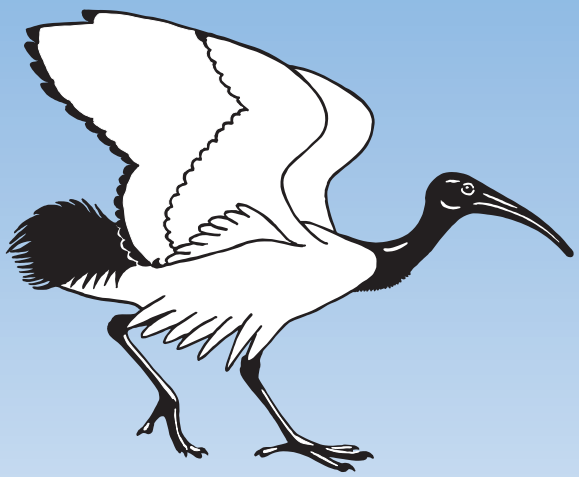
Bulletin of the British Ornithologists' Club



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CLUB ANNOUNCEMENTS

The 1014th meeting of the Club was held in the upstairs room at the Barley Mow, 104 Horseferry Road, London, SW1P 2EE, on 24 March 2025. Twenty-three people were present: Ms L. August, Mr J. Boorman, Ms R. Bowie, Ms C. Calvet, Cdr. M. B. Casement, RN, Mr S. Chapman, Dr R. A. Cheke, Mr A. Jackson, Mr M. Jennings, Mr R. Langley, Ms C. O'Carrol, Mr R. Portela-Miguez, Dr O. Prŷs-Jones, Dr R. Prŷs-Jones, Dr A. Richford, Mr D. Russell (*Speaker*), Ms A. Salvador, Mr G. de Silva-Wijeyeratne, Mr C. Slater, Mr C. W. R. Storey (*Chairman*), Ms L. Vaughn-Hirsch, Mr G. Wallbridge, Ms J. White.

Birds' nests, traditionally something of a 'Cinderella' subject in lectures on ornithology, seem recently to have come into their own during Club meetings. After the presentation by Dr Catherine Sheard in May 2024 on what birds' nests can teach us about evolution, less than one year later Douglas Russell, Senior Curator of Eggs and Nests at the Natural History Museum, Tring, spoke on *Interesting bird nests & eggs*, subtitled 'writing a popular book on 250 years of avian architecture'. This drew on the huge collections for which he is responsible and, more particularly, on his 2024 book of the same title that overviews them, which was enthusiastically reviewed in the last issue, *Bull. Brit. Orn. Cl*. 145: 1–2. For each of a broad cross-section of bird families, Douglas used a particularly interesting example, usually nest and egg(s), occasionally one or other only, and spanning specimens collected over more than a quarter of a millennium from 1768 to 2020, in order to interweave discussion of their history, ecology and conservation. Altogether, an unusual and most stimulating evening. His talk is now freely available to view on the Club's YouTube channel: https://www.youtube.com/channel/UCnPR9Y0Ya6gV35XpUBqAXBA.

CORRIGENDUM

In *Bull. Brit. Orn. Cl*. 145: 8, in the paper by Boersma *et al*. (2025) discussing an ornithological survey of Fergusson Island, Papua New Guinea, at the start of the section entitled 'New distributional records for Fergusson Island', it was stated that the authors recorded five species without published records anywhere in the D'Entrecasteaux Archipelago. However, as the remainder of the paragraph made clear, this total should have read six species.

Friends of the BOC

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

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

The *Bulletin* and other BOC publications

Since volume 137 (2017), the *Bulletin* of the BOC has been an online journal, published quarterly, that is available to all readers without charge. Furthermore, it does not levy any publication charges (including for colour plates) on authors of papers and has a median publication time from receipt to publication of five to six months. Prospective authors are invited to contact the *Bulletin* editor, Guy Kirwan (GMKirwan@

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aol.com), to discuss future submissions or look at http://boc-online.org/bulletin/bulletin-contributions. Back numbers up to volume 136 (2016) are available via the Biodiversity Heritage Library website: www.biodiversitylibrary.org/bibliography/46639#/summary; vols. 132–136 are also available on the BOC website: http://boc-online.org/

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

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A new subfamily for *Robsonius* (Locustellidae)

by George Sangster, Jimmy Gaudin & Per Alström

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Summary.—Phylogenetic analysis has shown that the ground warblers (*Robsonius*) are the sister-group of all other species of Locustellidae, which in turn consists of two major clades. This suggests that three subfamilies may be recognised: Locustellinae new rank, comprising the genera *Helopsaltes* and *Locustella*, Megalurinae new rank, comprising the genera *Poodytes*, *Malia*, *Cincloramphus*, *Megalurus*, *Elaphrornis*, *Schoenicola*, *Catriscus* and *Bradypterus*, and another, monotypic subfamily comprising the genus *Robsonius*, for which we introduce the name Robsoniinae.

