*Sterna saundersi* Hume'. These are considered to be the specimens to which Saunders & Salvin (1896) referred, one of which was examined by Snow in 1981 (Clancey 1982). J. J. F. J. Jansen and P. Kamminga shared images of the mounted specimen at Naturalis, Leiden. All specimen details are given in Table 3.

TABLE 3

Details of three *Sternula* specimens from South Africa considered by Saunders & Salvin (1896) to be *saundersi*.

Museum	Specimen no.	Collecting date (inferred)	Locality	Species data from labels	Sex	Label and other notes
NHMUK	Unregistered (Shelley no. 3931)	19 March 1878	Durban Bay	Shelley Mus. ' <i>Sterna balaenarum</i> ' E Mus. Howard Saunders ' <i>Sterna saundersi</i> Hume'	M	Sea Gull
NHMUK	Unregistered (Shelley no. 3932)	19 March 1878	Durban Bay	Shelley Mus. <i>Sterna balaenarum</i> E Mus. Howard Saunders ' <i>Sterna saundersi</i> Hume'	F	Common small sea gull found in the Durban Bay. This bird must be a 'mature'
Naturalis	RMNH. AVES.210701	No date	Port Natal	' <i>St. natalensis</i> Verreaux'	F	Schlegel (1863, specimen b) Specimen mounted

**NHMUK specimens.**—Both are in non-breeding plumage, having a dusky crown with white forehead reaching midway above the eye, dark carpal bar and near-complete moult of the outer primaries with three (specimen 3931) and one (specimen 3932) unmoulted, heavily worn primaries. These outermost primaries show pale shafts in both birds, and on the upperside a blackish shaft to the otherwise greyish, freshly moulted second outermost primary in specimen 3932. The bill is all dark in both. Having been collected in mid March, it might be expected that adults of Little or Saunders's Terns would have plumage and bare-part colours more advanced into breeding condition (Olsen & Larsson 1995a,b). It is therefore likely that both are in their second-calendar year. The timing and unusual plumage of both birds may have been why they were originally identified as Damara then Saunders's Terns. Using Mullarney & Campbell (2022), both can be identified as Little Terns, based on the darker grey mantle and inner wing, as well as broader dark hood on the crown, and blackish shafts on the upperside of the newly moulted primaries is a feature of *S. a. albifrons*.

**Naturalis specimen.**—Photographed by staff at Naturalis (Fig. 10). There is no collection date, but it appears to be an adult, probably attaining breeding plumage with all-fresh primaries (so had probably recently completed wing moult), and partial breeding head pattern and bill coloration. From these characters, the collecting date is estimated to have been mid February to early April. It has dark primary shafts on the upperside but no clearly darker outer primaries, therefore supporting G. F. Mees' conclusion that this a Little Tern of the nominate race.



Figure 10. Little Tern *Sternula a. albifrons* collected at 'Port Natal' (now Durban), South Africa. Mentioned by Schlegel (1863) but no date of collection given. Cited by Saunders & Salvin (1896) as evidence of *saundersi* occurring in South Africa but lack of black outer primaries and darker grey inner upperwing show this to be a Little Tern (© Naturalis Biodiversity Centre, Leiden)

# Taxonomic status of the Western Hemispingus *Sphenopsis ochracea* (Thraupidae) and a review of species limits in the genus *Sphenopsis* P. L. Sclater, 1861

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**SUMMARY.**—The genus *Sphenopsis* P. L. Sclater, 1861, has recently been restored to recognise the genetic monophyly of four Neotropical tanager species, formerly placed in the genus *Hemispingus* Cabanis, 1851, which are little known and poorly represented in museum collections: Oleaginous Hemispingus *Sphenopsis frontalis* (von Tschudi, 1844), Black-eared Hemispingus *S. melanotis* (P. L. Sclater, 1855), Western Hemispingus *S. ochracea* (von Berlepsch & Taczanowski, 1884) and Piura Hemispingus *S. piurae* (Chapman, 1923). Only ten study skins of *S. ochracea* are known in collections; prior to this study, just seven were known and no collection had adults of both sexes. The paucity of specimens has caused a considerable amount of confusion about the morphology of *S. ochracea*, both in published literature and private discussions among ornithologists. To review species limits, I assembled and photographed a comprehensive sample of study skins of *Sphenopsis* species, including *S. ochracea* study skins of both sexes, under a single light source, and compared plumage characters to published colour standards. I also quantified and analysed morphometric variation. These data expose multiple errors in published literature and scientific illustrations, and support recognition of *S. ochracea* and *S. piurae* at species rank.

In June 2021, the chance discovery of three study skins of Western Hemispingus *Sphenopsis ochracea* (von Berlepsch & Taczanowski, 1884), a poorly known species of montane tanager (Thraupidae), in the Delaware Museum of Natural History (DMNH, now Delaware Museum of Nature & Science), prompted me to undertake a critical review of the genus *Sphenopsis* P. L. Sclater, 1861. At present, there is disagreement among the four major world checklists with respect to the number of species recognised in the genus (Table 1). In particular, the taxonomic status of *S. ochracea*, of which specimens are rare in collections, and *S. piurae* (Chapman, 1923) remain contentious. Here, I identify and rectify several sources of confusion, via specimen comparisons and a critical analysis of the literature.

On 22 April 2017, the South American Checklist Committee (SACC) of the American Ornithological Society (AOS) passed a measure to ‘Resurrect *Sphenopsis* for *Hemispingus melanotis* and *H. frontalis*’ (Proposal 730.10). The four major world checklists have also recognised the name *Sphenopsis* for these taxa, although some nomenclatural confusion remains. Burns *et al.* (2014) first proposed restoring the genus ‘*Sphenops* Sclater, 1862’ for this clade, then suggested ‘*Sphenopsis* Sclater, 1862’ (Burns *et al.* 2016). The first 192 pages of P. L. Sclater’s *Catalogue of a collection of American birds* (‘1862’), in which the name *Sphenops* first appeared, were published in late 1861 (see Coues 1879: 278). After the remaining pages (193–368) were published in 1862, an ‘Errata et Emendanda’ page was added to this work, which stated ‘for *Sphenops* read *Sphenopsis* in several places’. This retroactive amendment was intended to bring the earlier work in line with the ‘1861’ volume of *Proceedings of the Zoological Society of London*, published in April 1862, where the name *Sphenopsis* first

TABLE 1

Five alternative taxonomies of the genus *Sphenopsis* as presented in (from left to right) the present study; eBird/Clements checklist v.2021 (Clements *et al.* 2021); IOC world bird list v.12.1 (Gill *et al.* 2021); Howard & Moore v.4 (Dickinson & Christidis 2014); HBW/Birdlife International digital checklist v.6 (HBW & BirdLife International 2021). The South American Checklist Committee (SACC) of the American Ornithological Society (AOS) currently recognises two species (*S. melanotis*, *S. frontalis*) in line with eBird/Clements and Howard & Moore. The ‘linearised’ taxonomic sequence used in this study (see Appendix) was based on Price-Waldman (2019), wherein *S. melanotis* (*sensu lato*, as treated by eBird/Clements and Howard & Moore) was reconstructed as paraphyletic. Taxa recognised at species rank within each taxonomy are shown in boldface. Taxa for which study skins were not personally examined in the present study are denoted thus (—).

Present study	eBird/Clements	IOC	Howard & Moore	HBW/Birdlife
<i>S. melanotis melanotis</i>	<i>S. m. melanotis</i>	<i>S. m. melanotis</i>	<i>S. m. melanotis</i>	<i>S. m. melanotis</i>
<i>S. m. castaneicollis</i>	<i>S. m. castaneicollis</i>	<i>S. m. castaneicollis</i>	<i>S. m. castaneicollis</i>	<i>S. m. castaneicollis</i>
<i>S. frontalis frontalis</i>	<i>S. f. frontalis</i>	<i>S. f. frontalis</i>	<i>S. f. frontalis</i>	<i>S. f. frontalis</i>
<i>S. f. hanieli</i>	<i>S. f. hanieli</i>	<i>S. f. hanieli</i>	<i>S. f. hanieli</i>	<i>S. f. hanieli</i>
—	<i>S. f. ignobilis</i>	<i>S. f. ignobilis</i>	<i>S. f. ignobilis</i>	<i>S. f. ignobilis</i>
—	<i>S. f. flavidorsalis</i>	<i>S. f. flavidorsalis</i>	<i>S. f. flavidorsalis</i>	<i>S. f. flavidorsalis</i>
—	<i>S. f. iterata</i>	<i>S. f. iterata</i>	<i>S. f. iterata</i>	<i>S. f. iterata</i>
<i>S. piurae</i>	<i>S. m. piurae</i>	<i>S. p. piurae</i>	<i>S. m. piurae</i>	<i>S. p. piurae</i>
<i>S. ochracea</i>	<i>S. m. ochracea</i>	<i>S. ochracea</i>	<i>S. m. ochracea</i>	<i>S. ochracea</i>
—	<i>S. m. berlepschi</i>	<i>S. m. berlepschi</i>	<i>S. m. berlepschi</i>	<i>S. m. berlepschi</i>
—	<i>S. m. macrophrys</i>	<i>S. p. macrophrys</i>	<i>S. m. macrophrys</i>	<i>S. p. macrophrys</i>

appeared (see Duncan 1937: 72). According to the Code (ICZN 1999), if a ‘slip to be inserted into the work’ is circulated, containing the correction of a spelling, the corrected name ‘is to be accepted as clear evidence of an inadvertent error’ (Art 32.5.1.1) and ‘the name thus corrected retains the authorship and date of the original spelling’ (Art. 33.2.2). Therefore, *contra* Dickinson & Christidis (2014), the correct genus and authority is *Sphenopsis* P. L. Sclater, 1861, referring to the ‘Catalogue’, not the ‘Proceedings’.

The range of *S. ochracea*, which some checklists classify as a subspecies of Black-eared Hemispingus *S. melanotis* (P. L. Sclater, 1855), is restricted to montane forest on the west slope of the Andes in Ecuador and Colombia. Chapman (1926: 688) ‘[saw] no specimens from western Ecuador’ and included *S. ochracea* on the authority of von Berlepsch & Taczanowski (1884), whose two type specimens (both females) were collected by Siemiradzki in 1882/83, at Cayandede and Chaguarpata, Ecuador, respectively. The types were later transferred from von Berlepsch’s private collection to the Senckenberg Gesellschaft für Naturforschung (SMF), Frankfurt am Main (Hellmayr 1936: 427), where only one now survives: SMF 58282, a ‘[female]?’ collected by Siemiradzki at ‘Chaquarpata’ (= Chaguarpata, Chimborazo, see Paynter 1993: 35) on 5 March 1883 (G. Mayr *in litt.* 2022). This study skin (Fig. 1), which is evidently the only surviving syntype of *S. ochracea* (von Berlepsch & Taczanowski), was not designated as such in the SMF collection prior to this study.

To my knowledge, expeditions in the 20th century yielded only nine more study skins of *S. ochracea*. In chronological order of collection, they are: (1) MLZ 7451, a male collected in 1929 near Pallatanga, Ecuador, housed at the Moore Laboratory of Zoology (MLZ), Occidental College, Los Angeles, CA; (2) ANSP 149722, a male collected in 1941 in Nariño, Colombia, housed at the Academy of Natural Sciences of Drexel University (ANSP), Philadelphia, PA; a toepad of this specimen was recently sampled for phylogenomic research (Price-Waldman 2019); (3–5) DMNH 59270, 85569 and 85570, two males and a female collected in 1976 in Chiriboga, Ecuador, which were unidentified prior to the

present study; (6–7) WFVZ 48203 and 48204, two females collected in 1989 near Chiriboga, Ecuador, housed at the Western Foundation of Vertebrate Zoology (WFVZ), Camarillo, CA; and (8–9) MECN 5265 and 5267, male and female juveniles, respectively, collected in 1991 at Molleturo, Azuay, Ecuador, housed at Museo Ecuatoriano de Ciencias Naturales (MECN), Quito; genetic samples of these specimens were (ostensibly) analysed by García-Moreno *et al.* (2001). It is possible that un-databased specimens exist in some South American museums, but the taxon is absent from the collections at the Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Boyacá, Colombia (G. Bravo *in litt.* 2022) and Universidad Icesi, Cali, Colombia (G. Londoño *in litt.* 2022). To my knowledge, DMNH is the only collection with adult study skins of both sexes, and these were overlooked in the collection until June 2021.

Several points of confusion have arisen from the analyses of García-Moreno *et al.* (2001), which demand explanation. Rensen (2007) quoted this paper in SACC Proposal 284: ‘Within our limited sampling, we could not detect any differences to warrant separation of the east- and west-slope subspecies *melanotis* and *ochraceus*, neither at the molecular level nor based on the plumage characters’ (García-Moreno *et al.* 2001). However, this statement was unfounded because the *S. ochracea* samples in their study (MECN 5265 and 5267) were evidently not included in their morphological or phylogenetic analyses. Both vouchers were juveniles (i.e., unsuitable for analysis of plumage colour in adults) and deposited at MECN (N. Krabbe *in litt.* 2022); they were therefore unavailable to García-Moreno *et al.* (2001), whose morphology analysis was based on ‘[vouchered adult] specimens from the National Museum of Natural History (Stockholm) and [the Zoological Museum, Natural History Museum of Denmark] ZMUC’ (both of which lack specimens of *S. ochracea*). Furthermore, although the MECN samples were mentioned in the Methods and Discussion sections, they were absent from all phylogenetic analyses presented in the Results, including the table of genetic distances (see Figs. 2–4 and Table 1 in García-Moreno *et al.* 2001). Omission of these samples, and the ‘undescribed’ sample discussed below (ZMUC 104925), may also explain why they



Figure 1. Lateral view of SMF 58282, the only surviving syntype of *Sphenopsis ochracea* (von Berlepsch & Taczanowski, 1884), collected by Siemiradzki at Chaguarpata, Chimborazo, Ecuador, on 5 March 1883. The original field label reads: ‘*Hemispingus?* / ♀? / Chaguarpata (5700’) [= 1,737 m] / 5/III 83 / Siemiradzki’. The identification on the secondary (Berlepsch) label reads: ‘*Chlorospingus* [in black ink] *ochraceus*, Berl. & Tacz. [in pencil]’, with ‘*Chloro*’ crossed out and replaced by ‘*Hemi*’ in pencil, and ‘*melanotis*’ in pencil (© Gerald Mayr)

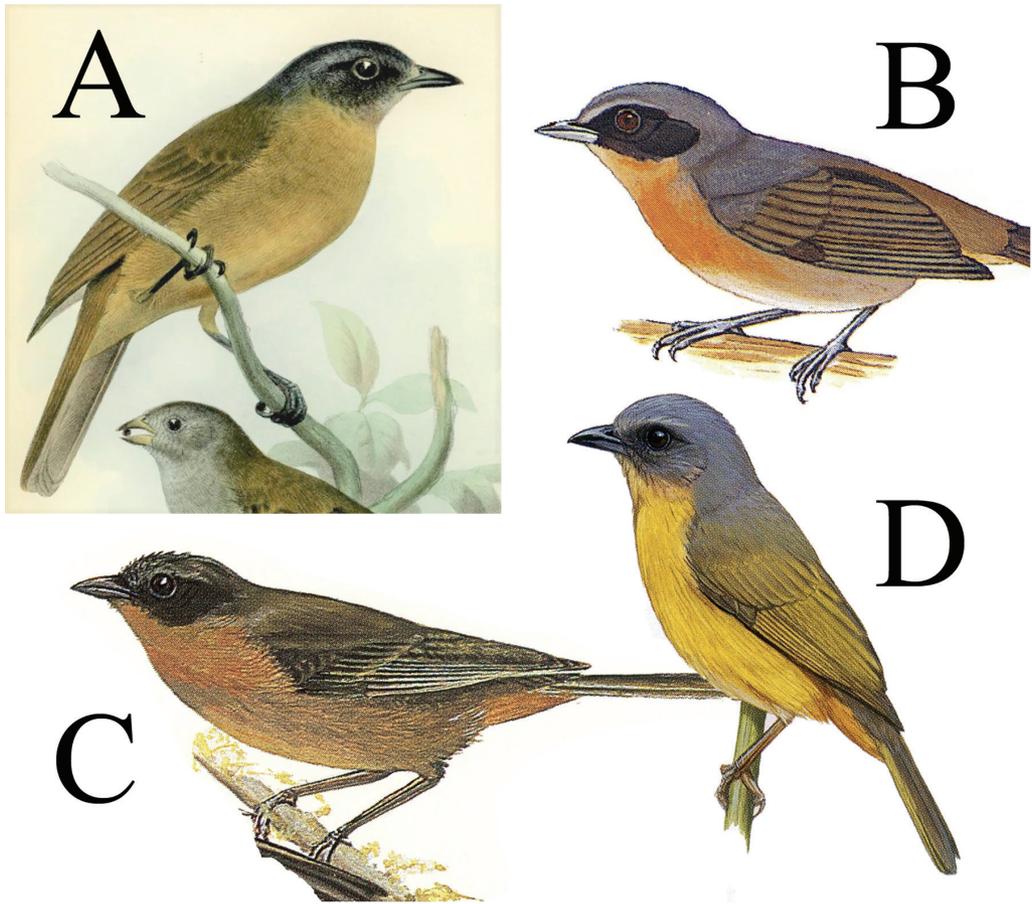


Figure 2. Four published illustrations of Western Hemispingus *Sphenopsis ochracea*: (A) lithograph by 'J. Smit', imprint by 'Hanhart', in von Berlepsch & Taczanowski (1884); (B) Ridgley & Greenfield (2001a); (C) Isler & Isler (1987); and (D) Hilty (2011).

were missing from DNA sequences deposited by García-Moreno *et al.* (2001) in GenBank ([www.ncbi.nlm.nih.gov](http://www.ncbi.nlm.nih.gov)).

Another source of confusion arose from the questionable identity of ZMUC 104925 ('O2308' in Appendix 2 in García-Moreno *et al.* 2001). This sample was inadvertently mentioned twice in their Methods section, and once in Appendix 2, with three different identifications! First, it was listed as '*H. frontalis frontalis*...from Imbabura, Ecuador'; then, it was listed as 'an undescribed form from Imbabura'; finally, in Appendix 2, it was listed as '*H. melanotis?* (undescribed)' from Imbabura. Notably, no mention of the *S. f. frontalis* sample from Imbabura appeared in Appendix 2 (García-Moreno *et al.* 2001). My enquiry into the status of this specimen revealed that ZMUC 104925 was collected by N. Krabbe, who initially identified it as '*Hemispingus [frontalis] frontalis*' on the specimen label. However, N. Krabbe (*in litt.* 2022) later reidentified the specimen as '*Hemispingus melanotis ochraceus*' after misinterpreting the phylogenies in García-Moreno *et al.* (2001). With help from P. Hosner (*in litt.* 2022), I confirmed Krabbe's initial identification (*S. frontalis*) via digital photographs of ZMUC 104925, which is evidently the only existing *S. frontalis* specimen from western Ecuador (N. Krabbe *in litt.* 2022). It is an immature, based on gonad and skull data, which no doubt contributed to the confusion.



Figure 3 (left). Lateral view of (Northern) Black-eared Hemispingus *Sphenopsis melanotis melanotis* (P. L. Sclater, 1855). From left to right, (1) ANSP 154444, adult female prepared by Kjell von Sneidern on 25 April 1942 at 'Toche, Tolima, Colombia'. (2) ANSP 154443, adult male, prepared by Kjell von Sneidern on 28 April 1942 at 'Toche, Tolima, Colombia'. (3) ANSP 165629, adult male, collected on 30 November 1950 on the 'Rio Rumiayaco, [Nariño] Colombia' (Matthew R. Halley)

Figure 4 (right). Lateral view of (Southern) Black-eared Hemispingus *Sphenopsis melanotis castaneicollis* (P. L. Sclater, 1858). From left to right, (1) ANSP 102295, adult female collected on 30 May 1931 at 'Oconeque, [Puno] Peru'. (2) ANSP 102285, adult male collected on 30 May 1931 at 'Oconeque, [Puno] Peru'. (3) ANSP 119323, adult male collected on 15 September 1922 at 'Sandillani, Yungas', La Paz, Bolivia. (4) ANSP 119336, adult incubating female collected on 9 December 1934 at 'Sandillani, Yungas', La Paz, Bolivia (Matthew R. Halley)

Finally, confusion as to the morphology of *S. ochracea* has also proliferated in part because of the variability and inaccuracy of published illustrations (Fig. 2). Unfamiliar with this taxon in the field, I initially suspected the DMNH study skins were undescribed, when I was unable to find a matching illustration. Subsequent research in the DMNH Archives revealed that their collectors also suspected them to be undescribed (see below). At that time (1976), the only published illustration of *S. ochracea* was the original plate in von Berlepsch & Taczanowski (1884), which inaccurately portrayed the taxon (Fig. 2). Correct identification of the DMNH specimens did not become clear until I carried them on loan to ANSP and compared them to ANSP 149722, a male *S. ochracea* from Nariño, Colombia, and a more representative sample of *Sphenopsis* taxa.

A recent phylogenetic analysis of ultraconserved elements (Price-Waldman 2019) indicates that *S. ochracea* (based on DNA from a toepad of ANSP 149722) is the sister group of Piura Hemispingus *S. piurae* (Chapman, 1923); this clade is the sister group of Oleaginous Hemispingus *S. frontalis* (von Tschudi, 1844), based on a sample of *S. f. frontalis* from Amazonas, Peru (MSB 31856); and these three taxa form a clade that is sister to Black-

eared Hemispingus *S. melanotis castaneicollis* (P. L. Sclater, 1858). The sample of '*S. melanotis*' in Price-Waldman's (2019) study was collected in Cuzco, Peru, within the range of *S. m. castaneicollis*. Therefore, the phylogenetic position of *S. m. melanotis* (*sensu stricto*) remains uncertain. These four species, and some other distinctive subspecies, including *S. frontalis hanieli* (Hellmayr & Seilern, 1914), were formerly placed in the genus *Hemispingus* Cabanis, 1851, before genetic data became available. To reassess the morphological characters of *Sphenopsis* species, in light of Price-Waldman's (2019) phylogenetic hypothesis, I assembled study skins under a single light source, to take digital photographs and compare plumage characters to published colour standards. I also quantified and analysed morphometric variation. Here, before explaining my comparative analysis, I briefly recount the history of the DMNH specimens, without which this study would have been impossible.

## History of the DMNH specimens

The overlooked skins of *S. ochracea* at DMNH were collected and prepared by researchers from the Yale Peabody Museum (YPM) in June and August 1976, during field work for the groundbreaking 'tapestry' research of Charles G. Sibley and Jon E. Ahlquist (Sibley & Ahlquist 1990). The expedition was financed by John E. duPont, founder of the DMNH, under an agreement wherein YPM (Sibley) would get the tissues (blood) for molecular research, and DMNH (duPont) the study skins and pickles. A total of US\$60,000 sent by duPont in support of YPM field work in South America, Africa and Asia is documented in correspondence between Sibley and Harold K. Light, Associate Director of DMNH, during April 1975–May 1977 (DMNH Archives). On 14 February 1977, just prior to receiving the last US\$10,000 check, Sibley wrote to duPont: 'I am most grateful to you for your generous help which has resulted in a DNA collection that otherwise never could have been made.' A list prepared at YPM, which includes two skins and one pickle of 'unknown tanagers', bears the following note in the margin: 'skins, skeletons, and pickles arrived as of 8/5/76 [5 August] All sent to Dupont' (DMNH Archives).