Phylogenetic analysis of mitochondrial and nuclear DNA sequences has revealed that multiple genera traditionally considered as babblers (Timaliinae Sundevall, 1836, *sensu* Deignan 1964) are actually members of, or are closely related to, other taxonomic groups, including Vireonidae Swainson, 1837, Muscicapidae Fleming, 1822, Turdidae Billberg, 1828, Elachuridae Alström, Hooper, Liu, Olsson, Mohan, Gelang, Manh, Zhao, Lei & Price, 2014, Locustellidae Bonaparte, 1854, Cisticolidae Sundevall, 1872, Pnoepygidae Gelang, Cibois, Pasquet, Olsson, Alström & Ericson, 2009, Sylviidae Leach, 1820, and Zosteropidae Bonaparte, 1853 (reviewed by Alström *et al*. 2013; see also Alström *et al*. 2014, Reeve *et al*. 2022). One of these genera is *Robsonius* Collar, 2006. The first two known species of *Robsonius* were originally described in the genus *Napothera* G. R. Gray, 1842, within the family Timaliidae (i.e. Cordillera Ground Warbler *Napothera rabori* Rand, 1960; Bicol Ground Warbler *Napothera sorsogonensis* Rand & Rabor, 1967). Collar (2006) noted that these two species share a combination of morphological and behavioural character states not found in *Napothera*, nor in other wren-babbler genera, and are thus best placed in a new genus. Collar (2006) proposed the genus name *Robsonius* for *N. rabori* and *N. sorsogonensis*.

The first phylogenetic study to address the relationships of *Robsonius* was that by Oliveros *et al*. (2012), who found that the genus was sister to several members of Locustellidae. In a comprehensive phylogenetic analysis of this family, *Robsonius* was placed as the sister-group of all other species of Locustellidae (Alström *et al*. 2018). The latter group, in turn, consisted of two major clades: one clade was formed by the genera *Helopsaltes* and *Locustella*, and the other comprised the genera *Poodytes*, *Malia*, *Cincloramphus*, *Megalurus*, *Elaphrornis*, *Schoenicola*, *Catriscus* and *Bradypterus*. A third species of *Robsonius*, Sierra Madre Ground Warbler *R. thompsoni*, was described by Hosner *et al*. (2013), who showed that *R. sorsogonensis* is sister to *R. rabori* and *R. thompsoni*.

Robsonius is now universally placed in Locustellidae (Dickinson & Christidis 2014, Collar *et al*. 2020, Fjeldså *et al*. 2020, Clements *et al*. 2022, Gill *et al*. 2023). The deep divergence between *Robsonius* and other members of Locustellidae (Alström *et al*. 2018, Oliveros *et al*. 2019) and the strong support for all three major clades (Alström *et al*. 2018) suggest that three subfamilies may be recognised: Locustellinae Bonaparte, 1854 new rank, comprising the genera *Helopsaltes* Alström *et al*., 2018, and *Locustella* Kaup, 1829; Megalurinae Blyth, 1875 new rank, comprising the genera *Poodytes* Cabanis, 1851, *Malia* Schlegel, 1880, *Cincloramphus* Gould, 1838, *Megalurus* Horsfield, 1821, *Elaphrornis* Legge, 1879, *Schoenicola* Blyth, 1844, *Catriscus* Cabanis, 1851, and *Bradypterus* Swainson, 1837; and

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another, monotypic subfamily for the genus *Robsonius*. 'Robsoniinae' was recently used as a family-group name for *Robsonius* but this represents a *nomen nudum*, as was indicated by the author by his use of square brackets (Gaudin 2023). Because no family-group name is available for *Robsonius*, we propose:

Robsoniinae, new subfamily

Type genus.—*Robsonius* Collar, 2006.

Diagnosis.—Same as for the type genus (Collar 2006). Thus, Robsoniinae differs from all other oscine passerines by a combination of: (i) absence of rictal bristles; (ii) part-feathered nares; (iii) broad white tips to the wing-coverts and outer 2–3 primaries; (iv) very copious, dense, elongate rump feathering; (v) fairly long and slightly hooked bill, as in *Turdinus* Blyth, 1844; (vi) high-pitched, insect-like main vocalisation; and (vii) habit of walking (Collar 2006: 108).

In addition, our alignment, using MUSCLE (Edgar 2004) as implemented in MEGA7 (Kumar *et al*. 2016), of the fifth intron of the nuclear gene β-fibrinogen (Fib5) datasets of Moyle *et al*. (2012), Oliveros *et al*. (2012) and Hosner *et al*. (2013) obtained from GenBank, shows that there is a 1 bp insertion (corresponding to position 268 of sequence JN826141[1] of *R. sorsogonensis*) and a 1 bp deletion (corresponding to position 541 of JN826141) that are synapomorphic for *Robsonius* (and hence Robsoniinae). The alignment used for assessing indels in the fifth intron of the nuclear gene β-fibrinogen is available at Zenodo (https://doi.org/10.5281/zenodo.15037864).