Fred C. Sibley (no relation), the YPM collections manager and expedition leader, was accompanied in the field by his teenage sons (David A. & Steven C. Sibley), a professor from Southern Connecticut University (Noble S. Proctor) and two graduate students (Keith B. Aubry and Carol A. Apruzzese). Hereafter, for simplicity, the surname 'Sibley' refers to Fred Sibley. The YPM team collected four specimens of *S. ochracea* in subtropical montane forest (2,000 m elevation) near the small village of Chiriboga, on an old and seldom-travelled road that descends the west slope of the Andes between Quito and Santo Domingo de los Colorados (Paynter 1993: 42, Ridgley & Greenfield 2001b: 41). The first specimen, collected on 12 June 1976, was a female (YPM field catalogue C-184). Sibley was uncertain of its identity and simply wrote 'Tanager' in the field catalogue (DMNH Archives). Later the same day, he caught and prepared two more specimens (C-202, C-203), which were identified as the 'same as C-184'. The second specimen (C-202) was a male with 1 mm testes, prepared as a study skin. The third (C-203) was pickled and sex was therefore not determined. To my knowledge, this is the only pickled specimen of *S. ochracea* ever collected. It was catalogued as DMNH 64739 in 1978, without any taxonomic identification in the ledger, and the DMNH pickle collection was transferred to ANSP in 2013. Finally, when the YPM team returned to the same road on 14 August 1976, they collected a fourth specimen (N-604, '*Tachyphonus* sp. nov.?'), a male with enlarged testes ('5 mm') that Aubry prepared as a study skin (DMNH Archives). After returning to the USA, Sibley shipped the field catalogues and specimens to David M. Niles, Associate Curator of birds at DMNH, with the following note:

'Ecuador — Fred Sibley *et al.* — all specimens from July 17 on are included in this shipment...Specimens prior to July 17 have already been sent to you. Missing skins were left in Ecuador. No pickles or skeletons should be missing...We have noted a *Synallaxis*<sup>1</sup> and *Tachyphonus* as sp. nov. just to make us feel good — we have not checked out either of these very well. Will of course be interested to know what they come out as.' (DMNH Archives)

Niles and Gene K. Hess, the DMNH Collections Manager, catalogued and databased nearly 5,000 study skins that arrived at the DMNH in the 1976 accession from YPM, of which >1,500 skins were from Ecuador. They were evidently (and understandably) puzzled by the tanagers. On a list of corrections to the YPM catalogue, Niles wrote 'C-184, 202, N-604, the mystery tanagers, may be *Hemispingus* sp.? or *Tachyphonus* sp.?; they'll be intensively checked at AMNH'. Niles did not realise that the American Museum of Natural History, New York (AMNH) collection lacks specimens of *S. ochracea*, despite its extensive holdings of South American tanagers, so a trip there would have been insufficient to resolve the problem. On 30 September 1977, Sibley wrote again to Niles: 'Did anything ever come out of that one Ecuador tanager we were hoping was a new species? Would love to go back to Ecuador before O'Neil [*sic*]<sup>2</sup> collects all the undiscovered birds of South America.' Niles responded on 30 January 1980: 'I did finally get up to AMNH for a short day, and ran all of our South American suboscine problems through their collections (the Tanagers await, still)' (DMNH Archives).

The tanager problem was still unresolved in 1986, when Niles left DMNH, and in 2007, when Hess retired. By this time, only one of the unidentified study skins had been catalogued, on 27 January 1977, under the uncertain identity '*Tachyphonus* sp.' (DMNH 59270). None was entered into the DMNH collections database, which caused the specimens to remain 'hidden' from outside researchers. In 2001, Jean L. Woods was hired as curator of birds. For various reasons, the collections manager position remained vacant until 2021, when I was hired and found the rare specimens in a 'hold-up' cabinet, where they had apparently been stored since the 1970s. When asked about the skins, Woods did not have any information about their identity or history (J. Woods pers. comm. 2021). After her departure, in December 2021, I was promoted to interim curator of birds and completed the present study.

## Methods

I catalogued, databased and pest-treated the novel *S. ochracea* skins at DMNH, then hand-carried them on loan to ANSP, for direct comparison with ANSP 149722 (*S. ochracea* male) and study skins of *S. melanotis*, *S. m. castaneicollis*, *S. f. frontalis*, *S. f. hanieli* and *S. piurae*. For each specimen, I used colour standards in Smithe (1975) to score the plumage colour on eight body parts (dorsal: crown, back, tail; ventral: throat, breast, belly, vent, tail). I also scored the ventral plumage of *S. ochracea* in published illustrations to assess their accuracy. To assess morphometric variation, I recorded the following five measurements from every specimen, unless the body part was damaged: (1) wing length (WG), measured with a ruler from the carpal joint to the tip of the longest primary; (2) tarsometatarsus (tarsus) length (TR), measured with callipers from the intertarsal joint to the distal end of the final leg

<sup>1</sup> After visiting the American Museum of Natural History (AMNH), Niles identified the '*Synallaxis*' specimen as *Cranioleuca curtata griseipectus* Chapman, 1924, which is a junior synonym of *C. c. cisandina* (Taczanowski, 1882) (see Bond 1945).

<sup>2</sup> John P. O'Neill, former director of the Louisiana State University Museum of Natural Science, Baton Rouge, described 15 new species and one subspecies from South America during his career.

TABLE 2

Plumage colour of species in the genus *Sphenopsis*, scored using study skins ( $n = 43$ ) in the Academy of Natural Sciences of Drexel University, Philadelphia (ANSP) and Delaware Museum of Nature & Science, Greenville (DMNH) collections (see Appendix for lists of specimens examined). The codes 'tail-D' and 'tail-V' denote the dorsal and ventral surface of the tail, respectively. Numbers are taken from Smithe (1975): (18) Orange Yellow; (23) Raw Umber; (28) Olive-Brown; (49) Greenish Olive; (51) Citrine; (82) Blackish Neutral Gray; (83) Dark Neutral Gray; (89) Jet Black; (119A) Hair Brown; (121) Vandyke Brown; (121A) Prout's Brown; (123A) Cinnamon; (123B) Clay Color; (123C) Yellow Ocher; (124) Buff; (129) Dark Brownish Olive; (136) Raw Sienna; (223D) Tawny Olive.

Species	Crown	Back	Tail-D	Tail-V	Throat	Breast	Belly	Vent
<i>S. melanotis melanotis</i>	83 <sup>3</sup>	83 <sup>7</sup>	28 <sup>3</sup>	23	123A	123A	124	123A
<i>S. m. castaneicollis</i>	82	83 <sup>7</sup>	28 <sup>3</sup>	28	89 <sup>3</sup>	136	124	136 <sup>4</sup>
<i>S. frontalis frontalis</i>	49 <sup>1,3,5</sup>	49 <sup>3</sup>	28 <sup>3</sup>	28	18 <sup>6</sup>	51 <sup>5</sup>	51 <sup>5</sup>	51 <sup>5</sup>
<i>S. f. hanieli</i>	49 <sup>3</sup>	49 <sup>1,3</sup>	28 <sup>3</sup>	28	123C <sup>4</sup>	123B	123B	123A
<i>S. piurae</i>	89 <sup>3</sup>	119A	28 <sup>3</sup>	28 <sup>4</sup>	89 <sup>3</sup>	136	136 <sup>4</sup>	136 <sup>4</sup>
<i>S. ochracea</i>	83 <sup>1</sup>	129 <sup>2</sup>	28 <sup>3</sup>	28	223D	123B <sup>3</sup>	223D	123A

<sup>1</sup>slightly browner

<sup>2</sup>slightly lighter and more olive

<sup>3</sup>slightly darker

<sup>4</sup>slightly lighter

<sup>5</sup>slightly more yellow

<sup>6</sup>slightly duller, less bright

<sup>7</sup>slightly more olive

scale; (3) tail length (TL), measured with a ruler from the insertion point of the two central rectrices to the tip of the longest rectrix; (4) bill length (BL), measured with callipers from the anterior edge of the right nare to the tip; and (5) bill width (BW), measured with callipers at the anterior edge of the nares. Finally, I chose 3–4 exemplary specimens of each species for digital reference photographs, which I took under diffuse natural light passing through a large laboratory window.

## Results

The four *Sphenopsis* species, including *S. ochracea*, and two taxa currently classified as subspecies (*S. m. castaneicollis*, *S. f. hanieli*), have unique and diagnosable plumage phenotypes, with negligible individual variation within each taxon (Table 2, Figs. 3–7). The only plumage trait with no discernible differences among *Sphenopsis* taxa was the colour of the uppertail, which was slightly darker than Olive-Brown (Color 28).

Some distantly related *Sphenopsis* taxa share ventral colour characters to the exclusion of more closely related taxa. For example, *S. piurae* and *S. m. castaneicollis* have the same colour throat (Jet Black, Color 89), breast, and vent (Raw Sienna, Color 136), although they are not sister taxa (see Price-Waldman 2019). Similarly, the colour of the vent is identical in *S. ochracea*, *S. m. melanotis* and *S. f. hanieli* (Cinnamon, Color 123A), and also in females of the distantly related Flame-crested Tanager *Loriotus cristatus* (Linnaeus, 1766), which was formerly placed in *Tachyphonus* (Burns *et al.* 2014). The colour of the vent is also similar in females of Fulvous-crested Tanager *Tachyphonus surinamus* (Linnaeus, 1766). This may explain Sibley's initial suspicion that the DMNH skins were an undescribed species of *Tachyphonus*.

Published illustrations of *S. ochracea* varied greatly in ventral coloration, from slightly darker than Spectrum Yellow (Color 55) in Hilty (2011), to slightly darker than Flesh Ocher (Color 132D) in Isler & Isler (1987). In contrast, specimens of *S. ochracea* were invariably Tawny Olive (Color 223D) on the throat and belly, and slightly darker than Clay Color (Color 123B) on the breast. Published illustrations have also typically shown some black on the cheeks, and a faint gray supercilium (see Fig. 2), but the three *S. ochracea* skins



Figure 5 (left). Lateral view of Oleaginous Hemispingus *Sphenopsis frontalis* (Chapman, 1923). From left to right, (1) ANSP 141983, adult female *S. f. frontalis* prepared by Kjell von Sneidern on 20 March 1939 at 'La Costa, Huila, Colombia'. (2) ANSP 185826, adult male *S. f. frontalis*, prepared by Tristan J. Davis on 22 July 1992 at 'Panguri; ca. 12 km NE San Francisco del Vergel', Zamora Chinchipe, Ecuador. (3) ANSP 83780, adult male *S. f. frontalis*, collected on 15 September 1922 at 'Baeza, Ecuador'. (4) ANSP 67191, adult male *S. f. hanieli*, collected on 3 March 1914 at 'Galeparo; Curro Del Avito, Venezuela' (Matthew R. Halley)

Figure 6 (right). Lateral view of Piura Hemispingus *Sphenopsis piurae* (Chapman, 1923). From left to right, (1) ANSP 116357, adult female prepared by M. A. Carriker, Jr., on 21 June 1933 at 'Palambra, D. Piura', Peru. (2) ANSP 116352, adult male, prepared by M. A. Carriker, Jr., on 22 June 1933 at 'Palambra, D. Piura', Peru. (3) ANSP 116358, adult male, prepared by M. A. Carriker, Jr., on 24 August 1933 at 'Chira, D. Cajamarca', Peru (Matthew R. Halley)

from Chiriboga, Ecuador (one female, two males) possess no trace of these characters; and they are faint in ANSP 149722 (Fig. 7) and SMF 58282 (Fig. 1). In photos, the plumage of SMF 58282 appears slightly foxed after nearly 140 years, but its warm brown plumage and greyish crown (like modern specimens of *S. ochracea*, Fig. 7) lack the greenish tinge of *S. frontalis* (Fig. 5) and ZMUC 104925, the formerly misidentified *S. frontalis* skin from Imbabura discussed above (P. Hosner *in litt.* 2022).

There were subtle differences in size among taxa, all of which exhibited a general pattern of male-biased sexual size dimorphism in the length of the wings and tail, which was not evident in other morphometric traits (Table 3). However, although these data are generally informative about size variation in the genus, sample sizes were too small for a more robust statistical analysis.

## Discussion

The scarcity of specimens of *S. ochracea* in major collections, and problems stemming from the analyses of García-Moreno *et al.* (2001), have caused much confusion. Most illustrated works portray the external phenotype of *S. ochracea* inaccurately (e.g., Isler &



Figure 7. Lateral view of Western Hemispingus *Sphenopsis ochracea* (von Berlepsch & Taczanowski, 1884). From left to right, (1) DMNH 85570, adult female prepared by Fred C. Sibley on 12 June 1976 at 'Chiriboga, km. 45, Quito-Santo Domingo (Old Rd.) 2000 m, Pichincha, Ecuador'. YPM field series = C 184. (2) DMNH 59270 (YPM N-604), adult male, prepared by Keith B. Aubry on 15 August 1976 at 'Chiriborga [= Chiriboga], 2000 m, Old Quito-Santo Domingo Rd., Pichincha, Ecuador'. At the time it was prepared, the bird weighed 21.5 g and had enlarged testes ('5 mm'). (3) DMNH 85569, adult male, prepared by Fred C. Sibley on 12 June 1976 at 'Chiriboza [= Chiriboga], km. 45, Quito-Santo Domingo (Old Road) 2000 m, Pichincha, Ecuador'. YPM field series = C 202. When prepared, the bird weighed 16 g and testes were not enlarged ('1 mm'). (4) ANSP 149722, adult male, prepared by Kjell von Sneider on 3 April 1941 at 'Mayasquer, Nariño, Colombia, Pac[ific] side / 7800 ft.' [=2,377 m] (Matthew R. Halley)

TABLE 3

Morphometrics of taxa in the genus *Sphenopsis*, recorded from adult male ( $n = 21$ ) and female ( $n = 15$ ) study skins in the Academy of Natural Sciences of Drexel University, Philadelphia (ANSP) and Delaware Museum of Nature & Science, Greenville (DMNH) collections. Sample sizes and means ( $\pm$  SD) are given for each taxon, within each sex class (female, male), for the following variables: (WG) wing length, (TR) tarsometatarsus length, (TL) tail length, (BL) bill length, and (BW) bill width. All measurements in mm.

Sex	Species	<i>n</i>	WG	TR	TL	BL	BW
female	<i>S. melanotis melanotis</i>	5	73.2 $\pm$ 1.6	19.9 $\pm$ 0.3	62.8 $\pm$ 2.4	8.2 $\pm$ 0.3	3.9 $\pm$ 0.1
	<i>S. m. castaneicollis</i>	3	61.7 $\pm$ 1.5	21.3 $\pm$ 2.1	55.0 $\pm$ 2.8	7.6 $\pm$ 0.4	3.7 $\pm$ 0.3
	<i>S. frontalis frontalis</i>	5	69.5 $\pm$ 2.8	19.4 $\pm$ 0.8	61.0 $\pm$ 4.0	8.3 $\pm$ 0.1	3.5 $\pm$ 0.0
	<i>S. f. hanieli</i>	0	–	–	–	–	–
	<i>S. piurae</i>	1	68	21.7	61	8.8	3.2
	<i>S. ochracea</i>	1	67	23.5	56	8.4	4.1
	male	<i>S. m. melanotis</i>	2	75.0 $\pm$ 2.8	19.5 $\pm$ 0.1	63.0 $\pm$ 5.7	8.4 $\pm$ 0.4
<i>S. m. castaneicollis</i>		6	69.3 $\pm$ 1.5	21.1 $\pm$ 1.4	60.0 $\pm$ 1.8	7.8 $\pm$ 0.5	3.7 $\pm$ 0.2
<i>S. f. frontalis</i>		6	73.7 $\pm$ 3.4	19.4 $\pm$ 1.4	62.7 $\pm$ 2.4	8.5 $\pm$ 0.1	3.5 $\pm$ 0.1
<i>S. f. hanieli</i>		1	70	19.9	–	8.5	3.5
<i>S. piurae</i>		3	70.0 $\pm$ 0.0	21.9 $\pm$ 1.5	63.3 $\pm$ 5.8	8.7 $\pm$ 0.0	3.4 $\pm$ 0.1
<i>S. ochracea</i>		3	72.5 $\pm$ 0.7	22.2 $\pm$ 0.1	60.5 $\pm$ 0.7	9.1 $\pm$ 0.0	4.2 $\pm$ 0.0

Isler 1987, Ridgley & Greenfield 2001a, Hilty 2011). The data presented here, including digital photographs of males and females taken under natural light (Figs. 3–7), serve to clarify the distinctiveness of the external morphology of *S. ochracea* and its closest relatives. Hopefully, this will be sufficient to prevent future researchers from erroneously concluding that overlooked specimens of *S. ochracea* in collections are undescribed. For clarity of

reference, the synonyms and nomenclatural combinations of *S. melanotis*, *S. frontalis*, *S. piurae* and *S. ochracea*, with lists of specimens examined and brief commentaries under each taxon, are provided in the Appendix.

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## Appendix

SACC Proposal 284 (Remsen 2007), which sought to ‘Recognize *Hemispingus piurae* as a species’ by splitting it from *H. melanotis*, failed to garner enough votes to pass (two yes, seven no). At the time, most committee members were unconvinced by ‘weak’ genetic data (i.e., too few base pairs) published by García-Moreno *et al.* (2001) and García-Moreno & Fjeldså (2003), which suggested that *S. piurae* was sister to *S. melanotis* + *S. frontalis*. Recently, a different and fully supported topology—(*(ochracea, piurae), frontalis*), *melanotis*)—was reconstructed with UCE data, bolstering the case for treating *S. piurae* and *S. ochracea* at species rank (Price-Waldman 2019).

Remsen (2007) contended that *S. piurae* and *S. m. castaneicollis* were ‘much more similar to each other than either is to nominate *melanotis* (no superciliary, pale throat) of e. Ecuador’, but this depends on whether one prioritises some plumage characters (e.g., throat colour, supercilium) over others (e.g., back and/or belly): *S. m. melanotis* and *S. m. castaneicollis* are the same colour on the back (slightly more olive than Dark Neutral Gray, Color 83) and belly (Buff, Color 124), to the exclusion of *S. piurae* and other *Sphenopsis* taxa. Furthermore, genomic data suggest that plumage characters shared by *S. piurae* and *S. m. castaneicollis* are homoplastic, which bolsters the case for species rank (Price-Waldman 2019). Nevertheless, until the phylogenetic relationship of *S. melanotis* (*sensu stricto*) is resolved, I recommend following Hilty (2011) and Gill *et al.* (2021) in recognising *S. piurae* and *S. melanotis* at species rank, and retaining *S. m. castaneicollis* as a subspecies of *S. melanotis*.

Therefore, in the following taxonomy, I recognise four species arranged according to a ‘linearised’ phylogeny following Price-Waldman (2019). Synonyms, taxonomic combinations and principal citations of *S. melanotis*, *S. frontalis*, *S. piurae* and *S. ochracea* are followed by lists of specimens examined and general comments. Type localities and whereabouts of type specimens are provided for each taxon.

### *Sphenopsis melanotis* (P. L. Sclater) Black-eared Hemispingus (Figs. 3–4)

*Chlorospingus melanotis* P. L. Sclater, 1855.

Syntype: NHMUK 1844.12.29.19, in Natural History Museum, Tring: ‘Bogotá’, Colombia (see Warren & Harrison 1971: 343).

*Chlorospingus castaneicollis* P. L. Sclater, 1858, Sclater 1861: 90, Taczanowski 1884: 520.

Holotype: NHMUK 1885.6.12.883: ‘Interior of Peru...bordering on Bolivia’ (see Warren & Harrison 1971: 96).

*Chlorospingus berlepschi* Taczanowski, 1880, Taczanowski 1884: 521.

Holotype: Lost, formerly in Museum and Institute of Zoology of the Polish Academy of Sciences, Warsaw (MIZ): ‘Ropaybamba’, Junín, Peru (see Mlíkovský 2009: 148).

*Hemispingus castaneicollis* von Berlepsch 1912: 1094 (in part).

*Hemispingus melanotis* von Berlepsch 1912: 1095, Isler & Isler 1987: 78.

*Hemispingus berlepschi* von Berlepsch 1912: 1095.

*Hemispingus melanotis stresemanni* Sztolcman & Domaniewski, 1927: 190.

Holotype: MIZ 34227: ‘Baños sur Rio Pastaza’ (= Baños), Ambato, Ecuador (see Mlíkovský 2009: 154).

*Hemispingus melanotis melanotis* Hellmayr 1936: 426, Isler & Isler 1987: 78, Hilty 2011: 167.

*Hemispingus melanotis berlepschi* Hellmayr 1936: 428, Zimmer 1947: 17, Isler & Isler 1987: 78, Hilty 2011: 167.

*Hemispingus melanotis castaneicollis* Hellmayr 1936: 428, Zimmer 1947: 17, Hilty 2011: 167.

**SPECIMENS EXAMINED:** *S. m. melanotis* (two males, five females, one unsexed): Colombia: Tolima: Toche (male: ANSP 154443; female: ANSP 154445, 154447–449; unsexed: ANSP 154444); Nariño: río Rumiayaco (male: ANSP 165629); ‘N. Grenada’ (female: ANSP 7731). *S. m. castaneicollis* (six males, five females, one unsexed): Peru: Puno: Sto. Domingo mine (male: ANSP 102288, 102290, 102294; female: ANSP 102289, 102292); Oconeque (male: ANSP 102285); Bolivia: Cochabamba: San Jacinto (unsexed: ANSP 133555); La Paz: Calabatea (male: ANSP 119327); Sandillani (male: ANSP 119323; female: ANSP 119324, 119325, 119328).

**COMMENTS:** The phylogenetic placement of the nominate subspecies *S. m. melanotis* within the genus *Sphenopsis*, and its relationship to *S. m. castaneicollis*, remain unresolved because the ‘*S. melanotis*’ sample analysed by Price-Waldman (2019) was collected in Cuzco, Peru, within the range of *S. m. castaneicollis*, and no sample of *S. m. melanotis* from the eastern Andes of Colombia or Ecuador was included. Notwithstanding, the data in Price-Waldman (2019) at least confirm the distant relationship of *S. m. castaneicollis* and *S. piurae*, the phenotypic similarity of which has been emphasised in debates over species rank (see Remsen 2007). Here, following tradition, I treat *S. m. castaneicollis* as a subspecies of *S. melanotis* and, following Hilty (2011) and Gill *et al.* (2021), elevate *S. ochracea* and *S. piurae* to species rank, removing them from the synonymy of *S. melanotis*. Nevertheless, further study may yet indicate that *S. m. castaneicollis* also deserves species rank, as suggested by homoplastic patterns of plumage colour revealed by phylogenomic analysis (Price-Waldman 2019).

*Sphenopsis frontalis* (von Tschudi)  
Oleaginous Hemispingus  
(Fig. 5)

*Hylophilus frontalis* von Tschudi, 1844.

Lectotype: MHNN 92.8817, in Muséum d'Histoire Naturelle de Neuchâtel, Switzerland (*vide* Hellmayr 1936: 423); eastern slope of Andes, Junín, Peru (Desfayes 1994: 90).

*Sphenops* [*sic*] *ignobilis* Sclater 1861: 160 (see Coues 1879: 278 for publication date).<sup>3</sup>

*Sphenopsis ignobilis* P. L. Sclater, 1862a: 379 (see Duncan 1937: 72 for publication date).

Holotype: NHMUK 1885.6.12.876: 'in Brasilia' = Mérida, Venezuela (see Paynter & Storer 1970: 265).<sup>4</sup>

*Chlorospingus oleagineus* P. L. Sclater, 1862b: 110, Taczanowski 1884: 516.

Holotype: NHMUK 1885.6.12.877: 'In Nov. Granada int.' = Bogotá, Colombia (see Warren & Harrison 1971: 402).

*Chlorospingus ignobilis* Sclater & Salvin 1871: 784 (see Dickinson 2005 for publication date), Sclater & Salvin 1879: 504.

*Chlorospingus frontalis* Taczanowski 1884: 517, von Berlepsch & Hellmayr 1905: 8.

*Chlorospingus frontalis ignobilis* von Berlepsch & Hellmayr 1905: 9.

*Hemispingus frontalis* von Berlepsch 1912: 1094, Isler & Isler 1987: 77, Hilty 2011: 167.

*Hemispingus frontalis oleagineus* von Berlepsch 1912: 1094.

*Hemispingus frontalis ignobilis* von Berlepsch 1912: 1094, Chapman 1925: 13, Hellmayr 1936: 424, Hilty 2011: 167.

*Hemispingus hanieli* Hellmayr & von Seilern, 1914: 87.

Holotype: ZSM 13925, in Zoologische Staatssammlung, Munich (*vide* Hellmayr 1936): Galipán, Cerro del Ávila, Distrito Federal, Venezuela (see Hellmayr & von Seilern 1914: 87, Paynter & Storer 1970: 266).

*Hemispingus frontalis frontalis* Chapman 1921: 122, Chapman 1925: 13, Zimmer 1947: 17, Isler & Isler 1987: 77, Hellmayr 1936: 423.

*Hemispingus frontalis iteratus* Chapman, 1925: 13, Hellmayr 1936: 425, Isler & Isler 1987: 77.

Holotype: AMNH 188022, in American Museum of Natural History, New York: Carapas, Mt. Turumiquire, Sucre, Venezuela (see LeCroy 2012: 68).

*Hemispingus frontalis hanieli* Chapman 1925: 13, Hellmayr 1936: 425, Isler & Isler 1987: 77, Hilty 2011: 167.

*Hemispingus* [*sic*] *frontalis flavidorsalis* Phelps & Phelps, Jr., 1953: 140.

Holotype: Colección Ornitológica Phelps, Caracas (COP 55625, 'on deposit' at AMNH according to Phelps & Phelps 1953): Cerro Jurustaca, upper río Negro, Sierra de Perijá, Zulia, Venezuela (see Paynter & Storer 1970: 265).

*Hemispingus frontalis flavidorsalis* Isler & Isler 1987: 77, Hilty 2011: 167.

SPECIMENS EXAMINED: *S. f. frontalis* (six males, five females, one unsexed): Colombia: Caldas: Salento (female: ANSP 154474); Cauca: El Tambo (male: ANSP 141981); San Antonio (female: ANSP 141982); Huila: La Candela (male: ANSP 155593, 155594; unsexed: 155591); La Costa (female: ANSP 141983); Tolima: Toche (female: ANSP 154472). Ecuador: Napo: Baeza (male: ANSP 83779, 83780). Peru: Junín (female: ANSP 91539). *S. f. hanieli* (one male): Venezuela: 'Galeparo, Curro del Avito' (ANSP 67191).

COMMENTS: In addition to rectifying the identity of ZMUC 104925 (see introduction), which was a source of confusion for García-Moreno *et al.* (2001), my study confirms that *S. f. frontalis* and *S. f. hanieli* are divergent and diagnosable, relative to other *Sphenopsis* species, and from each other. The adult plumage of *S. f. hanieli* differs from *S. f. frontalis* in colour, especially on the ventral surface, and has 'a sharply defined superciliary stripe' as emphasised in the original description ('Ein scharf abgesetzter Superciliarstreif', Hellmayr & von Seilern 1914: 87). Given the surprising degree of homoplasy in plumage colour uncovered by phylogenomic analysis (Price-Waldman 2019), re-evaluating the taxonomic status of *S. f. hanieli*, and other *S. frontalis* subspecies not included in this study, should be prioritised by future researchers. Here, following tradition, I have treated *S. f. hanieli* as a subspecies of *S. f. frontalis*, although additional data may support classifying it at species rank.

*Sphenopsis piurae* (Chapman)  
Piura Hemispingus  
(Fig. 6)

*Hemispingus castaneicollis* von Berlepsch 1912: 1094 (in part).

*Hemispingus piurae* Chapman, 1923, Hilty 2011: 167.

Holotype: AMNH 174541, Palambra, Piura, Peru (see LeCroy 2012: 69).

*Hemispingus castaneicollis chapmani* Sztolcman & Domaniewski, 1927.

<sup>3</sup> Spelling corrected in 'Errata et Emendanda' slip (see introduction).

<sup>4</sup> The registration number of this specimen was mis-transcribed in Warren & Harrison (1971) and has now been corrected in the NHMUK digital catalogue (A. L. Bond *in litt.* 2022).

Holotype: lost, formerly in the Museum and Institute of Zoology of the Polish Academy of Sciences, Warsaw (MIZ): Tambillo, Cajamarca, Peru (see Mlíkovský 2009: 154).

*Hemispingus melanotis piurae* Hellmayr 1936: 427, Zimmer 1947: 17, Isler & Isler 1987: 78.

*Hemispingus melanotis macrophrys* Koepcke, 1961: 22, Isler & Isler 1987: 78.

Holotype: UNMSM 0630, in Museo de Historia Natural 'Javier Prado', Lima: Sunchubamba, Otuzco, La Libertad Department, Peru (see Plenge 1979: 7).

SPECIMENS EXAMINED: (four males, one female): Peru: Piura: Palambla (male: ANSP 116350, 116353, 116354, 116357; female: ANSP 116352).

COMMENTS: As explained above, I consider the morphological and molecular data reviewed here to be sufficient to alleviate concerns of data deficiency that arose during debate of SACC Proposal 284 (Remsen 2007), bolstering the case for recognizing *S. piurae* at species rank.

*Sphenopsis ochracea* (von Berlepsch & Taczanowski)  
Western Hemispingus  
(Fig. 7)

*Chlorospingus ochraceus* von Berlepsch and Taczanowski, 1884.

Syntype: SMF 58282, in Senckenberg Gesellschaft für Naturforschung (SMF), Frankfurt am Main (Hellmayr 1936: 427): Chaguarpata, Chimborazo, Ecuador (see Paynter 1993: 35).<sup>5</sup> The original field label reads: '*Hemispingus?* / ♀? / Chaguarpata (5,700') [= 1,737 m] / 5/III 83 / Siemiradzki'.

*Hemispingus ochraceus* von Berlepsch 1912: 1095, Hilty 2011: 168.

*Hemispingus melanotis ochraceus* Hellmayr 1936: 427, Isler & Isler 1987: 78.

SPECIMENS EXAMINED: (three males, one female): Colombia: Nariño: Mayasquer (male: ANSP 149722); Ecuador: Pichincha: Chiriboga (male: DMNH 59270, 85569; female: DMNH 85570).

COMMENTS: Evidence presented here confirms that *S. ochracea* and *S. melanotis* are diagnosable by plumage colour (Table 2), *contra* García-Moreno *et al.* (2001), whose conclusions were unfounded (see above). Furthermore, Price-Waldman (2019) has demonstrated the genetic diagnosability of *S. ochracea* and its surprising sister relationship to *S. piurae*, which further bolsters the case for species rank for these taxa.

<sup>5</sup> The type status of this specimen was not recognised in the SMF collection prior to this study (G. Mayr *in litt.* 2022).

# Breeding distribution and status of Great Frigatebird *Fregata minor* in Chile

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**SUMMARY.**—We clarify the breeding status of Great Frigatebird *Fregata minor* in Chile, and describe the discovery of a new breeding colony at the Islas Desventuradas, which becomes the species' south-easternmost outpost in the Pacific. However, recent suggestions that it breeds on Rapa Nui appear to be unconfirmed, and there are no records at all for the Juan Fernández archipelago. Based on currently available data, in Chile the species breeds in August–September and December–January, with some minor fluctuations in egg laying. Based on published and unpublished accounts, we estimate c.200–300 breeding pairs in Chile, with the largest population and main breeding site at Isla Salas y Gómez, and a small population far to the east on Isote González in the Islas Desventuradas.

Frigatebirds are highly aerial birds of mainly tropical distribution (Orta 1992, Nelson 2005). Adults have sexually dimorphic plumage, but a complex series of plumage changes can make identification at sea difficult prior to adulthood (Nelson 1976, Howell 1994). Great Frigatebird *Fregata minor* breeds on tropical and subtropical oceanic islands, and rarely feeds in coastal waters (Diamond 1973, Nelson 2005). Nests are flimsy platforms of small twigs and, depending on island and nesting substrate, can be placed on vegetation or the ground; the latter are often cemented with guano. They lay a single-egg clutch and have a long breeding cycle that lasts c.8 months with a long post-fledging dependency (Nelson 1976, 2005). Consequently, they do not nest annually and presumably breed only every two years (Nelson 1976).

Since at least 1870, it was known that a species of frigatebird occurs in waters around Rapa Nui. Its identity was determined as '*Tachypetes aquila*' based on the feathers used in the crown of a high-ranking islander, which were brought back to the Museo Nacional de Historia Natural, Santiago, Chile, by Ignacio Gana (Philippi 1873). At that time just two species of frigatebirds were recognised, but following the work of Mathews (1914) and Rothschild (1915) five species were generally accepted. Murphy (1936: 919) mentioned that, in a letter from J. T. Nichols, a frigatebird was observed in April c.1,480 km west of the island of San Félix; and indicated that a *Fregata* sp. nested on Salas y Gómez without specifying the species but considered it the easternmost breeding site for any frigatebird in the Pacific. This comment was based on MacFarlane's (1887) account of a visit to the last-named island. Lönnberg (1921) in his notes on birds of Easter Island did not mention the presence of frigatebirds at Rapa Nui. However, Chapin (1935) observed c.8–10 birds on 12–19 January 1935, and was the first to postulate that they were Great Frigatebird. In their main text Goodall *et al.* (1951) did not mention any frigatebird in Chile, but in the appendix reported that a *Fregata* was present on Salas y Gómez, based on a communication by Ottmar Wilhelm, who visited the island in 1937. Nevertheless, in the second supplement to *Birds of Chile* (Goodall *et al.* 1964) the species around Rapa Nui and Salas y Gómez was indicated to be Great Frigatebird, based on independent notes by Martin Moynihan and Thor Heyerdahl. However, in the absence of a specimen, Johnson (1965) stated that the

birds around both islands could be either Great Frigatebird or Magnificent Frigatebird *Fregata magnificens*. King (1967) placed the individuals on Rapa Nui as Great, but it is unclear why; he included the species as a possible visitor. In the ornithological literature, it was not until Millie *et al.* (1969) took a specimen on Rapa Nui that the species concerned was identified definitively as Great and not Magnificent Frigatebird (also Johnson *et al.* 1970, Millie & Johnson 1970, Johnson *et al.* 1972). However, the species had been correctly identified considerably earlier, by Métraux (1940) in an ethnological paper overlooked by ornithologists. Thereafter, Devillers (1972) reported four specimens of Great Frigatebird, two each in Brussels and Paris, taken by Israel Drapkin on Motu Nui, off Easter Island, on 31 December 1934. These specimens formed part of a series of seabirds collected at Motu Nui, and mentioned by Métraux (1940), during the Franco-Belga Anthropological-Archaeological expedition (July 1934–January 1935) to Easter Island, divided among several museums, including the Institut Royal de Sciences Naturelles de Belgique, Brussels, the Muséum national d'Histoire naturelle, Paris, Western Foundation of Vertebrate Zoology, Camarillo, CA, and perhaps others. Schlatter (1984) in his summary of the birds of Chile's oceanic islands included *F. minor* as a breeder on Salas y Gómez and visitor to Rapa Nui.

Here, our goal is to clarify the breeding distribution, phenology and status of Great Frigatebird in Chile, in light of some equivocal reports. Furthermore, we provide information on a new breeding colony.

## Field work and Methods

The Chilean offshore islands include, from east to west, Rapa Nui, Salas y Gómez, the Islas Desventuradas and Juan Fernández archipelago. As part of avifaunal surveys of Chile's subtropical oceanic islands, we visited the Islas Desventuradas on three occasions, landing on San Ambrosio (26°19'S, 78°54'W) on 10–12 December 2019, and Isote González (26°18'S, 80°05'W) on 14–15 December 2020 and 23 August 2021. The avifauna of Islas Desventuradas is the least known of Chile's offshore groups. It consists of three main islands, San Ambrosio, San Félix and Isote González, and a series of rocky outcrops, the most important of which are the Bass islets and Roca Catedral. The easternmost island is San Ambrosio (26°19'S, 78°54'W) and the westernmost San Félix (26°16'S, 80°07'W). The centre of the archipelago is 927 km from the mainland at about the latitude of Caldera in northern Chile. All islands lack fresh water and have very scant vegetation. Until recently, San Ambrosio was much more vegetated but over a period of *c.*50 years (1970–2020) introduced goats and rabbits heavily grazed the island, and it will be many years before it is restored (see Marín *et al.* 2020, Marín & González 2021). MM visited Rapa Nui (27°07'S, 109°23'W) on 9–23 August 2009, and a general description and most findings were published in Marín & Caceres (2010), whilst RG visited Rapa Nui on 26 April–1 May 2018. Additionally, we compiled data from other recently available accounts. For Salas y Gómez (26°28'S, 105°21'W; often misspelled Sala y Gomez), we rely on published and unpublished sources. Given that many published positions and distances are equivocal, our data are all taken from marine charts: British Admiralty 4002, 4608, and SHOA (Servicio Hidrográfico y Oceanográfico de la Armada, Chile) 510, 2311, 2410, 2411 and 2510.

## Results and Discussion

Since the arrival of humans at Rapa Nui, Great Frigatebird seems never to have been abundant there, perhaps because there was pressure to obtain the species' feathers, which were used in crowns of high-ranking individuals and therefore valuable (Philippi 1873). From the 1930s the few published and unpublished reports generally involve small numbers,

with max. four at Rapa Nui, and most reports are from nearshore islets like Motu Nui and Motu Iti, albeit still usually of few individuals, e.g., Chapin (1935), Anon. (1993), Montero (1993), Marín & Caceres (2010) and references therein. However, Millie *et al.* (1969) noted 20–30 arriving to roost on Motu Nui in December 1968, Jaramillo *et al.* (2008) reported *c.*35 in March 2003 and Lazo (2010) saw 15 in February 2010. There is possibly some seasonality to the species' presence, but this is hard to assess using the available data; there are also some post-2010 reports on eBird ([www.ebird.org](http://www.ebird.org)) of larger numbers, however, several of these include birds from more than one area and some involve year-round observations, making analysis difficult. In 1993, some scenes in the film *Rapa Nui* (1994) required frigatebirds flying around in the background. Because of the lack of birds in the area, two ornithologists, M. Sallaberry and P. Harrison, were hired to transport frigatebirds from Salas y Gómez to Motu Nui. Initially, 34 individuals were brought and fed 150 kg of fish daily; according to Sallaberry 140 birds were eventually relocated, presumably via multiple trips (Anon. 1993). Consequently, this introduction temporarily bolstered the population at Rapa Nui. Most reports are from Motu Iti, Motu Nui and Motu Kao Kao, some of the islets off Rapa Nui and on which the birds roost.

All frigatebirds have an unusual breeding biology in several aspects including long incubation and nestling periods and nestling dependency. Great Frigatebird has an incubation period of *c.*55 days, a nestling period of 4–6 months and young remain at the colony another 5–12 months, so the species is capable of producing only one young every two years (Nelson 1976, 2005). In some colonies egg laying occurs over five to six months, but at others year-round (Nelson 1976, Metz & Schreiber 2002).

For Rapa Nui, there are several papers including biogeographical and ecological analyses that consider Great Frigatebird a breeder there, e.g., Flores *et al.* (2014) and Plaza *et al.* (2020), but Plaza *et al.* (2020) listed temperate-breeding species like Arctic Tern *Sterna paradisaea* and Southern Giant Petrel *Macronectes giganteus* as formerly nesting on one of the nearshore islets at some time in the 20th century, which is extremely unlikely. Such claims inevitably diminish their other results. Nonetheless, the initial report of nesting (Lazo 2010, 2011) was based on an observation of males, females and immatures on one of the islets and on Peninsula Poike on Rapa Nui itself, but Lazo (2010: 11) indicated that no real evidence, e.g., of a nest, was obtained. The presence of young birds does not necessarily prove local breeding, as young are highly mobile and can disperse >2,000 km (Weimerskirch *et al.* 2017). Salas y Gómez, the most likely source for the birds at Rapa Nui, is just 389 km to the north-east. If Great Frigatebird has indeed started to breed on Rapa Nui, this needs to be documented and not listed as fact based on conjecture, although it quite possibly did breed there in the past but abandoned the colonies after human arrival.

Salas y Gómez is seldom visited by ornithologists, however MacFarlane (1887) who visited on 5 March 1884 was probably the first to report a frigatebird breeding in Chile, which he identified as *Fregata aquila* (see above), but he did not specify if he found eggs or chicks. Firm evidence of breeding by frigatebirds at the island did not come until almost 100 years later, in early November 1981, when Narvarte & Cristino (1982) published photos of small nestlings (unidentified to species) in full white down being guarded / brooded by adults, indicating that they were between two and four weeks old (Metz & Schreiber 2002). No further information was given but based on the photos egg laying had probably started by mid / late August. Based on an unpublished report by P. Scott in 1972, Schlatter (1984) reported Great Frigatebird as breeding at Salas y Gómez, with *c.*100 pairs. Subsequently, Harrison & Jehl (1988) visited Salas y Gómez twice, in March 1985 and 1986. In 1985, they found 24 nestlings ranging from one-third grown to nearly fledged, and in 1986 they found the remains of 20 nestlings. Vilina & Gazitua (1999) visited the island on 6–11 December



Figure 1. The northern end of Islote González, Islas Desventuradas, Chile, with Punta Bari, Isla San Félix, in the background; the arrow indicates the plateau where Great Frigatebirds *Fregata minor* were nesting (Manuel Marín)



Figure 2A–B. Two different nests of Great Frigatebird *Fregata minor*, Islote González, early December 2020, showing the quantity of plastic debris used as nesting material, including rope, plastic packaging, and metal wire, indicated by arrows (Manuel Marín)

1997 and found 101 active nests, 23.7% with eggs, 45.5% small nestlings and 30.6% large nestlings. Pedro Lazo visited in February and September 2011 (Lazo 2011); in February, he reported 115 nestlings, or a minimum of 115 pairs, i.e., a similar total to Vilina & Gazitua (1999). However, this presumably represents only part of the island's population given that there are usually two breeding periods (see above) probably involving different cohorts. Unfortunately, Lazo (2011) did not mention numbers in September, providing only a photo of an adult incubating an egg, as would be expected at that time, but Lazo (2014) suggested the presence of similar numbers in the December / January and August / September breeding periods. Overall, however, in the only table given by Lazo (2014) his totals are of little use, as they represent a three-year average of all birds counted during the course of



Figure 3. The single Great Frigatebird *Fregata minor* nestling found on Isote González, Islas Desventuradas, Chile, 23 August 2021 (Rodrigo González)

each year and the combined numbers in two different areas (Rapa Nui and Salas y Gómez), and thus most likely involve duplication.

It is surprising that the species was added relatively recently to the avifauna of Islas Desventuradas by Aguirre *et al.* (2009), who also mentioned a secondhand report that it might breed there. We observed the species on all three of our visits and found it nesting on Isote González in August 2021. During our first visit to Isote González on 14–15 December 2020, on the west side *c.*100 m above sea level we accessed a small plateau with a sheer cliff to its north and east, and to the west a slope 20–30 m by 200 m at a 40–60° angle before dropping to the sea (Fig. 1). Here, we found seven empty nests from previous seasons, which had obviously been used multiple times as some had several layers of guano cementing them to the ground. They were built on rocks and were platforms of sticks and plastic debris, mainly string and rope of various sizes, and some contained metal wire, probably from the nearby naval base (see Fig. 2A–B). Also in December 2020, we observed a max. five Great Frigatebirds, an adult female and four immatures of different ages (no males were seen). In August 2021, in the same area we observed four adults, three females and one male, plus a well-grown nestling still in the nest, feathered but with much white down on the nape, breast, belly, flanks and shoulders (Fig. 3). It was five to six months old, suggesting eggs were laid late December–early January. Also in August 2021, one of the adult females regularly sat on a fresh nest (no guano in its top layer) and was perhaps preparing to lay.

Based on the literature, and the data compiled here, we can establish that in this region: (1) Great Frigatebird seems to have two distinct egg-laying seasons involving different cohorts, one starting in late August–September and the other in December–early January, probably with small inter-year variations. Therefore, colonies might show some activity year-round. (2) Currently there are only two islands where the species nests in Chile:

Isla Salas y Gómez and Isote González. (3) At both sites, the species nests on the ground, whereas elsewhere in its extensive distribution Great Frigatebird usually nests on trees or bushes. (4) Speculation that the species breeds at Rapa Nui requires confirmation, as there is nothing to document this claim. (5) Isote González becomes the species' south-easternmost breeding site in the South Pacific (2,646 km east of Salas y Gómez).

The species is not numerous in Islas Desventuradas, but there are at least 8–10 pairs from different breeding cohorts. Such small numbers are the most likely explanation for the lack of records until recently. Based on the available evidence, we estimate a population of 200–300 breeding pairs in Chile, or more than double the total given by Schlatter (1984). Ideally, however, the colonies should be surveyed during both breeding seasons and across two consecutive years, to provide a more precise estimate of the population. For the Juan Fernández archipelago, to the best of our knowledge no frigatebird species has been reported there.

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# On the wrong side of the Atlantic: first record of wild Greater Flamingo *Phoenicopterus roseus* in Brazil and in the Americas?

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**SUMMARY.**—We present the first report of Greater Flamingo *Phoenicopterus roseus* in Brazil, an individual at Araruama, Rio de Janeiro state, in late November 2021 until at least early April 2022, and discuss hypotheses to explain its appearance so far from the species' normal distribution. We believe that it was either an escapee from a captivity or a genuine vagrant that reached Brazil due to bad weather. We also reviewed earlier reports of this species in the Americas on citizen science databases, all of which pertained either to misidentifications, a single escaped individual, or taxonomic misclassification. Given the species' ability to make long-distance movements, including over-water dispersal, we contend that the *P. roseus* in Brazil was the first record for South America and the first wild bird in the Americas.

Phoenicopteridae comprises six modern species of flamingos in three genera: *Phoenicopterus*, *Phoenicoparrus* and *Phoeniconaias* (Gill *et al.* 2021). These pink to reddish tall-standing wading birds are well known for their unique body features, bright coloration and social behaviours (del Hoyo *et al.* 2020), being one of the most easily recognised bird groups among ornithologists, birdwatchers and the general public alike (Rose *et al.* 2014, Delfino & Carlos 2021). Greater Flamingo *Phoenicopterus roseus* is the most widespread and second most abundant species in the family, with a global population estimated at 680,000 individuals in the wild and 8,324 in captivity (FSG 2021). Distributed from southern Africa to southern Europe, India and the Middle East, it usually occurs at saline lagoons, lakes and other coastal wetlands (Balkız *et al.* 2007, 2010, del Hoyo *et al.* 2020). It is present year-round in a number of regions, but seasonal at some sites and is present only sporadically in others (Johnson 1989, Sanz-Aguilar *et al.* 2012, del Hoyo *et al.* 2020).

Greater Flamingo performs seasonal movements but also undertakes highly irregular patterns of displacement, varying among locations, populations and time of year (Johnson 1989, Balkız *et al.* 2007, 2010, Lees & Gilroy 2021). Significant seasonal movements occur among Mediterranean, North African and Middle Eastern populations in response to adverse weather conditions, with a certain degree of site fidelity (Johnson 1989, Balkız *et al.* 2010, del Hoyo *et al.* 2020). Nevertheless, some erratic or nomadic records are available, reflecting food availability and wetland condition (Johnson 1989, Kumssa & Bekele 2014, Bensaci *et al.* 2015, Kumar & Rana 2021, Lees & Gilroy 2021). In some cases, inclement weather (or other factors) can lead to birds appearing far outside the normal range, e.g., in Siberia, northern Europe and China (Johnson 1989, del Hoyo *et al.* 2020). Here, we report the first observation of a Greater Flamingo in Brazil and review other reports in the Americas. Possible explanations for the bird's appearance on the 'wrong' side of the Atlantic are discussed. We believe that it could be the first wild record in the Americas.

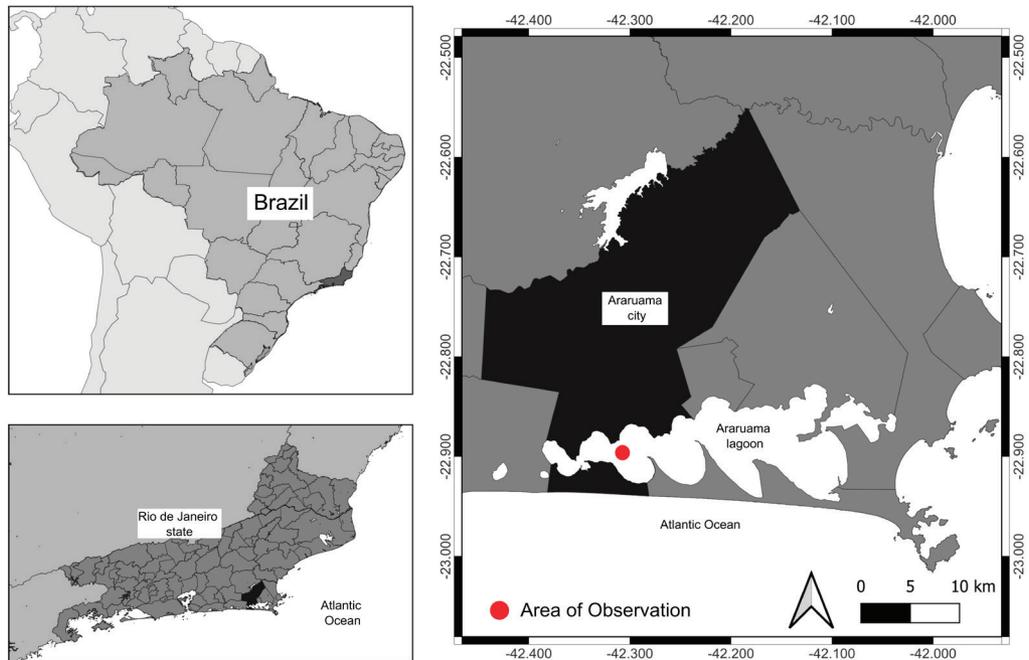


Figure 1. Lagoa de Araruama, the largest permanent hypersaline lagoon in the world, showing the location of the first record of Greater Flamingo *Phoenicopterus roseus* in Brazil, near Araruama.

## First record of Greater Flamingo in Brazil

The first record of a Greater Flamingo in Brazil was near Araruama ( $22^{\circ}54'54.2''\text{S}$ ,  $42^{\circ}22'05.0''\text{W}$ ), Rio de Janeiro state, on the south-east coast of Brazil, where it was first seen on 28 November 2021 (Fig. 1). It was found by a group of birdwatchers near Araruama salt pans, Praia Seca, close to Lagoa de Araruama, a hypersaline lagoon with 160 km of shoreline, 37 km long and up to 13 km wide. The mean depth of the lagoon is 2–3 m (Kjerfve *et al.* 1996) (Fig. 1).

Analysis of feather pattern and bare-parts coloration of the individual suggests it was a near-adult (Johnson *et al.* 1993), as the grey on the head, neck and chest indicates the bird was not fully mature, despite the colour of the bare parts and presence of full-coloured feathers on other tracts (Johnson *et al.* 1993, Shannon 2000, Chiale *et al.* 2018) (Fig. 2). Flamingos older than one year are already independent and can move long distances (Barbraud *et al.* 2003, del Hoyo *et al.* 2020).

Despite being similar to congeners (Chilean Flamingo *P. chilensis* and American Flamingo *P. ruber*), the Greater Flamingo was identified by three distinctive characters (Fig. 2). (1) Greater Flamingo has a slightly larger bill, with the distal third black and the culmen ridge and basal region being white or slightly pinkish; Chilean and American Flamingos have the bill almost half black, with the basal half white (Chilean Flamingo) or orange (American Flamingo) (Jenkin 1957, Kear 1969, Mascitti & Kravetz 2002) (Fig. 2). (2) Greater Flamingo has entirely pinkish legs, with no difference in colour between the tarsometatarsus, tibiotarsus and intertarsal joint. The pattern is very similar to American Flamingo, but the latter has the joint slightly more pinkish or reddish than the rest of the leg; Chilean Flamingo has the tarsometatarsus and tibiotarsus yellow or grey, with only the intertarsal joint and feet pink (Kear 1969, Johnson *et al.* 1993, del Hoyo *et al.* 2020). (3) Greater Flamingo has pale pink or white feathers, with some reddish ventrally, but



Figure 2. Greater Flamingo *Phoenicopterus roseus*, Lagoa de Araruama, Rio de Janeiro state, Brazil, showing three distinctive characters used for identification: (1) the colour and pattern of the bill, (2) the pink legs and ankles; (3) the pale pink feathers on the body; the arrows highlight the grey lower head and neck, used to estimate the individual's age, and the damaged feathers in the right wing (Hélio Pereira)

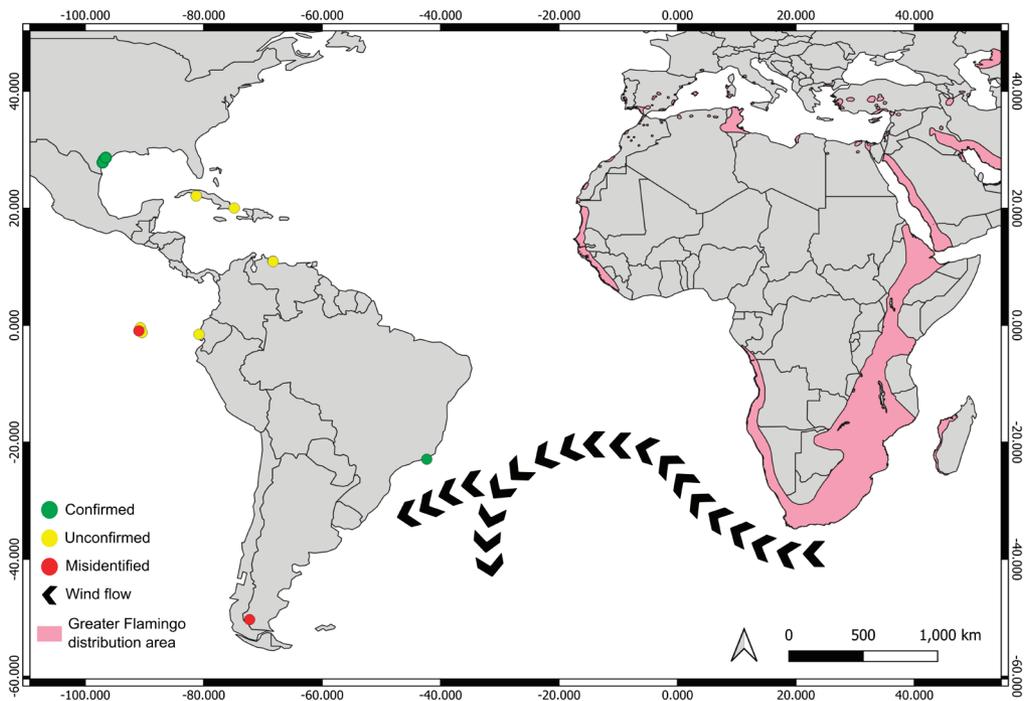


Figure 3. Map of previous records of Greater Flamingo *Phoenicopterus roseus* in the Americas, showing confirmed, unconfirmed and incorrect reports, together with the natural distribution of the species in Africa. The arrows indicate hypothetical wind-flows that could help the flamingo to arrive at the Brazilian coast.

American Flamingo has all of the body orange or red, and Chilean Flamingo has red only in the tail and rear body (Johnson *et al.* 1993, Amat & Rendón 2016, Freeman *et al.* 2016, Chiale *et al.* 2018) (Fig. 2).

The bird appeared very wary and flew off when approached too closely. Some remiges on the right wing were missing and others were damaged (Fig. 2), evidence of either molt, predation or aggressive interactions, but perhaps injury during flight (Matyjasiak *et al.* 2018). The bird joined a few Chilean Flamingos also present at Lagoa de Araruama, and was observed until at least 9 April 2022 (E. Pimenta; <https://www.wikiaves.com.br/4793780>).

## Greater Flamingo in the Americas

Despite this being the first record for Brazil, it is not the first Greater Flamingo to be reported in the Americas. Via the Global Biodiversity Information Facility (GBIF; <https://www.gbif.org/>), eBird (<https://ebird.org/>) and WikiAves (<https://www.wikiaves.com.br/>) we found 19 reports of the species in the Western Hemisphere (Table 1) between 1993 and 2018, in Texas (USA), the Galápagos Islands (Ecuador), Venezuela, Cuba, and once in southern Argentina (Fig. 3). For 11 records, photographs permitted identification, but in one the photo was not very clear and in two the observers had misidentified the species (Table 1). For eight of these records the photos involved Greater Flamingos, all of them in Texas (USA). For the other eight records, no photograph or description was provided.

Because Greater Flamingo is easily mistaken for young American or Chilean Flamingos, photos or a description of distinctive characters is essential to correctly identify the species (Austen *et al.* 2016). Another probable cause of misidentification in digital platforms is use of the former taxonomic classification of Greater and American Flamingos, i.e., as two

TABLE 1

Reports of Greater Flamingos *Phoenicopterus roseus* in the Americas in two different databases: GBIF and WikiAves, and the new record for Brazil. Records were classed as undocumented (Undoc.) or documented (Doc.) and confirmed identification (Conf.), unconfirmed (Unconf.) or misidentification (Misid.) due to either observer error or, especially, outdated taxonomy.

Country	Date	Locality	Status	Photograph	Source
Argentina	17 Feb 2018	Laguna Nimez	Misid.	Doc.	GBIF (3389153657)
Brazil	28 Nov 2021	Lagoa de Araruama	Conf.	Doc.	WikiAves (WA4622214)
Cuba	10 Mar 2016	Parque Nacional Ciénaga de Zapata, Playa Larga	Unconf.	Undoc.	GBIF (1339221161)
	17 Nov 2016	Parque Nacional Ciénaga de Zapata, Playa Larga	Unconf.	Doc.	GBIF (1580260816)
Ecuador	24 Nov 2016	Las Salinas	Unconf.	Undoc.	GBIF (1580273277)
	30 Dec 1994	Punta Cormorant, Isla Floreana, Galápagos Islands	Unconf.	Undoc.	GBIF (1038766660)
	3 Jan 1995	Isla Rábida, Galápagos Islands	Unconf.	Undoc.	GBIF (1038765835)
	10 Apr 2003	Punta Cormorant, Isla Floreana, Galápagos Islands	Unconf.	Undoc.	GBIF (922868615)
	29 Feb 2012	Puerto Villamil, Isla Isabela, Galápagos Islands	Misid.	Doc.	GBIF (1835272665)
USA	8 Mar 2016	Puerto López, Galápagos Islands	Unconf.	Undoc.	GBIF (1339484501)
	26 Dec 2013	Texas	Conf.	Doc.	GBIF (2445083523)
	4 Jan 2014		Conf.	Doc.	GBIF (2423049643)
	24 Sep 2016		Conf.	Doc.	GBIF (3070478318)
	24 Sep 2016		Conf.	Doc.	GBIF (3058714305)
	26 Sep 2016		Conf.	Doc.	GBIF (2573963639)
	20 Nov 2016		Conf.	Doc.	GBIF (3058721315)
Venezuela	26 Nov 2016		Conf.	Doc.	GBIF (3058741307)
	21 Dec 2016		Conf.	Doc.	GBIF (3058691305)
	23 Mar 2013	Cuare Nature Reserve	Unconf.	Undoc.	GBIF (922920489)
	23 Mar 2013	Parque Nacional Morrocoy	Unconf.	Undoc.	GBIF (922877009)

subspecies of the same species, *P. r. ruber* and *P. r. roseus*. In some observations, the number of individuals reported was not consistent with a vagrant in the Americas, indicating that these records were misidentified (or misclassified) American Flamingos (Table 1). The observation in Argentina involved misidentified Chilean Flamingo.

The eight records in Texas involved the same individual, an escapee from Kansas Zoo, observed frequently since 2013 in the area, with a yellow ring on the right leg typical of that facility (<https://edition.cnn.com/2022/04/01/world/escaped-flamingo-492-texas-scn/index.html>). We believe that the Brazilian Greater Flamingo in 2021 is the first record of the species in the wild not only for Brazil but also South America. Two hypotheses could explain its presence: the bird was an escapee from a facility or private collection; or the bird was a natural vagrant.

### Lost or escapee?

Brazil has strict regulations about breeding and keeping exotic bird species in private collections, which is permitted only for conservation and environmental education, mainly in captive facilities and zoos regulated by the Instituto Brasileiro do Meio Ambiente e Recursos Naturais (IBAMA), Instituto Chico Mendes de Biodiversidade (ICMBio) and

Ministério Brasileiro do Meio Ambiente (MMA) (Brazil 1967, 1998, IBAMA 2011). All birds kept legally must be registered and banded according to norms of the Centro Nacional de Pesquisa e Conservação de Aves Silvestres (CEMAVE) (ICMBIO 2021). As the Greater Flamingo in Rio de Janeiro was not ringed, and we have found no reports of a missing flamingo, the probability that it was from a zoo or captive facility seems low. There is the possibility of an escape from an illegal facility, but birds the size of a flamingo with such distinctive features would be very difficult to keep undetected.

The second and, in our estimation, more probable explanation is that the flamingo originated in Africa (or elsewhere in its regular range) and, due to adverse weather, reached Brazil. Flamingos can fly up to 600 km per night, being capable of travelling very long distances between colonies and non-breeding areas in a short period of time, with few stopovers (Johnson *et al.* 1989, Johnson & Cézilly 2007). Greater Flamingos are capable of over-water dispersal, moving significant distances over the Indian Ocean and Mediterranean Sea (Johnson *et al.* 1989), with sightings of the species in Madagascar, the Maldives and Seychelles (Johnson & Cézilly 2007). Nevertheless, crossing the Atlantic is very unlikely, except in adverse weather like strong winds, storms, or drastic changes in temperatures (Johnson 1989, Richardson 1990, Clairbaux *et al.* 2019). Such conditions can cause individuals to become lost.

Araruama is more than 5,600 km from Namibia, the nearest point on the African mainland. Southern Africa has a large number of wetlands, many of them used by Greater and Lesser Flamingos during November–February (del Hoyo *et al.* 2020). Furthermore, the west coast of Africa was affected by thunderstorms and winds up to 80 km/h during 21–27 November (SAWS 2021, NMS 2021), the week before the Greater Flamingo appeared in Brazil, possibly explaining the record (Fig. 3). In the Atlantic, south-east trade winds blow from *c.*30°S along the coast of Africa, then over the Atlantic to South America (Longhurst & Pauly 1987), which could have aided vagrancy to coastal Brazil, like other Old World birds such as Western Reef Heron *Egretta gularis* (Fedrizzi *et al.* 2007).

That the bird was a vagrant rather than an escapee is suggested by its behaviour: vigilant and avoiding humans, reinforcing the idea that the bird was not used to human presence and probably wild (Yosef 2000, Beauchamp 2006), because captive birds are often more habituated to humans and have lower reaction distances (Delfino & Carlos 2021).

## Conclusions

The record of a Greater Flamingo in coastal Rio de Janeiro, Brazil, is the first in the country, South America and potentially the first wild individual in the Americas. It was probably a young adult that flew over the Atlantic due to storms on the west coast of Africa, showing the capacity of the species, and flamingos in general, to make long-distance movements (Balkız *et al.* 2007, 2010, del Hoyo *et al.* 2020).

We also draw attention to the importance of correct identification of birds on citizen science platforms, preferably with updated taxonomy, and photographs, to support identification and locate potential errors. Such platforms are important tools, not only contributing to conservation and management programmes but helping to identify future occurrence patterns, habitat use and distribution expansions (Greenwood 2007).

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# Pteruthiidae and Erpornithidae (Aves: Corvides): two new family-group names for babbler-like outgroups of the vireos (Vireonidae)

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The Old World genera *Erpornis* Hodgson, 1844, and *Pteruthius* Swainson, 1832, were long considered babblers Timaliidae (Deignan 1964, Sibley & Monroe 1990, Howard & Moore 1991). This was based on gross morphology (in *Erpornis*, similarity to *Yuhina*; in *Pteruthius*, bold plumage pattern reminiscent of, e.g., the laughingthrush genus *Garrulax*) and biogeography (presence alongside many 'other' species of babblers in the Oriental region), rather than phylogenetic analysis.

In the first molecular phylogenetic analysis of babblers, Cibois *et al.* (2002) found that the species known as '*Yuhina*' *zantholeuca* was not closely related to other species of *Yuhina* but was placed in an unresolved position near the crows *Corvus* and cuckooshrikes *Coracina*. As a consequence, the species was removed from *Yuhina* and placed in the monotypic genus *Erpornis* (Cibois *et al.* 2002). *Erpornis* was subsequently found to be closely related to the New World vireos Vireonidae (Barker *et al.* 2004). Another study showed that *Pteruthius* does not belong with the babblers but is sister to the *Erpornis*-Vireonidae clade (Reddy & Cracraft 2007). These findings were corroborated by Jønsson *et al.* (2016), Oliveros *et al.* (2019) and Stervander *et al.* (2020).

Following the discovery that *Erpornis* and *Pteruthius* represent successive sister groups of the vireos, they were lumped within an expanded Vireonidae in several taxonomies (Dickinson & Christidis 2014, Winkler *et al.* 2015, Fjeldså *et al.* 2020b). Placing *Erpornis* and *Pteruthius* in Vireonidae was probably necessitated by the lack of available family-group names for these two taxa. However, a good reason to refrain from placing *Erpornis* and *Pteruthius* into Vireonidae is that it changes the meaning of Vireonidae and affects several aspects of the systematics and biogeography of the family. For example, the time to their most recent common ancestor (MRCA) is shifted at least ten million years backwards (Stervander *et al.* 2020: fig. A2.1), the geographic origin of the MRCA shifts from the Americas to Asia, and the synapomorphies and diagnostic character states of 'Vireonidae' are modified. One can argue that these changes were unnecessary and potentially confusing. Given the long stability of the meaning of the name Vireonidae (e.g. Sharpe 1903, Wetmore 1930, Mayr & Amadon 1951, Deignan 1964, Wolters 1980, Sibley & Monroe 1990, Dickinson 2003), the alternative taxonomic solution, to exclude *Erpornis* and *Pteruthius* and place these in new family taxa, should be proposed. For example, Slager *et al.* (2014), who were aware of the close relationship of *Erpornis* and *Pteruthius* to the vireos, used the name Vireonidae in its traditional sense, i.e. for the New World taxa alone, excluding *Pteruthius* and *Erpornis*.

Placing *Erpornis*, *Pteruthius* and Vireonidae in separate family taxa is in line with the current classification of Passeriformes, as reviewed in Fjeldså *et al.* (2020a). Fjeldså *et al.* (2020b) followed the idea, within Passeriformes, of temporal banding (Avisé & Johns 1999), in which the classification at higher ranks (i.e. families and genera) should correspond to groups of similar age, based on calibrated phylogenies. They did not, however, establish a strict cut-off line (as had Jønsson *et al.* 2016 for Corvides), knowing that confidence intervals of nodes are often wide and can vary among analyses (e.g. Oliveros *et al.* 2019, Stervander

TABLE 1  
Divergence times of *Pteruthius* and *Erpornis* from Vireonidae calculated in various dated phylogenies.

<i>Pteruthius</i>	<i>Erpornis</i>	Source
27.5–27.7 Mya	22.4–22.5 Mya	Reddy & Cracraft (2007)
23 Mya	21 Mya	Jönsson <i>et al.</i> (2016)
15 Mya	-	Moyle <i>et al.</i> (2016)
17 Mya	12.5 Mya	Oliveros <i>et al.</i> (2019)
27.5 Mya	21 Mya	Stervander <i>et al.</i> (2020)

TABLE 2  
Taxa treated as families (*sensu* Fjeldså *et al.* 2020b) that were inferred to be of equal or younger age than *Pteruthius*. Taxa marked with an asterisk were inferred to be younger than both *Pteruthius* and *Erpornis*.

Chronogram	Taxa
Oliveros <i>et al.</i> (2019)	Dendrocolaptidae, Xenopidae, Furnariidae, Malaconotidae, Pityriasisidae, Aegithinidae, Platysteiridae, Vangidae, Lamprolidae, Rhipiduridae, Ifritidae, Paradisaeidae, Corvidae, Platylophidae, Laniidae, Paradoxornithidae, Sylviidae, Timaliidae, Leiothrichidae, Pellorneidae, Buphagidae, Sturnidae, Mimidae, Polioptilidae, Troglodytidae, Viduidae, Estrildidae, Rhodinocichlidae, Plectrophenacidae, Emberizidae, Cardinalidae, Mitrospingidae*, Thraupidae*, Passerellidae, Parulidae*, Icteridae*, Calyptophilidae* and Phaenicophilidae*.
Stervander <i>et al.</i> (2020)	Furnariidae, Dendrocolaptidae, Xenopidae, Platyrhinchidae, Tachuridae, Rhynchocyclidae, Chaetopidae, Eupetidae, Dicruridae, Lamprolidae*, Rhipiduridae*, Corcoracidae*, Platylophidae*, Paradisaeidae*, Laniidae*, Corvidae*, Melampittidae, Ifritidae*, Monarchidae*, Machaerirhynchidae, Artamidae*, Cracticidae*, Rhagologidae, Aegithinidae, Pityriasisidae*, Malaconotidae*, Platysteiridae*, Vangidae*, Sylviidae, Zosteropidae, Timaliidae, Pellorneidae, Leiothrichidae, Polioptilidae, Troglodytidae, Buphagidae, Sturnidae, Mimidae, Urocynchramidae, Ploceidae, Amblyospizidae, Viduidae*, Estrildidae*, Passeridae, Fringillidae, Plectrophenacidae*, Rhodinocichlidae*, Emberizidae*, Calyptophilidae*, Mitrospingidae*, Thraupidae*, Cardinalidae*, Passerellidae*, Phaenicophilidae*, Icteridae* and Parulidae*.

*et al.* 2020). Most taxa treated as families by Fjeldså *et al.* (2020b), however, diverged around 20 Mya, a date similar to estimates for the *Erpornis* lineage and the *Pteruthius* clade (Table 1). In the chronogram of Oliveros *et al.* (2019), 38 taxa treated as families (*sensu* Fjeldså *et al.* 2020b) are of equal or younger age than *Pteruthius* and six of these are also of equal or younger age than *Erpornis* (Table 2). Similarly, in the unconstrained chronogram of Stervander *et al.* (2020), 56 taxa treated as families (*sensu* Fjeldså *et al.* 2020b) are of equal or younger age than *Pteruthius* and 28 of these are also of equal or younger age than *Erpornis* (Table 2).

Because no family-group names are available for *Erpornis* and *Pteruthius*, we propose:

## Erpornithidae new family

**Type genus** *Erpornis* Hodgson, 1844

**Diagnosis** Small passerines (body length 12.0–13.5 cm) with rather plain plumage and distinct yellow vent and tail. Differs from all species of Vireonidae by combination of (i) short erect crest, (ii) uniform head without pale supercilium behind the eye or pale eye-ring, (iii) lack of wingbars, (iv) plain tertials and (v) pale pink legs.

Differs from all species of Pteruthiidae by combination of (i) slender bill, (i) short erect crest, (iii) lack of sexual dimorphism in plumage, (iv) greenish head and upperparts, (v) lack of a dark eyestripe and (vi) uniform greenish wings without wingbars.

**Included taxa** *Erpornis zantholeuca* Blyth, 1844.

## Pteruthiidae new family

**Type genus** *Pteruthius* Swainson, 1832

**Diagnosis** Small passerines (body length 11.5–21.0 cm) with short stout bill and colourful plumage (except the Green Shrike-Babbler *P. xanthochlorus* complex). Differs from Vireonidae by (i) sexual dimorphism in plumage and (ii) head pattern, with black head (in male Black-headed Shrike-Babbler *P. rufiventer*), black head with white supercilium (males of the Pied Shrike-Babbler *P. flaviscapis* complex), ear-coverts bordered by dark crescent and reddish throat (Black-eared Shrike-Babbler *P. melanotis* complex), dark lores, pale supercilium behind eye and reddish throat (Chestnut-fronted Shrike-Babbler *P. aenobarbus* complex), or plain greyish head with dark lores but no pale supercilium (*P. xanthochlorus* complex).

Differs from *Erpornis* by combination of (i) stout bill, (ii) lack of crest, (iii) sexual dimorphism in plumage, (iv) black or well-marked head in most species (except the *P. xanthochlorus* complex), and (v) wings either black with yellowish or chestnut tertials (in *P. flaviscapis* complex), black or dark brown with white to rufous-buff wingbars (*P. melanotis* and *P. aenobarbus* complexes), or greenish with paler wingbars (*P. xanthochlorus* complex).

**Included taxa** A single genus (*Pteruthius*) with nine or 19 species, depending on whether divergence in songs (Rheindt & Eaton 2009; Gill *et al.* 2021) or diagnosability of plumage (Reddy 2008), respectively, is used as the taxonomic criterion for species limits.

## Discussion

An alternative solution would be to treat Erpornithidae as a subfamily of Vireonidae, based on (i) the view that placement of the Asian *Erpornis* with the New World vireos conveys useful biogeographic information because it would emphasise the Asian origin of Vireonidae, (ii) the fact that in the phylogeny of Oliveros *et al.* (2019) only a small number of families are younger than Erpornithidae, and these are all in the nine-primaried New World oscines, and (iii) the age of Erpornithidae is younger than a large number of nodes within families in the phylogeny of Oliveros *et al.* (2019), which means that if temporal banding is applied to these groups, many new families should be named.

Ranking is obviously subjective, and therefore disagreements about the ‘appropriate’ rank cannot be solved empirically. In this case, ranking *Erpornis* as a subfamily and placing it in Vireonidae has two negative consequences: it results in an unnecessary change of the name of the vireos (‘Vireoninae’) and attaches the name ‘Vireonidae’ to a different, larger, older and geographically much more widespread group. We are not convinced by the arguments in favour of merging *Erpornis* with the vireos in a single family. First, merging the Asian *Erpornis* with the New World vireos in itself would not convey any information about the geographic origin of the vireos. Rather, the origin of a particular group, i.e. the direction of past geographic movement, is inferred from mapping the geographic range of multiple groups on a phylogeny. Second, whereas in the phylogeny of Oliveros *et al.* (2019) only six families were younger than Erpornithidae, and these were all in the nine-primaried New World oscines, in the phylogeny of Stervander *et al.* (2020) no fewer than 28 were of equal or younger age than *Erpornis* (Table 2), and these were not restricted to the nine-primaried New World oscines. Several nine-primaried New World oscine taxa were ranked as families by Barker *et al.* (2013) to keep the names of several major previously recognised groups stable (e.g. Thraupidae, Cardinalidae, Icteridae, Parulidae). We agree with this approach because it serves nomenclatural stability, even if it results in relatively ‘young’ family-level taxa. We have applied this approach to Erpornithidae

and Pteruthiidae, so that Vireonidae can be maintained for the vireos. Third, the fact that several lineages in other families are older than Erpornithidae does not imply that these should also be ranked as families. Only when temporal banding is enforced with a strict threshold will there be a need to change the rank of these taxa, and we believe this is not necessary. Ranking *Erpornis* as a family is in line with the current classification of Passeriformes, as reviewed in Fjeldså *et al.* (2020a), which is only loosely based on temporal banding.

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# Radiographic analysis of Meinertzhagen's redpoll specimens: testing a purported case of fraud

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**SUMMARY.**—Based on a detailed analysis of the external appearance of redpoll *Acanthis* skins, Knox (1993) explicitly accused the collector Richard Meinertzhagen of having stolen specimens from the Natural History Museum bird skin collection and re-labelling them. Here, I test Knox's results using independent evidence of the internal appearance of the specimens in question derived from radiography. Radiographic evidence strongly supported Knox's overall conclusion of fraud by Meinertzhagen but revealed limitations inherent in his attempt to determine the collection history of bird skins using external appearance alone. Although results in such investigations are inherently likely to be probabilistic rather than certain, a multi-factorial approach, taking a wide array of evidence into account, is most likely to engender confidence in the outcome.

The publication of Knox (1993) comprised the first focused investigation of long-standing anecdotal evidence that the ornithologist Richard Meinertzhagen had fraudulently acquired and relabelled at least part of his huge bird skin collection. In 1954, Meinertzhagen presented the entire bird skin collection he still retained, nearly 20,000 specimens, to the then British Museum (Natural History), now Natural History Museum (NHMUK), following a close, but often acrimonious, relationship with the institution spanning c.40 years. Following its handover, he continued to work on his collection in the museum in South Kensington, London, until prevented from doing so by increasing frailty in the years preceding his death in 1967. In the early 1970s, the entire NHMUK bird research collections, including the Meinertzhagen skins, were moved from London to the museum's site in Tring, where they continue to be held.

The possibility of fraud in Meinertzhagen's bird skin collection had first been alluded to in print by Clancey (1984), in an article providing an overview of the NHMUK bird collections at Tring, but by this time it had already been the subject of discussion and investigation over many years by staff and ornithological associates of NHMUK (cf. Cocker 1989, Rasmussen & Prÿs-Jones 2003, Garfield 2007, Prÿs-Jones *et al.* 2019). Knox's (1993) investigation involved close external examination of Meinertzhagen's redpoll (*Carduelis* spp., now *Acanthis* sp.—see below) skins, and comparisons of these with other redpoll specimens held by the NHMUK, as a by-product of research into the taxonomy of the group (Knox 1988). His conclusions, based on a combination of subjective and objective assessment of skin preparation styles, provided compelling, but not definitive, evidence that Meinertzhagen had committed fraud.

Two questions in particular arise from the research and allegations of Knox (1993). The first concerns whether it is possible to produce independent evidence that will substantiate or refute allegations based on external preparation style alone concerning the genuine or fraudulent status of Meinertzhagen's specimens. The second relates to whether any fraud committed pertains to specific and limited parts of Meinertzhagen's bird collection or affects

it more generally. Here, I address the first of these issues by using radiographic techniques to reveal the internal structure of the redpoll skin specimens studied by Knox (1993).

Redpoll taxonomy has moved on since Knox (1993) was published. First, it is now generally accepted that redpolls comprise a separate genus, *Acanthis* (Zuccon *et al.* 2012). Secondly, recent genetic studies indicate that all redpolls may be best viewed as comprising a single species *A. flammea*, despite the extent of phenotypic variation among them (Lifjeld 2015, Mason & Taylor 2015, Funk *et al.* 2021). For my purposes here, this change is less important than facilitating an easy comparison with Knox's (1993) study. When necessary, specimens discussed below are therefore designated in inverted commas by the subspecific names (*flammea*, *cabaret*, *rostrata*, *hornemanni*, *exilipes*) then in use to designate phenotypic distinctiveness.

## Methods

The redpoll specimens x-rayed for this study included all those referenced by their NHMUK registration numbers in Knox (1993). They comprised 22 skins from the Meinertzhagen collection and 19 from other NHMUK collections from which Knox suspected that Meinertzhagen might have stolen specimens that he then relabelled as his own. I undertook the radiography on the NHMUK Solus-Schall x-ray machine, with a beryllium window tube at 1 m and using Kodak Industrex-M film, at 30 kV and 10 mA for an exposure time averaging 35 seconds.

Some of the x-rayed redpoll specimens produced largely opaque images in which details of bone structure were obscured to a greater or lesser extent. This was presumed to be caused by these skins having been treated with arsenic, formerly employed as a preservative during preparation by some collectors (Harrison & Cowles 1970). Arsenic, especially mixed with chalk as in arsenical soap, would be expected to absorb x-rays, causing opacity (M. Moore & P. Morris *in litt.* 1996). To test for this, I removed samples of a few mg of skin from just inside the belly incision of eight of the x-rayed redpoll specimens, chosen to include birds producing both relatively clear and largely opaque images and to encompass a diversity of putative origins. Three of these specimens were subsequently re-sampled by removing a small amount of stuffing material from an orbit of each. These samples were submitted blind to the Chemistry Dept. of Royal Holloway, Univ. of London, to test for the presence of arsenic by mass-spectrometry.

A full list of the NHMUK registration numbers of all specimens x-rayed and sampled for arsenic is provided in Table 1, together with dates of collection, sex, collection localities and collectors, as recorded on their labels, plus a cross-reference to the specimen identification codes used in the text and on the radiographic images figured herein. Finally, minor errors made by Knox (1993) in his specimen referencing are corrected.

## Results

**Radiographic evidence.**—Subheadings used below follow those in Knox (1993) for ease of comparison.

1. *Blois, France, 1953.* On Fig. 1, specimens A–C are the three Meinertzhagen skins, phenotypically '*cabaret*', labelled as having been collected in Blois, France, on 17 January 1953, by 'G.B.' (identity unclear) and then 'sent formalined' to Meinertzhagen. Specimens D–J are the seven extant skins, also '*cabaret*', from a series of 13 originally registered in NHMUK, taken by R. B. Sharpe at Hanwell, Middlesex, England, on 17 November 1884. The radiographic images, however, indicate an identity of preparation style for each of specimens B–J inclusive, with A being unequivocally distinct. Points of similarity for B–J,

TABLE 1

All specimens mentioned in the paper are listed below, cross-referenced to their code used in the text and figures (NB – BB, JJ and MM were not used). Information on collection date (no year of collection is available for the Lenz specimens), sex (M = male, F = female), locality and collector is that shown on the relevant specimen labels. Specimens A–T are phenotypically species *flammea* and U–RR species *hornemanni* according to the taxonomy used by Knox (1993). Meinertzhagen specimens sampled for arsenic have an asterisk (\*) against their code.

Code	NHMUK reg. no.	Collection date	Sex	Locality	Collector
A*	1965.M.17376	17 Jan 1953	M	Blois, France	'G.B.' for R. Meinertzhagen
B	1965.M.17377	17 Jan 1953	M	Blois, France	'G.B.' for R. Meinertzhagen
C*	1965.M.17378	17 Jan 1953	F	Blois, France	'G.B.' for R. Meinertzhagen
D	1886.10.20.39	17 Nov 1884	M	Hanwell, England	R. B. Sharpe
E	1886.10.20.40	17 Nov 1884	M	Hanwell, England	R. B. Sharpe
F	1886.10.20.41	17 Nov 1884	M	Hanwell, England	R. B. Sharpe
G*	1886.10.20.42	17 Nov 1884	M	Hanwell, England	R. B. Sharpe
H*	1886.10.20.45	17 Nov 1884	F	Hanwell, England	R. B. Sharpe
I	1886.10.20.46	17 Nov 1884	F	Hanwell, England	R. B. Sharpe
J	1886.10.20.49	17 Nov 1884	F	Hanwell, England	R. B. Sharpe
K	1965.M.17330	7 Dec 1932	M	Asknish, Scotland	R. Meinertzhagen
L*	1965.M.17331	7 Dec 1932	M	Asknish, Scotland	R. Meinertzhagen
M*	1965.M.17332	4 Dec 1932	M	Asknish, Scotland	R. Meinertzhagen
N	1965.M.17333	7 Dec 1932	M	Asknish, Scotland	R. Meinertzhagen
O*	1965.M.17335	7 Dec 1932	M	Asknish, Scotland	R. Meinertzhagen
P*	1965.M.17357	5 Dec 1932	F	Asknish, Scotland	R. Meinertzhagen
Q	1965.M.17352	30 Aug 1955	M	North Atlantic (60°N, 14°W)	R. Meinertzhagen
R	1965.M.17347	22 Nov 1920	M	Taynish, Scotland	R. Meinertzhagen
S	1965.M.17343	17 Nov 1920	M	South Uist, Scotland	R. Meinertzhagen
T	1965.M.17348	21 Oct 1920	M	Taynish, Scotland	R. Meinertzhagen
U	1965.M.17379	21 Oct 1920	M	Mull, Scotland	R. Meinertzhagen
V	1965.M.17396	30 Aug 1955	M	North Atlantic (60°N, 14°W)	R. Meinertzhagen
W	1937.10.17.309	28 May 1937	M	Moskusokse Fjord, Greenland	C. G. & E. G. Bird
X	1937.10.17.310	12 Oct 1936	M	Myggbukta, Greenland	C. G. & E. G. Bird
Y	1937.10.17.312	4 Nov 1936	M	Myggbukta, Greenland	C. G. & E. G. Bird
Z	1937.10.17.313	4 Nov 1936	M	Myggbukta, Greenland	C. G. & E. G. Bird
AA	1937.10.17.314	4 Nov 1936	M	Myggbukta, Greenland	C. G. & E. G. Bird
CC	1937.10.17.315	9 Nov 1936	M	Myggbukta, Greenland	C. G. & E. G. Bird
DD	1937.10.17.316	21 May 1937	M	Myggbukta, Greenland	C. G. & E. G. Bird
EE	1937.10.17.317	1 Oct 1936	F	Mackenzie Bay, Greenland	C. G. & E. G. Bird
FF	1937.10.17.318	16 Oct 1936	F	Myggbukta, Greenland	C. G. & E. G. Bird
GG	1965.M.17387	6 Mar 1938	?	Inari, Lapland, Finland	R. Meinertzhagen
HH	1965.M.17386	6 Mar 1938	F	Inari, Lapland, Finland	R. Meinertzhagen
II	1965.M.17384	6 Mar 1938	M	Inari, Lapland, Finland	R. Meinertzhagen
KK	1965.M.17383	24 Feb 1938	F	Rovaniemi, Lapland, Finland	R. Meinertzhagen
LL	1965.M.17314	7 Mar 1938	F	Inari, Lapland, Finland	R. Meinertzhagen
NN	1965.M.17385	7 Mar 1938	M	Inari, Lapland, Finland	R. Meinertzhagen
OO	1886.3.31.16	1 Feb	F	Moscow, Russia	Dr Lenz
PP	1886.4.3.15	17 Feb	M	Moscow, Russia	Dr Lenz
QQ	1884.9.25.19	1 Mar	M	Moscow, Russia	Dr Lenz
RR	1965.M.17382	24 Feb 1938	?F	Rovaniemi, Lapland, Finland	R. Meinertzhagen

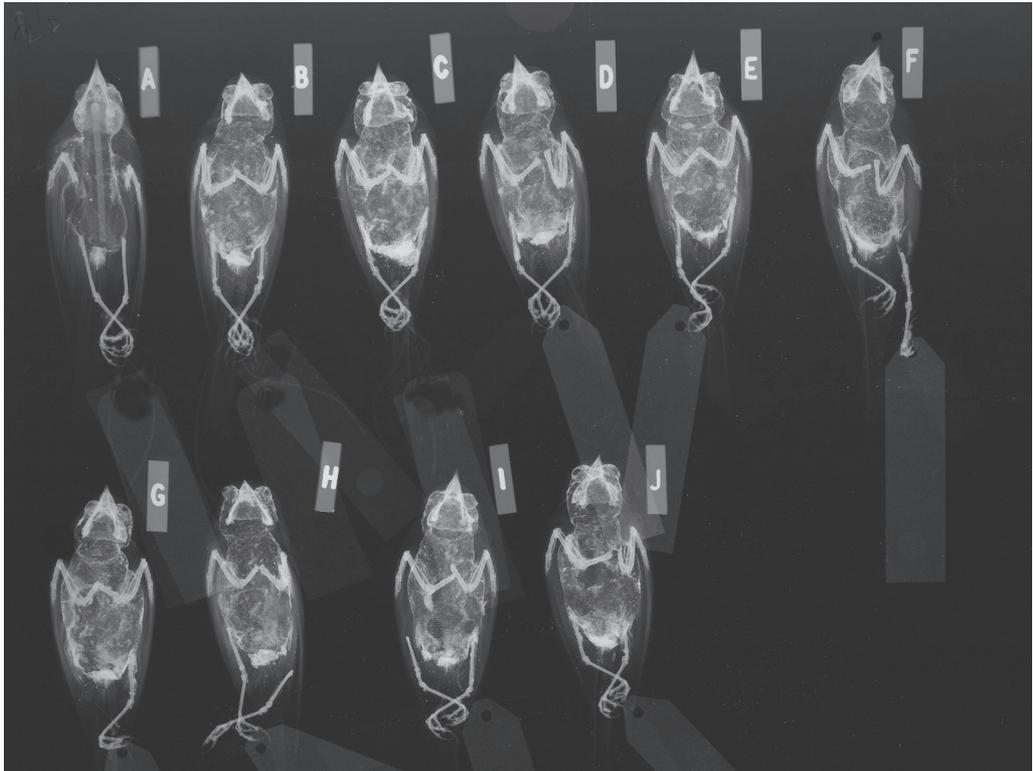


Figure 1. Radiographs of Meinertzhagen redpoll *Acanthis* skins from Blois, France (A–C) and of Sharpe redpoll skins from Hanwell, England (D–J). Full details of each specimen can be found in Table 1.

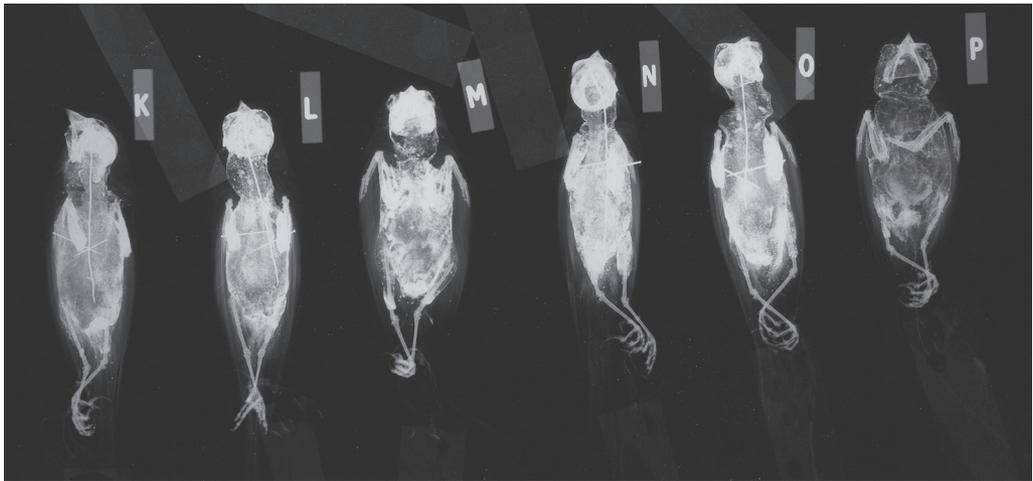


Figure 2. Radiographs of Meinertzhagen redpoll *Acanthis* skins from Asknish, Scotland. Full details of each specimen can be found in Table 1.

but of difference to A, include the unusual cut-away rear skull, severance of the wing bones through the humerus, absence of a support stick, and overall extent and pattern of lighter and darker areas on the images. These results corroborate the conclusions of Knox (1993), based on external skin preparation style, who identified specimens B and C as closely

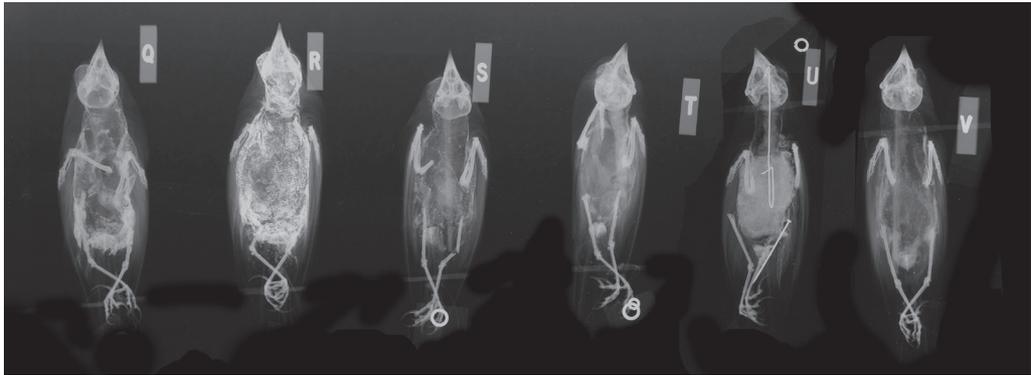


Figure 3. Radiographs of Meinertzhagen *Acanthis* redpoll skins from the North Atlantic (Q and V) and Scotland (R–U). Full details of each specimen can be found in Table 1.

matching Sharpe's Hanwell series, but specimen A as clearly different. Moreover, there is no indication that any of A–C has ever been in formalin, which has the attributes of making the skin rubbery, so that it does not shrink back and the feathers tend not to lie flat, and the specimen difficult to prepare.

2. *Asknish, Argyll, 1932*. On Fig. 2, specimens K–P are the six redpolls labelled by Meinertzhagen as having been collected by himself at Asknish, Argyll, Scotland, between 4 and 7 December 1932. Specimens K, L, N and O, which are all phenotypically '*flammea*', are each highly opaque and show close similarity to each other in visible internal preparation style, including a thin longitudinal wire support and pinned wings. Specimen M, also '*flammea*', is also highly opaque but otherwise shows differences from the foregoing, most notably in lacking either an internal support wire or pinned wings. Specimen P, a '*cabaret*', is totally distinct in preparation style from the other Argyll specimens, but identical to Sharpe's Hanwell series (D–J, Fig. 1). These results precisely corroborate the conclusions of Knox (1993) based on external appearance.

3. *North Atlantic, 60°N, 14°W, 1955, and 4. West coast of Mull, Scotland, 1920*. On Fig. 3, specimens Q and V are respectively '*rostrata*' and '*hornemanni*', both labelled by Meinertzhagen as having flown on board a ship in the North Atlantic on which he was travelling on 30 August 1955. The radiographic evidence supports Knox's (1993) conclusion, based on external features, that these are different styles of skin; thus Q has a more hollowed-out skull, lacks a supporting stick and has an image showing greater opacity around the tail base and tibial regions.

By contrast, the radiographic images refute Knox's (1993) opinion from external evidence that specimen V closely matches another Meinertzhagen specimen, U, which is labelled as a '*?exilipes*' collected on the island of Mull in 1920 (Fig. 3). U appears to be a re-made skin, in which a wedge of stuffing fills the body cavity but does not reach the neck, and a supporting wire extends from the front of the skull into the mid-body cavity. The radiographic images do, however, tend to confirm Knox's (1993) further opinion that U differs in preparation style from two other '*flammea*' (R and S), purportedly collected by Meinertzhagen in Scotland in 1920. In fact, these three skins, R, S and U, plus a fourth, T, with similar data but which Knox was unable to locate, are strikingly heterogenous in preparation style (Fig. 3).

Comparisons of the radiographs of U and V with those shown in Fig. 4 of specimens of '*hornemanni*' taken in Greenland in 1936 (X–Z and AA, CC, EE and FF) and 1937 (W and DD) by the brothers C. G. & E. G. Bird reveals V, but not U, to be very similar, in particular

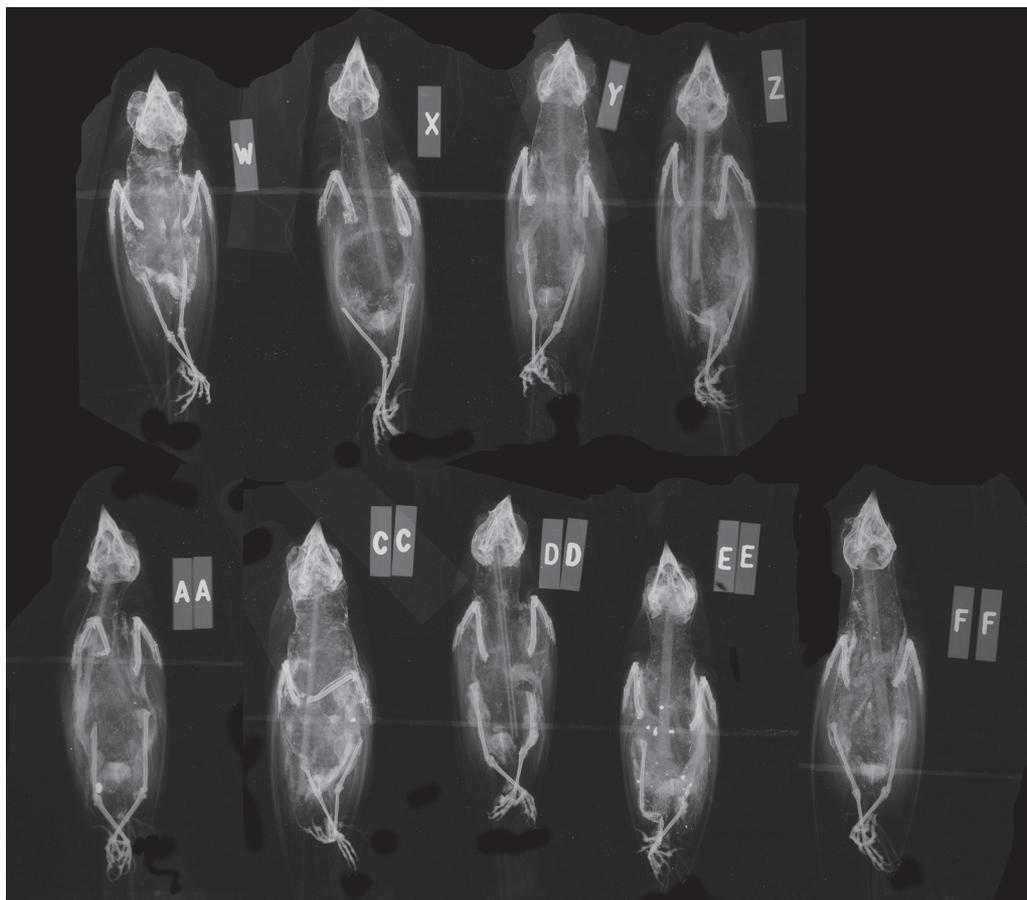


Figure 4. Radiographs of C.G. & E.G. Bird redpoll *Acanthis* skins from Greenland. Full details of each specimen can be found in Table 1.

to their 1936 specimen preparation style. Although Knox (1993) recorded two specimens as missing from the Bird brothers' 1936 series, there is now only a single redpoll skin from the entire NHMUK Bird brothers' Greenland series that cannot be accounted for. This is the October 1936 male registered as 1937.10.17.311 (listed in error by Knox as 1937.10.17.11), which Knox correctly deduced from plumage features must be specimen V. Contrary to Knox (1993), however, specimen U is almost definitely not a Bird brothers' skin.

5. *Finland, 1938*. Knox (1993) examined 21 redpoll skins, almost all 'exilipes' purportedly collected by Meinertzhagen in northern Finland in February/March 1938, and found that they fell into three groups based on external make-up. In Fig. 5, GG–II are three of the 17 specimens that Knox suggested from external appearance might be Meinertzhagen's own style of preparation, whereas KK, LL and NN are in a different style that Knox claimed closely matched a Moscow series obtained by NHMUK in the 1880s from the London dealer P. A. Holst and collected by a Dr Lenz (Sharpe 1888, 1906); according to Knox, the single representative of the third style is RR.

The radiographs concur with these conclusions by revealing pronounced differences in internal appearance between the three groups, but consistency within each of the two groups comprising more than one specimen. Furthermore, KK, LL and NN show very similar radiograph images to OO–QQ, which are all from the Moscow series; the intact

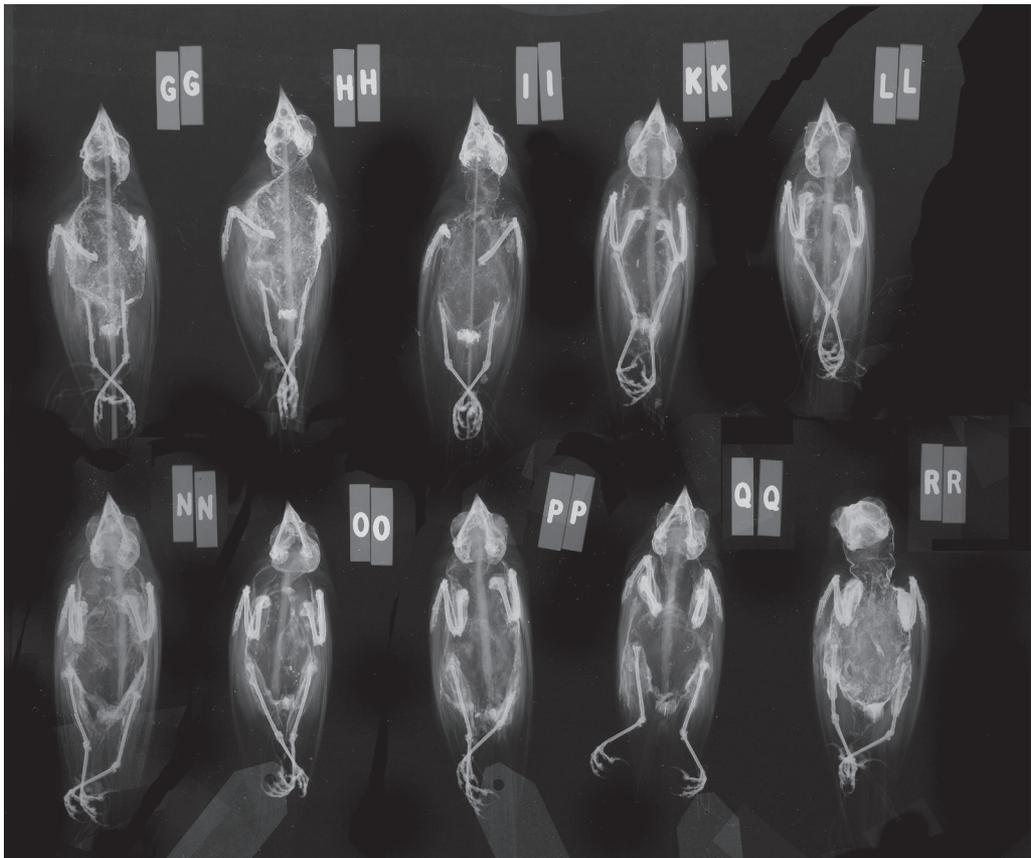


Figure 5. Radiographs of Meinertzhagen redpoll *Acanthis* skins from Finland (GG–NN and RR) and Lenz redpoll skins from Moscow, Russia (OO–QQ). Full details of each specimen can be found in Table 1.

humeri, carefully disarticulated from the pectoral girdle elements, are particularly striking in this regard. Although only two of Holst's Lenz redpolls registered into the NHMUK collection are now unaccounted for, a third might easily have been unregistered or acquired by Meinertzhagen from another collection (*cf.* Knox 1993).

**Evidence of arsenic.**—Samples of skin for arsenic analysis were removed from eight specimens: two of Meinertzhagen's Blois birds, one of which (C) closely matched the Hanwell series on both external and radiographic evidence, whereas the other (A) did not (Fig. 1); two Hanwell specimens (G and H) (Fig. 1); and four of Meinertzhagen's Scottish birds, three of which (L, M and O), comprising two different preparation styles, were highly x-ray opaque, whereas the fourth (P), identical in style to the Hanwell series, was not (Fig. 2). The results of testing unambiguously divided the specimens into two distinct groups. Five (A, C, G, H and P) contain no detectable arsenic, whereas the other three (L, M and O) each contain high levels of the element.

The three specimens re-analysed using stuffing recovered from their orbits included the two Hanwell birds, G and H, which again showed no evidence of arsenic above background levels despite having their stuffing visibly contaminated with an unidentified powder, presumably used during their preparation. The third was a Meinertzhagen Scottish specimen, O, for which the analysis again revealed the presence of substantial arsenic despite lacking visible preservative on its stuffing.

## Discussion

Taken as a whole, the results presented above amply confirm the main thrust of Knox's (1993) argument. There is very strong evidence from specimen preparation style (internal and external), in combination with current gaps in series of birds that were entered into the NHMUK registers, that Richard Meinertzhagen stole skins from the NHMUK and relabelled them with data that made it appear that he had collected them. This finding therefore confirms the informal and private conclusions of some influential ornithologists of an earlier generation who had studied specimen material from both the NHMUK's and Meinertzhagen's skin collections. As an example, around 1939/1940 Claud Ticehurst wrote to Hugh Whistler explicitly accusing Meinertzhagen of having stolen NHMUK skins of various Himalayan finch species he was studying, concluding 'But what a fool Dick [= Richard Meinertzhagen] is! Does he think for a moment that I am hoodwinked over these skins? Almost every skinner indelibly stamps his name on every skin he makes.' (NHMUK Archives).

Nevertheless, the present study also reveals some limitations as to what can be deduced from external examination of skins alone, highlighting that the above statement by Ticehurst on skin make-up style should be taken as no more than a generality. Skins that appear very similar externally can at times show much more obvious differences when their internal preparation style is investigated, as demonstrated by the way that Knox (1993) was misled into believing that specimen U (Fig. 3) could be from the Bird brothers' Greenland series (Fig. 4). The question of potential variability in the preparation style of individuals (including Meinertzhagen) over time, especially in an era when collectors frequently had assistants working with them who were not always acknowledged, also must be borne in mind.

Despite the above, it should be emphasised that the degree of variability exhibited in skin make-up style in specimens supposedly collected by Meinertzhagen himself at particular times and places is striking. Six redpoll skins (K–P, Fig. 2), supposedly taken by him over four days in 1920, are prepared in three different styles; of the three tested for arsenic, two involved its use as a preservative whereas one did not. Arsenic use appears to have been a characteristic of particular collectors; thus, for example, various Russian collectors such as Nikolai Przhevalsky made skins that are almost invariably highly opaque when x-rayed, and ornithologists such as Robert Tytler and Elliott Coues were so keen on using powdered arsenic that they may have suffered early deaths from its side effects (Prÿs-Jones *et al.* 2021). The limited evidence adduced in the current study suggests that skins are largely opaque due to arsenic use in their preparation, but that more limited opaque flecking, e.g. as exhibited by the Hanwell skins (D–J, Fig. 1), can have other causes.

A further complication that may intrude into interpretations of skin specimen preparation style is re-making, whereby a prepared skin is relaxed and then re-prepared. This tends to obscure, although not usually completely, both the external and internal handiwork of the original preparator, as described by Rasmussen & Collar (1999) and Kennerley & Prÿs-Jones (2006) in their respective analyses of the true origins of two fraudulent rarities in Meinertzhagen's collection, namely a Forest Owlet *Athene blewitti* and the supposed second European record of Gray's Grasshopper Warbler *Helopsaltes fasciolatus*. Re-making is unusual, however, and of the specimens discussed in this paper only U showed evidence of it, as described above.

Finally, it should be emphasised that the process of trying to restore original data to Meinertzhagen specimens that evidence indicates have been stolen and relabelled is fraught with difficulty and almost always must be treated probabilistically. The NHMUK bird skin

collection is enormous, approaching three-quarters of a million specimens, and in reconciling register entries with numbers of specimens currently present it is almost inevitable that inconsistencies will occur, as exemplified by the two specimens mentioned in the Results section that Knox (1993) was unable to locate. Even when specimens are seemingly unaccountably missing, there may be reasons other than theft for their apparent absence that require investigation (Knox & Walters 1992). Moreover, although Meinertzhagen spent most time working in NHMUK, he also visited many other museums, in particular the bird collection of Walter Rothschild, formerly at Tring but since the early 1930s largely held by the American Museum of Natural History, New York. The description of the activities of the ornithologist 'Dr. Cyril Cunningham', whom Miriam Rothschild (1983) recorded as stealing specimens from Walter Rothschild's collection and discarding their labels, in fact relates to Richard Meinertzhagen, although she did not wish this to become public knowledge during her lifetime (Prÿs-Jones *et al.* 2019). There is also strong evidence that Meinertzhagen removed specimens from other museums, including St Peterburg and Paris (C. Vaurie *in* Cocker 1989: 274) as well as Stockholm (C. Edelstam pers. comm.).

In conclusion, radiography has proved to be a valuable tool for confirming, and occasionally correcting, information derived from external skin appearance in documenting specimen fraud that Richard Meinertzhagen clearly committed during his ornithological career. A further paper will examine the apparent scope of such fraud with reference to Meinertzhagen's Asian bird collection.

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# Cryptic species-level diversity in Dark-throated Oriole *Oriolus xanthonotus*

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**SUMMARY.**—Borneo is part of the Sundaland biodiversity hotspot, yet this large tropical island still harbours much unrecognised biodiversity. In this integrative study, we combine the results from phylogenomic, bioacoustic, biometric and morphological analyses, and show that the Sundaic species Dark-throated Oriole *Oriolus xanthonotus* comprises two species-level taxa, both of which occur on Borneo. The eastern species, here re-named Ventriloquial Oriole *O. consobrinus*, is characterised by plumage distinctions, most notably a more male-like coloration in females, and a characteristic ventriloquial song unique among the region's orioles. The precise contact zone of the two species on Borneo is incompletely mapped. Their populations on Borneo show pronounced character displacement whereby individuals of *O. xanthonotus* on other landmasses are significantly larger than Bornean individuals, presumably to prevent non-adaptive hybridisation with the larger Ventriloquial Oriole along their Bornean contact zone.

Borneo, the third largest island on Earth, forms part of the South-East Asian equatorial rainforest belt known as Sundaland (Fig. 1). The island boasts unusually high avian diversity and is well known ornithologically for its distinct montane endemic avifauna, featuring roughly 1–2 dozen endemic bird species depending on taxonomic treatment (MacKinnon & Phillipps 1993, Eaton *et al.* 2021). However, despite being *c.*500 km from the nearest part

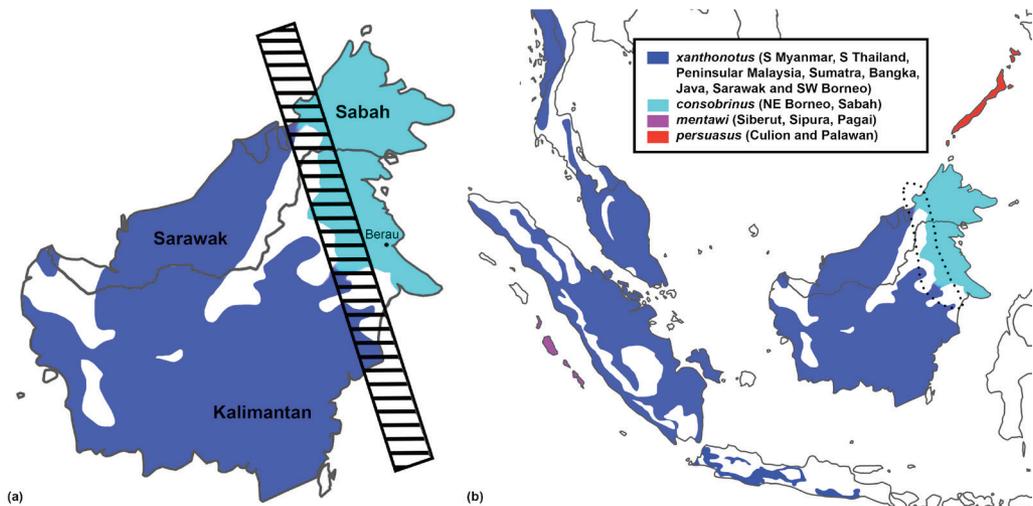


Figure 1. Distribution map of Dark-throated Oriole *Oriolus xanthonotus*, following Walther & Jones (2020). (a) Distribution of Bornean *O. x. xanthonotus* and *O. x. consobrinus*. Barred rectangle refers to possible contact zone between the two taxa. (b) Distribution map of all four taxa within the *O. xanthonotus* complex.

of the Asian mainland in the Malay Peninsula, Borneo's endemic lowland avifauna has traditionally been considered rather limited. In the taxonomic traditions of the 20th century, the vast majority of Borneo's lowland rainforest birds were considered part of more widely distributed Sundaic species whose ranges often also include Sumatra, Java and Peninsular Malaysia (MacKinnon & Phillipps 1993, Sheldon *et al.* 2015). It has taken a steady stream of molecular and bioacoustic work to reveal that the populations of some Bornean lowland or hill forest birds are more distinct than previously anticipated, a few even at species level, thereby further boosting the island's number of endemic species (Moyle *et al.* 2005, Lim *et al.* 2010, 2017, Moyle *et al.* 2011, Ng *et al.* 2016, 2017a, Gwee *et al.* 2019, Cros *et al.* 2020).

Borneo's distribution of lowland endemism constitutes one of the world's most unusual biogeographic patterns, whose origin continues to require a satisfactory explanation. The greatest part of Borneo's lowland endemic birds—both among species traditionally recognised and those elevated to species via recent research—is restricted to the north-east of the island. Here labelled 'Sabah endemics' or 'Sabah specialists', these species are almost entirely confined to the state of Sabah, although some are known to spill over slightly into adjacent parts of North and East Kalimantan, Sarawak, and even Brunei. Most Sabah endemics are replaced over the rest of Borneo by a more widespread sister species that usually also occurs on Sumatra, Peninsular Malaysia, and sometimes even Java. This biogeographic division into Sabah and the remainder of Borneo along a suture zone, comprising multiple roughly parallel contact zones among avian taxa, exists against the backdrop of a conspicuous lack of geographic boundaries (Sheldon *et al.* 2009, Rheindt 2021), as the position of Borneo's largest rivers and mountains is incongruent with the divide.

The cataloguing of Borneo's avian endemism remains far from complete. Recent taxonomic treatments have suggested that splits between Sabah and the rest of Borneo may become necessary in approximately another dozen bird species (Eaton *et al.* 2021). In this study, we present evidence for one such taxonomic split in the Dark-throated Oriole *Oriolus xanthonotus* complex. This species is a typical Sundaic rainforest denizen, distributed from the southernmost tip of Myanmar in the Thai-Malay Peninsula through Sumatra, Java and Borneo to Palawan, in the south-west Philippines. Four subspecies have long been recognised, two of which occupy smaller marginal islands (*mentawi* on the three main Mentawai Islands of Siberut, Sipora and Pagi, off western Sumatra, and *persuasus* on Palawan and some smaller satellites; Fig. 1). Among the two more widespread subspecies, *consobrinus* is said to be restricted to northern, central and eastern Borneo (including Sabah), whilst nominate *xanthonotus* occurs in the remainder of Borneo, Sumatra, Java and the Thai-Malay Peninsula. The precise boundary between the two subspecies on Borneo remains to be elucidated.

Recent genomic work on Old World orioles (Jønsson *et al.* 2019) has uncovered unexpected relationships and divergences among Asian oriole species that possibly warrant taxonomic adjustments. Most of these refer to island taxa or populations otherwise isolated geographically. However, one complex that stands out is the Dark-throated Oriole, with two distinctive forms co-occurring on one landmass (Borneo) and presumably overlapping or abutting in range. Here we present parts of Jønsson *et al.*'s (2019) genomic data and add bioacoustic, biometric and morphological analyses to propose dividing Dark-throated Oriole into two species.

## Materials and Methods

For genomic analyses and methods we refer to Jønsson *et al.* (2019). For phenotypic analyses, we measured 59 specimens of Dark-throated Orioles deposited in the Raffles

TABLE 1

List of specimens measured. All specimens are from the Raffles Collection in the Lee Kong Chian Museum of Natural History, Singapore.

Taxon	Landmass or state of collection	Locality	Collection date	Sex	Specimen registration number
<i>xanthonotus</i>	Sarawak	'Belingeang' (probably Bukit Belingan south of Miri)	17/05/1917	Male	3.18788
<i>xanthonotus</i>	Sarawak	'Bukar', Samarahan (near Kuching)	25/10/1919	Male	3.18789
<i>xanthonotus</i>	Sarawak	'Bukar', Samarahan (near Kuching)	15/11/1919	Male	3.1879
<i>xanthonotus</i>	Sarawak	'Saribas'	01/03/1932	Male	3.18795
<i>xanthonotus</i>	Sarawak	'Lio Matu, Baram District' (now Lio Matoh, near Miri)	13/10/1920	Male	3.1878
<i>xanthonotus</i>	Sarawak	'Lio Matu, Baram District' (now Lio Matoh, near Miri)	23/10/1920	Male	3.18781
<i>xanthonotus</i>	Sarawak	'Long Musan', Baram, Sarawak	05/10/1920	Male	3.18782
<i>xanthonotus</i>	Sarawak	'Borneo, Baram'	05/03/1905	Male	3.18783
<i>xanthonotus</i>	Sarawak	'Sungei Lenian, Tenjar, Baram'	24/08/1919	Male	3.18786
<i>xanthonotus</i>	Sarawak	'Saribas'	01/01/1917	Male	3.18791
<i>xanthonotus</i>	Sarawak	'Saribas'	15/05/(illegible)	Male	3.18794
<i>consobrinus</i>	Sabah	'Bettotan' (now Betotan), Sandakan	11/08/1927	Male	3.18702
<i>consobrinus</i>	Sabah	'Bettotan' (now Betotan), Sandakan	14/08/1927	Male	3.18704
<i>consobrinus</i>	Sabah	'Bettotan' (now Betotan), Sandakan	22/08/1927	Male	3.18707
<i>consobrinus</i>	Sabah	'Bettotan' (now Betotan), Sandakan	22/08/1927	Male	3.18708
<i>consobrinus</i>	Sabah	Kudat	19/09/1927	Male	3.18713
<i>consobrinus</i>	Sabah	'Bettotan' (now Betotan), Sandakan	08/08/1927	Male	3.18698
<i>consobrinus</i>	Sabah	'Bettotan' (now Betotan), Sandakan	27/07/1927	Male	3.18697
<i>consobrinus</i>	Sabah	Rayoh	28/06/1928	Male	3.18718
<i>consobrinus</i>	Sabah	'Bettotan' (now Betotan), Sandakan	09/08/1927	Male	3.18700
<i>consobrinus</i>	Sabah	'Banguey Island' (now Banggi)	6/09/1927	Male	3.18694
<i>consobrinus</i>	Sabah	Kudat	17/09/1927	Male	3.18714
<i>consobrinus</i>	Sabah	'Malawalle Island' (now Malawali)	08/1927	Male	3.18716
<i>consobrinus</i>	Sabah	'Banguey Island' (now Banggi)	02/09/1927	Male	3.18693
<i>consobrinus</i>	Sabah	'Bettotan' (now Betotan), Sandakan	11/08/1927	Male	3.18701
<i>consobrinus</i>	Sabah	Rayoh	19/06/1928	Male	3.18717
<i>xanthonotus</i>	Sarawak	Baram	05/03/1905	Female	3.18784
<i>xanthonotus</i>	Sarawak	'South Paku, Paku Saribas'	28/10/1916	Female	3.18793
<i>xanthonotus</i>	Sarawak	Baram, Borneo	05/03/1905	Female	3.18785
<i>xanthonotus</i>	Sarawak	Wai Sa... Baram, Borneo	27/10/1920	Female	3.18787
<i>consobrinus</i>	Sabah	'Bettotan' (now Betotan), Sandakan	08/1927	Female	3.18712
<i>consobrinus</i>	Sabah	Kudat	09/1927	Female	3.18715
<i>consobrinus</i>	Sabah	'Bettotan' (now Betotan), Sandakan	13/08/1927	Female	3.18703
<i>consobrinus</i>	Sabah	'Bettotan' (now Betotan), Sandakan	24/08/1927	Female	3.18711
<i>consobrinus</i>	Sabah	'Bettotan' (now Betotan), Sandakan	27/07/1927	Female	3.18696

<i>consobrinus</i>	Sabah	'Banguay Island' (now Banggi)	07/09/1927	Female	3.18695
<i>consobrinus</i>	Sabah	'Bettotan' (now Betotan), Sandakan	09/08/1927	Female	3.18699
<i>consobrinus</i>	Sabah	'Bettotan' (now Betotan), Sandakan	19/8/1927	Female	3.18705
<i>consobrinus</i>	Sabah	'Bettotan' (now Betotan), Sandakan	21/08/1927	Female	3.18706
<i>xanthonotus</i>	Malay Peninsula	Chong Trang, North Malay Peninsula	01/12/1909	Male	3.18755
<i>xanthonotus</i>	Malay Peninsula	Temengoh now Temengor, Perak	02/08/1909	Female	3.18751
<i>xanthonotus</i>	Malay Peninsula	Cheras, Selangor	18/3/1908	Male	3.18769
<i>xanthonotus</i>	Malay Peninsula	Pelipak, Johor	29/3/1905	Male	3.18776
<i>xanthonotus</i>	Malay Peninsula	Pelipak, Johor	27/3/1905	Female	3.18775
<i>xanthonotus</i>	Malay Peninsula	Gunung Angsi, Negri Sembilan	4/1906	Female	3.18771
<i>xanthonotus</i>	Malay Peninsula	Klang, Selangor	14/1/1909	Male	3.18770
<i>xanthonotus</i>	Sumatra	Kota Pinang	4/6/1937	Male	3.18797
<i>xanthonotus</i>	Sumatra	Kota Pinang	5/7/1937	Male	3.18798
<i>xanthonotus</i>	Sumatra	Kota Pinang	7/8/1937	Male	3.18799
<i>xanthonotus</i>	Sumatra	Kerinci, Sumatra	28/11/1914	Female	3.18796
<i>xanthonotus</i>	Sumatra	Padang, Sumatra	14/11/1934	Male	3.18800
<i>xanthonotus</i>	Java	Wynkoops Bay now Pelabuhan Ratu	13/3/1920	Male	3.18804
<i>xanthonotus</i>	Java	Wynkoops Bay	8/3/1920	Male	3.18803
<i>xanthonotus</i>	Java	Wynkoops Bay	8/3/1920	Male	3.18802
<i>xanthonotus</i>	Java	Wynkoops Bay	7/3/1920	Male	3.18801
<i>xanthonotus</i>	Java	Wynkoops Bay	19/3/1920	Male	3.18805
<i>persuasus</i>	Palawan (Philippines)	Puerto Princesa	17/09/1925	Female	3.18808
<i>persuasus</i>	Palawan (Philippines)	Puerto Princesa	08/08/1925	Female	3.18806
<i>persuasus</i>	Palawan (Philippines)	Puerto Princesa	13/08/1925	Male	3.18807
<i>mentawi</i>	Sumatra	Siberut Island	24/9/1924	Male	3.3968
<i>mentawi</i>	Sumatra	Sipora Island	20/10/1924	Female	3.3969
<i>mentawi</i>	Sumatra	Siberut Island	16/9/1924	Male	3.3967

Collection of the Lee Kong Chian Museum, Singapore, including three *persuasus*, three *mentawi*, 21 *consobrinus* and 32 nominate *xanthonotus* (Table 1). The latter taxon was represented by specimens from across multiple major landmasses (Table 1). Specimens were arranged according to taxon, landmass, collection date and sex, and were measured as follows: flattened wing length (from the carpal joint to the tip), maxilla length (from the tip to where the bill meets the skull), tail length (from the longest rectrix tip to the uropygial gland) and tarsus length (from tibiotarsus). Measurements of each parameter were performed by a single person (MYW: tail and wings; NM: maxilla and tarsus). All specimens were inspected for plumage coloration. Biometric comparisons of individuals from different landmasses and taxa were undertaken using principal component analysis (PCA) via the 'prcomp' function in R version 4.0.2 (R Core Team 2020), with PCA plots drawn using the 'ggplot2' package. We also carried out t-tests in R to identify any traits that might be significantly different between taxa.

Old World orioles are known for their fluty and variable songs. Song structure, including number of elements as well as their frequency and duration, varies greatly within and

among populations. Therefore, bioacoustic analyses that include sonogram measurements of individual call notes are not meaningful because of difficulties in assigning homology. Bioacoustic variability notwithstanding, Dark-throated Oriole calls can be assigned to particular call types within each population based on composite properties such as call structure, number of elements and frequency modulation. Some of these call types are specific to a particular taxon, whereas others are shared. Our bioacoustic analysis therefore centred on mapping the overlap of call types among different taxa. We gathered a total of 147 sound recordings from xeno-canto ([www.xeno-canto.org](http://www.xeno-canto.org)), the Macaulay Library (<https://macaulaylibrary.org>) and private recordings (B. van Balen; available on request) for qualitative inspection. These vocalisations were categorised into 11 and ten call types for the eastern and western populations, respectively.

## Results

**Genomic analysis.**—Jønsson *et al.* (2019) analysed two mitochondrial and two genome-wide DNA data partitions across the genus *Oriolus*. We summarise and provide additional detail on the results of each of these four datasets with emphasis on the Dark-throated Oriole complex (Fig. 2).

Analysis of the single mitochondrial gene ND2 (1,041 base pairs [bp]) uniquely encompassed individuals of all four subspecies, including island representatives for Java, Sumatra, the Thai-Malay Peninsula, Borneo, Palawan and Mentawai. This analysis revealed

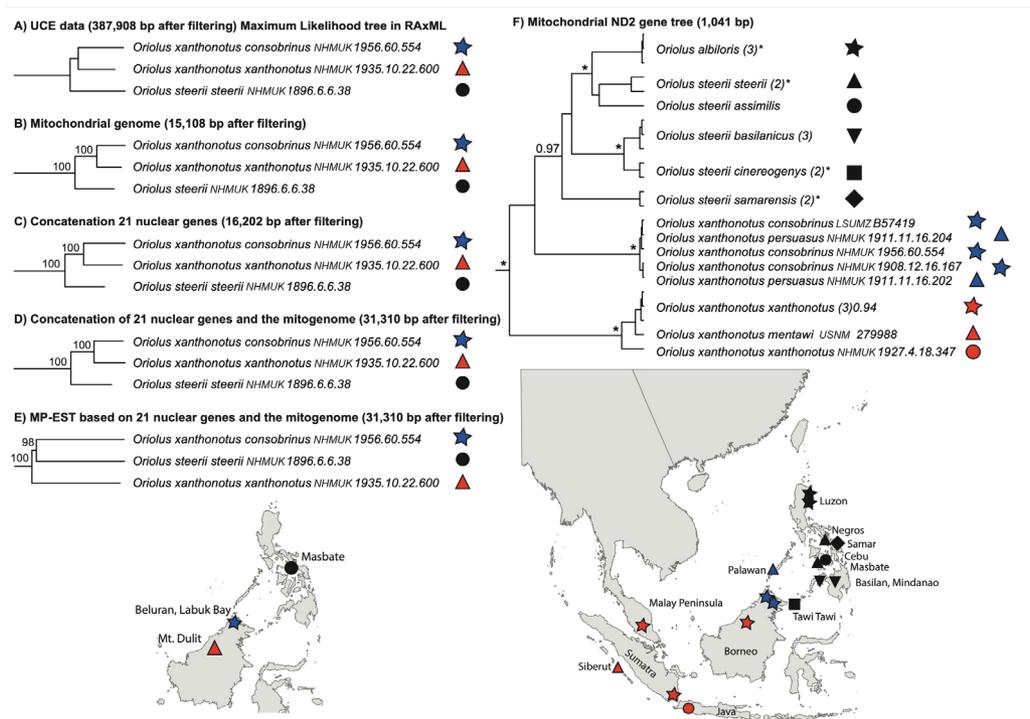


Figure 2. Phylogenetic trees based on four different data partitions adapted from Jønsson *et al.* (2019). A: nuclear ultraconserved element (UCE) loci; B: mitochondrial genomes; C: 21 independent nuclear sequence loci; F: mitochondrial NADH dehydrogenase 2 (ND2) gene sequences. D–E show trees based on a combination of the 21 nuclear sequence loci (C) and the mitochondrial genomes (B), constructed using the concatenation approach (D) and the species-tree approach as implemented in MP-EST (E). Maps show sampling localities for the phylogenetic trees placed above.

*O. xanthonotus* to be paraphyletic, with strong support for a closer relationship between the two eastern subspecies, *O. x. consobrinus* and *O. x. persuasus*, and the Philippine species White-lored Oriole *O. albiloris* and Philippine Oriole *O. steerii*, to the exclusion of the two western subspecies *O. x. xanthonotus* and *O. x. mentawi* (Fig. 2). Basal divergence between the 'western' dark-throated taxa (*O. x. xanthonotus* and *O. x. mentawi*) and the remaining orioles was estimated to have occurred c.7 million years ago, whereas divergence between 'eastern' dark-throated taxa (*O. x. consobrinus* and *O. x. persuasus*) and the two Philippine species was estimated to have occurred c.5 million years ago (fig. 1 in Jønsson *et al.* 2019).

For a smaller set of taxa representing all major *Oriolus* clades including an *O. x. xanthonotus* sample from Borneo, *O. x. consobrinus* and Philippine *O. steerii*, Jønsson *et al.* (2019) used shotgun sequencing to generate genome-wide sequences, resulting in the following four datasets:

In contrast to the single ND2 gene, analysis of more than 15,000 bp of the mitochondrial genome, containing ND2 and 15 other genes, supported monophyly of eastern and western representatives of Dark-throated Orioles (Fig. 2), with strong support for their being more closely related to each other than to Philippine Oriole (fig. 2B in Jønsson *et al.* 2019).

Analysis of a concatenation of 16 nuclear genes, amounting to >16,000 bp, agreed with the mitogenomic analysis in placing eastern and western Dark-throated Orioles closer to each other than to Philippine Oriole (Fig. 2; fig. 2C in Jønsson *et al.* 2019).

A concatenation of genome-wide ultra-conserved elements, amounting to almost 388,000 bp, and therefore surpassing the previous dataset almost 25-fold, had a more equivocal outcome: *O. x. xanthonotus* and *O. x. consobrinus* were placed as sister to each other, with Philippine Oriole as sister to these two, but with no strong branch support (Fig. 2). Moreover, the branch separating Philippine Oriole from the two dark-throated taxa was very short (fig. 2A in Jønsson *et al.* 2019).

In a species-tree analysis, as opposed to a concatenation analysis, using 21 nuclear genes and the entire mitogenome, *O. x. consobrinus* emerged as sister to Philippine Oriole, whilst nominate *O. x. xanthonotus* was more distant to these two, with fairly strong branch support (Fig. 2; bootstrap 98; see supplementary fig. S6 in Jønsson *et al.* 2019). This pattern was similar to the result of the ND2 analysis (Fig. 2). Species-tree analyses do not combine all loci into one super-alignment, but consider the phylogenetic information of each locus independently, and are widely regarded as the state of the art in phylogenetic analysis (e.g., Edwards *et al.* 2007).

**Morphometric analysis.**—The PCA plot for morphometric measurements clearly divided Sabah and Sarawak specimens along PC1, accounting for 38.8% of variation (Fig. 3). Generally, *O. x. xanthonotus* specimens from Sarawak grouped closer with *O. x. xanthonotus* individuals from the Thai-Malay Peninsula, Sumatra and *O. x. mentawi* from the West Sumatran Islands, whereas *O. x. consobrinus* from Sabah clustered more closely with *O. x. persuasus* from Palawan. Specimens of *O. x. xanthonotus* from Java were embedded with *O. x. xanthonotus* specimens from other landmasses (Fig. 3).

Morphometric measurements of Sabah vs. Sarawak specimens exhibited nearly non-overlapping ranges and significant differences in all parameters except tail length (Fig. 4). Javan *O. x. xanthonotus* emerged as significantly different in wing and tarsus length compared to other *O. x. xanthonotus* populations. In *O. x. mentawi* from the West Sumatran Islands, only wing length was significantly different from the nearby mainland Sumatran *O. x. xanthonotus* population.

**Plumage inspection.**—The plumages of *O. x. xanthonotus* from the Thai-Malay Peninsula were similar to those of *O. x. xanthonotus* from eastern Borneo but differed considerably

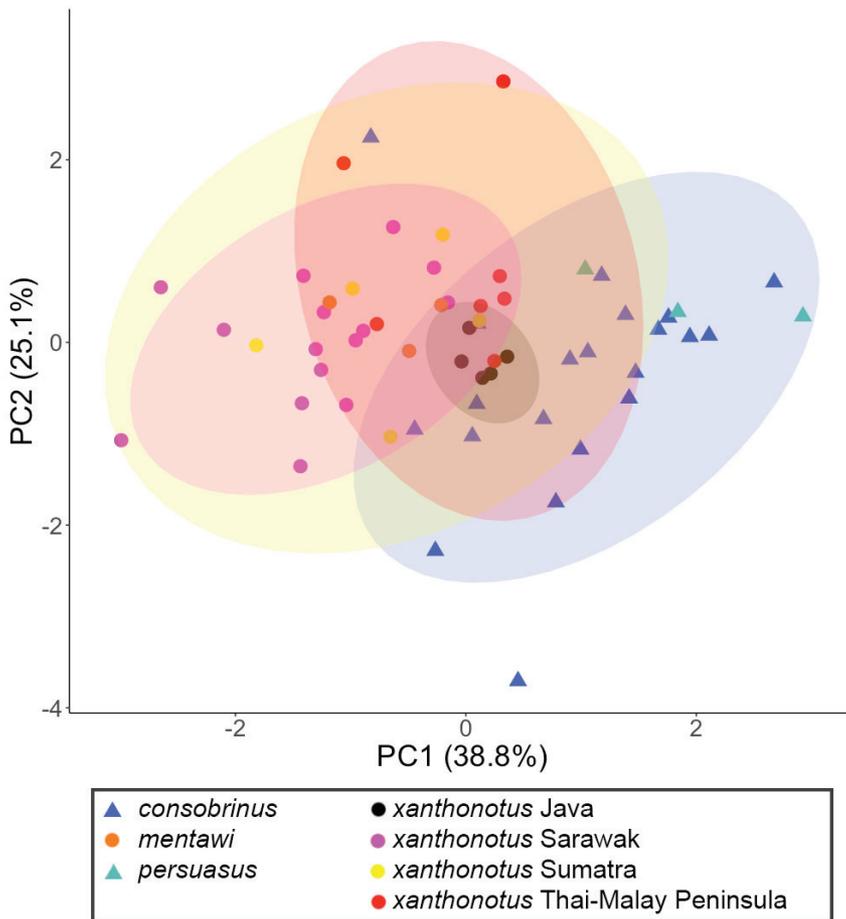


Figure 3. Principal component analysis plot for measurements across all four morphometric parameters. The 95% confidence interval ellipses are shown with the following colours: *O. x. consobrinus* (blue), *O. x. xanthonotus* Sarawak (pink), *O. x. xanthonotus* Java (grey) and the rest of the *O. x. xanthonotus* range (yellow). The percentage of total variation explained by each principal component (PC) is shown in parentheses.

from *O. x. consobrinus* in Sabah and *O. x. persuasus* on Palawan, which two showed similar plumage patterns.

Female *O. x. xanthonotus* has shorter, thinner and sparser streaking on the underparts, with a paler background coloration on the upper breast and a greyish-olive head that grades evenly into the upper mantle. This contrasts with female *O. x. consobrinus* and *O. x. persuasus*, which have longer, thicker and denser underparts streaking, a greyish background to the upper breast and a dark grey head that clearly contrasts with the upper mantle, giving their plumage a male-like character (Fig. 5).

Male *O. x. xanthonotus* also has shorter, thinner and sparser streaking on the underparts than both *O. x. consobrinus* and *O. x. persuasus*. Males of the latter show a diffuse border between the black throat and white upper breast, whereas *O. x. consobrinus* has a sharp divide between the black throat and white upper breast (Fig. 5).

**Bioacoustic analysis.**—We found two distinct vocal groups within the Dark-throated Oriole complex based on visual inspection of sonograms. Populations in the Thai-Malay Peninsula, Sumatra and Sarawak constitute one group separate from populations of Sabah and Palawan. Each of the two groups is characterised by sets of song and call types that

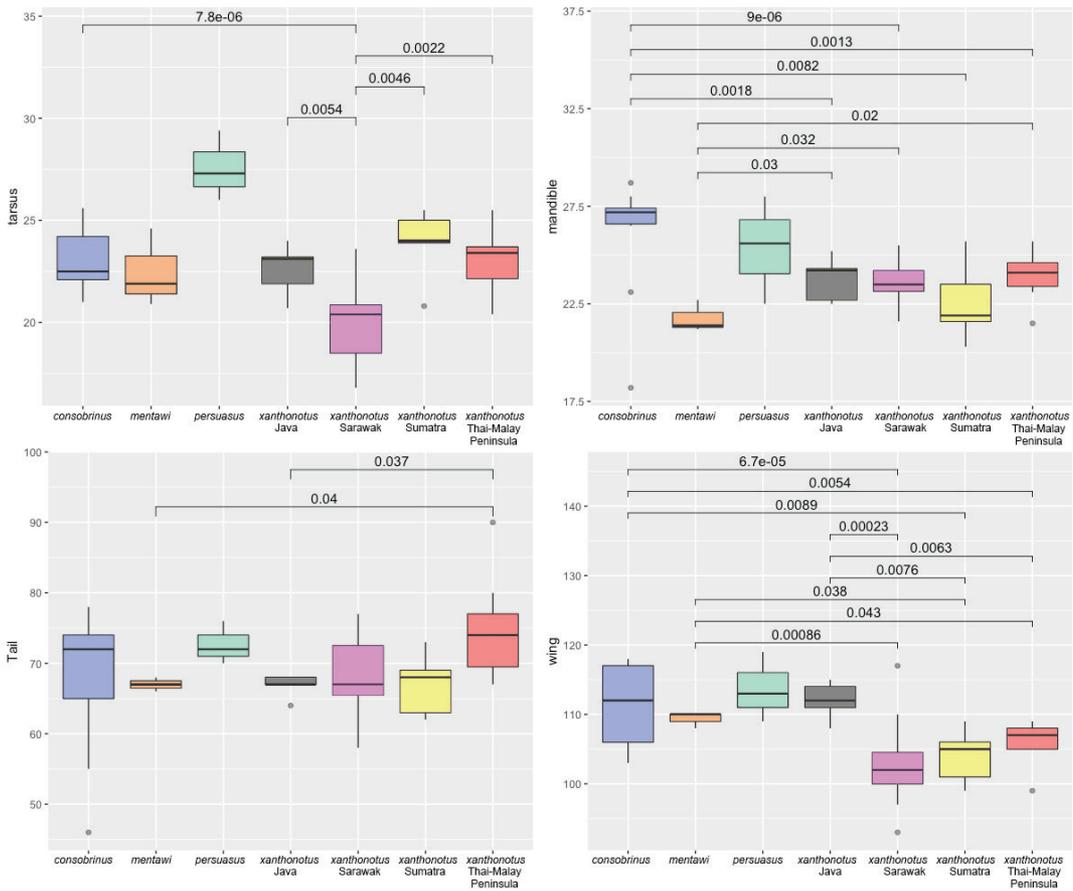


Figure 4. Box plots of morphometric measurements for tarsus (upper left), tail (lower left), maxilla (upper right) and wing length (lower right). Significant  $p$  values are shown above the plots for each corresponding pairwise comparison. Wing and tarsus comparisons involving *O. x. persuasus* overwhelmingly emerged as significant, and are not shown because of space constraints.

do not overlap (Figs. 6–7). At the same time, each group was found to emit call types of either inflected or deflected single notes which, however, differ greatly in duration between groups (Figs. 6–7: top row).

In contrast to the more conventional fluty multisyllabic oriole calls uttered by nominate *O. x. xanthonotus* (Fig. 6), the commonest calls in the Sabah and Palawan populations (*O. x. persuasus* and *O. x. consobrinus*) have a distinct ventriloquial quality (Fig. 7), more reminiscent of the sympatric Bornean Black Magpie *Platysmurus aterrimus*. Many of these ventriloquial calls exhibit a three-note structure, but with variations, sounding roughly like a monotonous *du-du-duuuu* with a variable ending, either inflected (e.g. XC 360969, XC 269344) or deflected (e.g. ML 202577).

Whilst *O. x. xanthonotus* from Java shares multiple call types with remaining nominate populations, we detected two unique call types (Fig. 6, blue frame) with a ‘bulbul-like’ (XC 618465) or ‘plaintive cuckoo-like’ (XC 393776) quality, quite unlike the typical fluty timbre that characterises the vocalisations of other populations. However, because of a low vocal sample size for Java, it is unclear whether these calls are of taxonomic importance or are merely rare vocal variants.



Figure 5. Photographs of female (left column) and male (right column) Dark-throated Oriole *Oriolus xanthonotus* specimens at the Lee Kong Chian Natural History Museum (Singapore). Dorsal (top row), ventral (middle row) and lateral views (bottom row). Specimens grouped by taxa, from left to right: Peninsular Malaysian *O. x. xanthonotus*, *O. x. mentawi*, *O. x. consobrinus* and *O. x. persuasus* (females); Peninsular Malaysian *O. x. xanthonotus*, Javan *O. x. xanthonotus*, *O. x. mentawi*, *O. x. consobrinus* and *O. x. persuasus* (males) (Movin Nyanasengeran)

## Discussion

**Character displacement on Borneo.**—Steep mensural differences between the two species on Borneo suggest that ecological and evolutionary character displacement may be moulding their body size and shape. Character displacement—also termed reinforcement—is an evolutionary phenomenon whereby populations of closely related species possess similar traits across most of their non-overlapping ranges, but adopt greater trait differences in areas where they co-occur thereby preventing competition (Brown & Wilson 1956, Hoskin *et al.* 2005). In South-East Asian birds, character displacement has been mapped for vocal traits in *Ptilinopus* fruit doves (Rheindt *et al.* 2011) and *Rhipidura* fantails (Ng *et al.* 2017b), but also for mensural characters in *Pachycephala* whistlers (Ashari *et al.* 2018) in a pattern reminiscent of Dark-throated Orioles on Borneo.

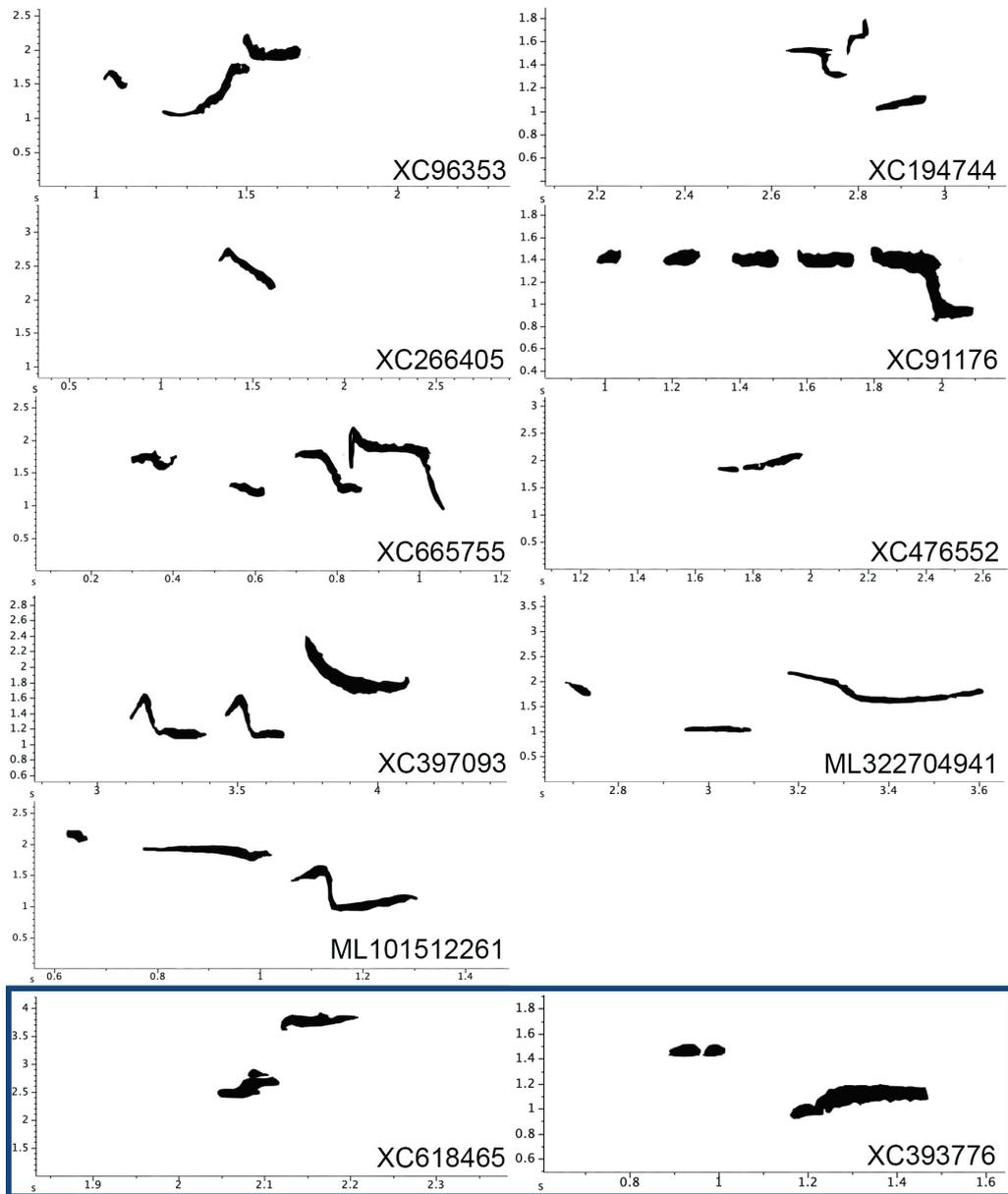


Figure 6. Sonograms of typical examples of the 11 song and call types identified across the Malay Peninsula, Sumatra, Java and Sarawak, reflecting the distribution of *O. x. xanthonotus*. Javan individuals were found to utter two unique call types that differ from all other recordings (blue frame). Frequency axis in kHz.

Measurements of tarsus length, wing length and bill length suggest that easterly *O. x. consobrinus* from Sabah is considerably larger than Bornean populations of nominate *O. x. xanthonotus*, with almost non-overlapping size ranges (Fig. 4). In a PCA combining all four morphometric characters, the ‘clouds’ of these two groups are nearly non-overlapping (Fig. 3). However, when Sabah *O. x. consobrinus* is compared with nominate *O. x. xanthonotus* outside Borneo, we find a large overlap in measurements, and differences are not significant (Figs. 3–4). Measurements of both Bornean populations (*O. x. xanthonotus* and *O. x.*

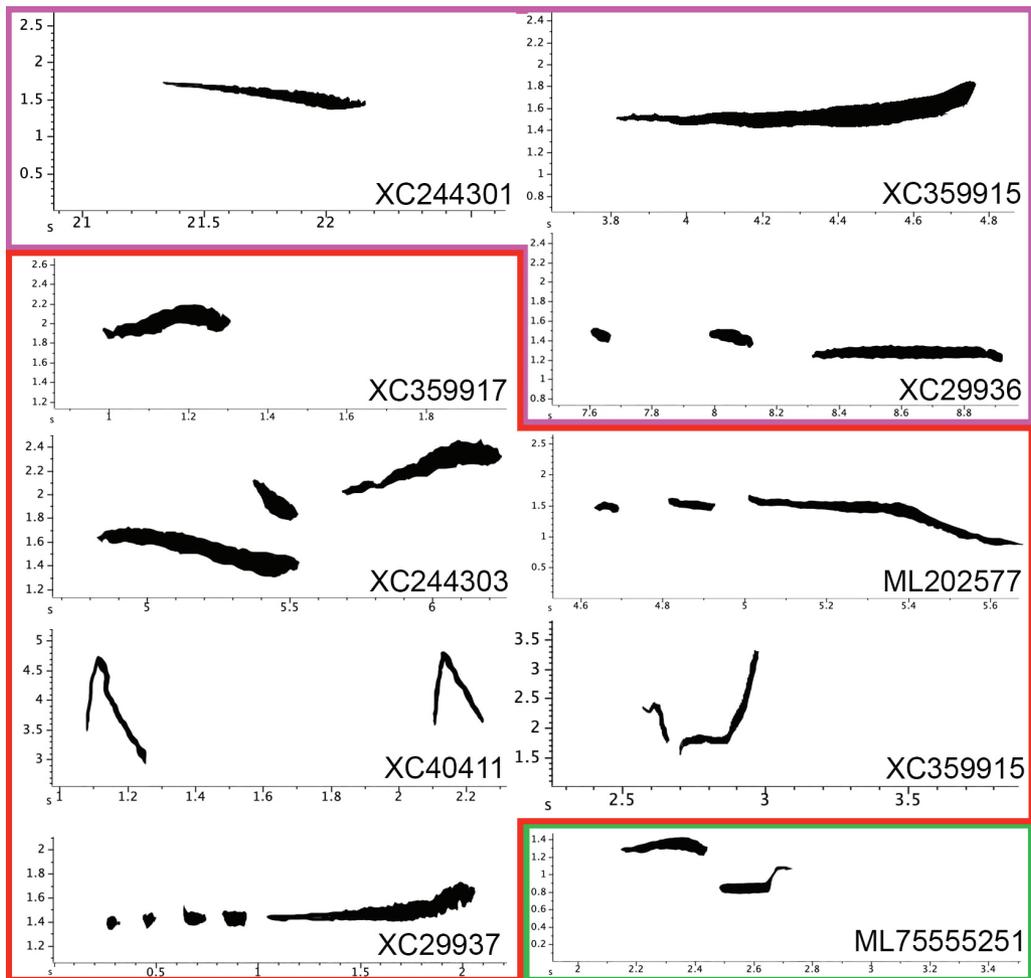


Figure 7. Sonograms of typical examples of the ten song and call types identified across Sabah and Palawan, reflecting the distribution of *O. x. consobrinus* and *O. x. persuasus*. The two populations shared three common call types (purple), whilst other call types may be distinct to each population, Sabah (red) and Palawan (green). Frequency axis in kHz.

*consobrinus*) may be driven apart to minimise the chances of reproductively suboptimal hybrid offspring in their contact zone. In biological terms, this has led to a Dark-throated Oriole (*O. x. xanthotus*) on Borneo that is much smaller than populations throughout the rest of the range, and outsize by the *O. x. consobrinus* which it encounters on Borneo.

**Mapping the contact zone in Borneo.**—The precise extent of the ranges of various Sabah endemics or Sabah specialties on Borneo remains incompletely known, especially for taxa that have only recently been recognised at species level (e.g. Glissando Babbler *Pellorneum saturatum* vs. Leaflietter Babbler *P. poliogene* and others; Eaton *et al.* 2021, Garg *et al.* 2022). The same uncertainty applies to Dark-throated Orioles. Whilst the internet permits access to much photographic and sound material from Sabah, there is hardly any such material from the rest of Borneo. As of November 2021, sound recordings deposited on [www.xeno-canto.org](http://www.xeno-canto.org) indicated that *O. x. consobrinus* extends south from Sabah at least to the Berau District of East Kalimantan (Fig. 1), where a recording by I. Woxvold has the vocal hallmarks of eastern *O. x. consobrinus* (XC 65382). Further north, the transition

between the two appears to be close to the borders of Sabah, as recordings and personal observations from Brunei indicate the presence of the western (*O. x. xanthonotus*) fluty song and plumage types there (NM pers. obs.). Field ornithologists and hobby birdwatchers can contribute much to our understanding of Bornean ornithology by filling such knowledge gaps and thereby helping to achieve a more complete mapping of the distribution of the island's bird species.

**Genomic evidence for a split.**—Jønsson *et al.*'s (2019) extensive genomic analyses produced a surprisingly heterogeneous picture of the phylogenetic relationships of Dark-throated Oriole taxa and closely allied species in the Philippines. Analysis of a widely used mitochondrial gene unexpectedly pointed to a close relationship between the two eastern subspecies of Dark-throated Oriole (*O. x. consobrinus* and *O. x. persuasus*), Philippine Oriole and White-lored Oriole, whereas western dark-throated taxa (*O. x. xanthonotus* and *O. x. mentawi*) were phylogenetically more distant (Fig. 2). Importantly, this paraphyletic arrangement of the Dark-throated Oriole was backed by strong branch support and would have been widely interpreted as reflecting the true relationships in the complex *c.*10–20 years ago before the advent of modern next generation sequencing technology. After expanding the mitochondrial dataset to include 15 additional genes, however, Jønsson *et al.* (2019) found that the odd paraphyletic arrangement of Dark-throated Orioles was not corroborated (Fig. 2), and that they may—after all—form a monophyletic species.

Use of mitochondrial DNA in phylogenetics is known to generate artefactual relationships in cases when DNA introgression and instances of hybridisation may have confounded its gene tree (e.g. Rheindt & Edwards 2011, Andersen *et al.* 2021). A new era of phylogenomics based on genome-wide DNA has revolutionised the field and made routine the use of nuclear DNA loci. The most extensive nuclear dataset analysed by Jønsson *et al.* (2019) encompassed almost 388,000 bp from across the nuclear genome of these orioles, surpassing the volume of the mitogenomic dataset 25-fold. This expansive dataset provided only weak support for a monophyletic placement of eastern and western Dark-throated Orioles (Fig. 2). In addition, a species-tree analysis of 21 nuclear genes combined with the mitogenomes shifted support back to placing eastern *O. x. consobrinus* closer to Philippine Oriole rather than to western *O. x. xanthonotus* (Fig. 2).

In summary, the most likely explanation for the heterogeneous outcome of phylogenomic analyses—despite the massive DNA sequence volumes investigated—is a similar timing for the split among three lineages, one of which is the ancestor of White-lored and Philippine Orioles, whilst the other two represent the eastern and western subspecies groups of Dark-throated Oriole, respectively. The earlier timing of the split between eastern and western Dark-throated Orioles, preceding the diversification between this lineage of orioles in the Philippines, strongly supports elevation of the eastern genetic clade of Dark-throated Oriole to species level as *O. consobrinus*.

**Biological evidence for a split.**—Our morphometric and plumage analyses largely corroborate the work of early museum taxonomists who documented considerable differences in coloration especially in females. Eastern females are considerably more contrasting, saturated and male-like in appearance, and no cline in such coloration differences was evident in our sample of 59 specimens. Male differences, while less pronounced, are nevertheless readily discernible in the field and in specimens (Fig. 5). There is variation in the female plumage, with *consobrinus* exhibiting a more blackish crown similar to male plumage compared to *xanthonotus* on Borneo. This tendency for females to develop male-like plumage occurs elsewhere in the genus *Oriolus* but rarely in sympatry (e.g., Black-and-crimson Oriole *O. cruentus*; Kirwan *et al.* 2021). In the parapatric

populations of *consobrinus* and *xanthonotus* on Borneo, these differences in female plumage may present a prezygotic impediment to gene flow.

Furthermore, there are substantial bioacoustic differences between eastern and western Dark-throated Orioles, which may even outweigh the color differences in reproductive importance. The western subspecies group utters many versions of a typical multisyllabic fluty oriole song (Fig. 6) roughly reminiscent of other species in the region (e.g., Black-naped Oriole *O. chinensis*). This typical fluty song is unknown in the eastern subspecies group, whose primary vocalisations chiefly comprise a series of ventriloquial calls reminiscent of Bornean Black Magpie *Platysmurus aterrimus* (Fig. 7).

On the combined basis of phylogenomic, biometric, bioacoustic and plumage data, we propose that the two eastern subspecies of Dark-throated Oriole (*O. x. consobrinus* [northern and eastern Borneo] and *O. x. persuasus* [Palawan]) be recognised as a separate species, *O. consobrinus*. We propose ‘Ventriloquial Oriole’ as the vernacular name of this newly recognised species, reflecting its characteristic song, which is unique among the region’s orioles. The western subspecies group—nominate *O. x. xanthonotus* and *O. x. mentawai*—still occupies the largest part of the distribution of this complex; therefore retention of the name ‘Dark-throated Oriole’ for the western group appears to be the best solution leading to the least nomenclatural disruption.

**Taxonomic uncertainty of the Javan population.**—‘*Oriolus Xanthonotus*’ [sic] was first described by Horsfield in 1821 with ‘Java’ as its type locality, rendering the taxonomic identity of the Javan population of special importance. In plumage and morphometrics, Javan specimens squarely fit within the range of variation displayed by nominate *O. x. xanthonotus* on other landmasses, especially Sumatra and the Thai-Malay Peninsula (Figs. 3–5). Therefore, use of the subspecies name *xanthonotus* as a moniker for the more westerly species of Dark-throated Oriole is not in doubt. In mtDNA, Javan populations are characterised by the deepest divergence within the *O. x. xanthonotus* cluster (Fig. 2), but still compatible with subspecies status. Vocal material from Java is currently limited, consistent with the defaunation that has occurred here during the last three decades (Eaton *et al.* 2015, Symes *et al.* 2018, Verma *et al.* 2020) leading to this population’s decline and endangerment. Whilst the existing vocal material is suggestive of some potential differentiation of Java’s nominotypical population (Fig. 6, blue frame), the possibility of unusual call variants cannot be eliminated, and more extensive sampling of Javan call notes is required.

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# First observations of parental care in Screaming Piha *Lipaugus vociferans*

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The family Cotingidae is endemic to the Neotropics and is notable for species that possess a great diversity of plumage ornaments and sounds, in addition to elaborate courtship behaviour (Podos & Cohn-Haft 2019, Winkler *et al.* 2020). In addition to its 'showy' representatives, e.g. species in the genera *Rupicola*, *Phoenicircus* and *Cotinga*, it also contains visually inconspicuous species like most of the genus *Lipaugus*.

Screaming Piha *Lipaugus vociferans* occurs in the humid Amazonian lowlands of northern South America with a disjunct population in the Atlantic Forest of eastern Brazil (Suzuki *et al.* 2020). It occupies the forest midstorey, mostly in dry-land upland forest, but also locally in seasonally flooded forest (Kirwan & Green 2011). Individuals are grey with no sexual dimorphism in plumage (Suzuki *et al.* 2020). Males gather in leks where they give their loud and unmistakable vocalisations (Kirwan & Green 2011).

The reproductive biology of most cotingids is poorly known. Data on parental care are scarce in the literature and difficult to obtain in the field, even for widely distributed and abundant species such as *L. vociferans* (Winkler *et al.* 2020). Here, we present new data on parental care for this species, as well as information about nestling diet and length of stay in the nest. We observed the nest for a total of ten hours, using binoculars and digital cameras with 50× and 60× zoom lenses. Videos and photographs were analysed to identify dietary items and deposited in the Macaulay Library via the eBird platform ([www.ebird.org](http://www.ebird.org)). The nest's height above ground was calculated using a Bushnell Yardage Pro Sport 450 Laser Rangefinder.

On 25 September 2021, we found a nest in an area of upland forest in the grounds of the Iracema Falls Hotel, municipality of Presidente Figueiredo, Amazonas, Brazil (01°58'59.34"S, 60°03'04.67"W). An adult *L. vociferans* was initially noticed holding an unidentified arthropod in its bill. Because the bird did not swallow the prey immediately, we continued to watch, suspecting it might be feeding young. After a few minutes, it flew to the nest, and fed a chick that we estimated to be five days old, given the presence of down covering the body. After feeding the chick, the adult remained at the nest for the next 15 minutes. The nest lacked a well-defined shape and comprised thin branches and rhizomorph fungus (Figs. 1, 2 and 4), best classified as a simple platform *sensu* Simon & Pacheco (2005). It was c.4 m from the forest edge, supported at the sides in a fork of narrow branches 11 m above ground. The nest tree was approximately 12 m tall and <30 cm dbh. The area around the nest held several *Euterpe* sp. palms, which may have contributed to the adult's choice of nest site.

We revisited the nest on 3, 9 and 12 October. We observed the adult leave the nest nine times, taking on average 22 minutes to return (min. 8, max. 89 minutes), permitting us to observe eight provisioning events (Table 1; ML 393817191, ML 393819751 and WA 4707161). On 3 October, the nestling, which had pink skin and a pale grey bill, still lacked wing-coverts, but already had feather pins, mainly on the wings, back and head, and the eyes appeared to be starting to open (Fig. 1). Usually, when the adult left the nest, it immediately



Figure 1. Adult Screaming Piha *Lipaugus vociferans*, covering the chick in the nest, Iracema Falls Hotel, Presidente Figueiredo, Amazonas, Brazil, 3 October 2021 (Priscilla de Jesus Diniz)



Figure 2. Nestling Screaming Piha *Lipaugus vociferans*, Iracema Falls Hotel, Presidente Figueiredo, Amazonas, Brazil, 9 October 2021 (Tomaz Nascimento de Melo)



Figure 3. Screaming Piha *Lipaugus vociferans* fledgling outside the nest, Iracema Falls Hotel, Presidente Figueiredo, Amazonas, Brazil, 12 October 2021 (Tomaz Nascimento de Melo)

TABLE 1  
Food items brought by the adult Screaming Piha *Lipaugus vociferans* to the nest.

Visit	Day	Food item	Description
1	3 October 2021	Fruit	Red fruit (perhaps <i>Erythroxylum</i> )
2	3 October 2021	Fruit	Probably <i>Euterpe/Oenocarpus</i> fruit
3	3 October 2021	Invertebrate	Orthopteran
4	3 October 2021	Invertebrate	Orthopteran (Tettigoniidae)
5	3 October 2021	Invertebrate	Araneae
6	9 October 2021	Anura	Green frog (eaten by the adult bird)
7	9 October 2021	Invertebrate	Unidentified arthropod
8	9 October 2021	Invertebrate	Unidentified arthropod
9	12 October 2021	Anura	Green frog

disappeared and was seen again only when it approached the nest. However, four times the adult concentrated its search for food in a radius *c.*100 m from the nest. On these occasions, it was observed foraging 10–15 m above ground.

Twice, we saw the adult bring a tree-frog of the genus *Boana* (Hylidae) to the nest. The first time, after a few seconds, the adult tried to feed the chick, which did not accept the food, and the adult subsequently swallowed the frog (Table 1; Fig. 4D). Similar behaviour was observed by a Rufous Piha *Lipaugus unirufus* in Costa Rica, with the adult swallowing food that the chick had refused several times (Kirwan & Green 2011). On 12 October, we again observed the adult bring a green frog to the nest, similar to the species in the first observation, but this time the nestling swallowed the food immediately upon it being proffered.



Figure 4. Food items brought to the nest by the adult Screaming Piha *Lipaugus vociferans*: (A) the chick with a probable *Euterpe/Oenocarpus* fruit that it was unable to swallow and subsequently dropped; (B) adult delivering an unidentified spider to the young; (C) adult delivering an orthopteran to the young; (D) adult offering an anuran to the nestling, which it later swallowed itself (see text) (Tomaz Nascimento de Melo)

On 9 October, we observed agonistic behaviour from the adult while at the nest, in response to the approach of a flock of Red-rumped Caciques *Cacicus haemorrhous*. The adult chased away a cacique as soon as it landed in the nest tree and then returned to the nest. Aggressive nest defence behaviour has been previously reported for *L. vociferans* and another Cotingidae, Purple-throated Fruitcrow *Querula purpurata* (Sick 1997). On the same day, we could see that the chick was completely covered in brownish feathers, with darker wing-coverts. The bill and eyes had adult-like coloration (Fig. 2). On the last day of observations (12 October), the young was already perched just beside the nest (Fig. 3). We thus infer that the chick fledged at age *c.*23–24 days.

Although *L. vociferans* is one of the commonest Cotingidae throughout its range, little is known concerning its reproductive biology (Kirwan & Green 2011). Nests in Brazil and French Guiana, built 7–12 m above ground, were of similar shape and composition to that described here, and also had a single egg or nestling (Érard 1982, Oniki & Willis 1982, Sick 1997, Buzzetti & Silva 2005). Parental care had not previously been described. During our observations, just one adult was seen at the nest at any one time. Although we cannot be sure it was always the same individual, in our experience, when both parents participate they are regularly seen together near the nest. Thus, we suspect single-parent care, consistent with female-only nesting behaviour described for other lekking cotingids (Kirwan & Green 2011). Nestling time (estimated at 23–24 days) is marginally shorter than in congeners. However, we may have under-estimated the chick's age at discovery. Cinnamon-vented Piha *L. lanioides* takes 25–26 days to fledge and Rufous Piha *L. unirufus* *c.*28–29 days (Skutch 1969, Willis & Oniki 1998).

*L. vociferans* feeds mainly on fruits and invertebrates (Kirwan & Green 2011). Consumption of vertebrates, like the small frogs we observed, has been reported only once before: a lizard of the genus *Anolis* (Whittaker 1996). Vertebrate predation, however, is known for at least 12 other cotingid species, amphibians being the second most preyed upon group after lizards (Lopes *et al.* 2005).

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# The type specimens of *Urospizias dampieri* Gurney Sr., 1882

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John Henry Gurney Sr. (1819–90) examined a series of raptors collected by Lieutenant (later Rear-Admiral) George Edward Richards (1852–1927) in New Britain that had been passed to him for examination by Canon H. B. Tristram (Gurney 1882a). Among them were three adult females, all taken at Blanche Bay in June 1879, of a species that he considered with some reservations to be *Urospizias etorques* Salvadori, 1875, from New Guinea, which is now treated as a junior synonym of *Accipiter hiogaster leucosomus* (Sharpe, 1874). Gurney (1882a) in fact based this assessment on four New Britain specimens, the three received via Tristram plus an adult male, collector unstated, preserved in the then British Museum (now Natural History Museum, NHMUK). His reservations were largely the result of not having to hand an adult *U. etorques* from New Guinea with which to compare the New Britain specimens.

Shortly thereafter, Gurney (1882b) revisited the issue, the Norwich Museum (later Castle Museum, Norwich) having now obtained an adult female *U. etorques* from the Astrolabe Mountains, New Guinea, collected by Andrew Goldie. This persuaded him that the New Britain specimens indeed formed a new species, which he named *Urospizias dampieri*, now *Accipiter hiogaster dampieri*, after the famous navigator William Dampier (1651–1715), who in 1699 had been the first European to discover the New Britain archipelago. As evidence, Gurney noted the smaller size of the New Britain females, as well as reiterating subtle plumage distinctions that he had previously mentioned (Gurney 1882a), derived from Salvadori's (1880) discussion of *U. etorques*. Although presenting mensural details for the New Guinea bird newly to hand, Gurney (1882b) did not repeat them for the New Britain birds, but instead referred to those already presented in Gurney (1882a).

Possibly due to this lack of precise mention of the relevant New Britain specimens in the species description by Gurney (1882b), the syntypes on which this taxon was based appear to have been overlooked subsequently. Checking the published catalogue of Tristram (1889: 59) reveals that he retained two of Richards's specimens (*a* and *b* under *Astur etorques*), which subsequently passed with much of his bird collection to what is now National Museums Liverpool (NML); these specimens are now registered as NML-VZ

TABLE 1  
Details of the syntypes of *Urospizias dampieri*, Gurney Sr., 1882.

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NML-VZ T10112 Female. Blanche Bay, New Britain. 22 June 1879. Coll. G. E. R[ichards]. Iris brown. Feet orange. Bill black, yellow at base.
NML-VZ T4422 Female. Blanche Bay, New Britain. 26 June 1879. Coll. G. E. R[ichards]. Iris brown. Feet orange. Bill black, yellow at base.
NHMUK 1955.6.N.20.2707 Female. Blanche Bay, New Britain. 26 June 1879. Coll. G. E. R[ichards]. Iris brown. Feet orange. Bill black, yellow at base.
NHMUK 1881.3.29.1 Male. New Britain. May 1878. G. B[rown].

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T10112 and NML-VZ T4422 (Table 1). However, there is no mention of them in the bird type catalogue of Wagstaffe (1978).

The third Richards specimen was passed with the rest of Gurney's raptors, previously held in the Castle Museum, Norwich, to NHMUK in 1954, where it is now registered as 1955.6.N.20.2707 (Table 1). Based on both the Gurney collection label it bears and on his complete but unpublished birds of prey catalogue (1889–91), this was seemingly acquired by Gurney for the Norwich Museum via Philip Sclater at the Zoological Society of London. This had already happened by the time Gurney (1884) revisited identification issues concerning *dampieri*, when he additionally confirmed that this specimen was one of the syntypes used in the original description. Again, however, there is no mention of it in the NHMUK bird type catalogue (Warren 1966).

The extremely limited information that Gurney (1882a) presented about the identity of the fourth specimen he examined amounted to merely that it was a male and in the British Museum. Nevertheless, checking the registers and collection of NHMUK indicates that it must have been specimen 1881.3.29.1, collected in New Britain in May 1878 by the Revd. George Brown (1835–1917), a Methodist missionary to Melanesia (see Beolens *et al.* 2014). Gurney (1882a) was published in January 1882, suggesting that he must have examined material he referenced therein prior to autumn 1881. Brown's specimen 1881.3.29.1 was accessioned into the British Museum collection in March 1881, in good time for this to have happened, and it is the sole male *dampieri* specimen present of which this is true. This specimen is also not mentioned by Warren (1966).

We therefore conclude that the four syntypes of the name *Urospizias dampieri* Gurney Sr., 1882, are those listed in Table 1.

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