Included taxa.—*Robsonius sorsogonensis* (Rand & Rabor, 1967), *R. rabori* (Rand, 1960) and *R. thompsoni* Hosner, Boggess, Alviola, Sánchez-González, Oliveros, Urriza & Moyle, 2013.

Discussion

With the growth of phylogenetic knowledge, taxonomic systems (classifications) are becoming more refined and include an increasing number of clade names. These names add precision to the hierarchical system of taxa. Naming clades enables straightforward discussion of the relevant taxa. Subfamilies have been used many times before in ornithology (e.g. Peters 1934, Mayr & Cottrell 1986, Sibley & Ahlquist 1990). In recent classifications, 78 subfamilies were recognised as part of 27 non-passerine families (Dickinson & Remsen 2013) and 98 subfamilies were included in 27 passerine families (Fjeldså *et al*. 2020). Examples of recently recognised subfamilies are Hypocryptadiinae Hachisuka, 1930, and Passerinae Vigors, 1825 (in Passeridae Vigors, 1825) and Plocepasserinae Des Murs, 1860, Bubalornithidae Iredale & Bannerman, 1921, and Ploceinae Sundevall, 1836 (in Ploceidae Sundevall, 1836; Fjeldså *et al*. 2020). Thus, the recognition of subfamilies in Locustellidae is consistent with the classification of other groups of birds.

Ironically, the name Robsoniinae is superfluous because the relevant clade already had a unique name, albeit at a lower rank (i.e. *Robsonius*). The reason it is named here as a subfamily is that in rank-based nomenclature, naming one taxon at a certain rank (e.g. subfamily Locustellinae) means that all other equally or more divergent branches (i.e. Megalurinae and Robsoniinae) within that clade (i.e. Locustellidae) should also be recognised at the same rank and be named. Introducing the name Robsoniinae was necessary in order to formally recognise two other subclades of Locustellidae (each comprising multiple genera), which in recent classifications did not have a unique taxonomic name, i.e. the clades here

[1] At the time of writing, this sequence was still listed as '*Napothera rabori*' on GenBank.

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called Locustellinae and Megalurinae. Under the rules of rank-based nomenclature, naming Robsoniinae is a necessary consequence of the taxonomic recognition of these other clades.

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New information on bird distribution in Bolivia

by Miguel Montenegro-Avila, Nicole A. Avalos, J. Luis Martínez, W. Sergio Pantoja, Romer Miserendino, Dirk Dekker, Tini Wijpkema, Jacob Wijpkema, Claribel Villarroel, Alberto Espinoza, Mauricio Herrera, Miguel Ángel Aponte Justiniano, Luis Alejandro Gálvez, Estela I. Torrez, Miguel A. Clavijo, Miglė Montrimaitė, Teodoro Camacho, Cindy Veizaga, Tomas Calahuma, Simon Graesboell Iversen, Mateo Tapia Vargas, Cristhian Trigo, Edith Sánchez, Javier Padilla & Diego Aliaga-Pantoja

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Summary.—Recent advances in our understanding of the Bolivian avifauna have been substantial; 1,452 species are now known for the country. This manuscript presents a compilation of records made between 2005 and the present, including records for 27 species that contribute to our understanding of elevational and geographic distributions and status of birds in Bolivia. Among the most noteworthy discoveries are further records of the only recently recorded Coscoroba Swan *Coscoroba coscoroba*, the first record of the globally threatened Horned Curassow *Pauxi unicornis* in Santa Cruz for more than a decade, evidence that Scaled Dove *Columbina squamata* might be becoming established in the east of the country, the second record of South American Painted Snipe *Nycticryphes semicollaris* in Bolivia, the fifth and sixth Bolivian records of Common Tern *Sterna hirundo* and the third national record of Purple-throated Cotinga *Porphyrolaema porphyrolaema*. These findings underscore the need for sustained research and documentation of Bolivia's avifauna.

Since the publication of the first dedicated field guide to the country's birds (Herzog *et al*. 2017) substantial advances have been made in our understanding of the distribution of various bird species in Bolivia, as evidenced by the publication of many new records (e.g. Lane *et al*. 2021, Aponte *et al*. 2022, Montenegro-Avila *et al*. 2022, 2023, 2024, Pantoja *et al*. 2022, van Els *et al*. 2023, 2024a), which have increased the total number of documented species in the country to 1,452 from the 1,435 species listed by Herzog *et al*. (2017). The present manuscript is a compendium of records made between 2005 and the present in all nine of the country's departments. We present records of 27 species, the significance of which lies in their contribution to our understanding of species distributions in regions of the country where ornithological exploration is still limited. This underscores the importance of continued research into the Bolivian avifauna, both to improve our understanding of species distribution and to inform conservation and effective habitat management.

Species accounts

Species names and order generally follow those of the South American Classification Committee (Remsen *et al*. 2025). ML numbers, corresponding to the catalogue numbers under which these photographs are archived in the Macaulay Library (https://macaulaylibrary.org), serve to identify specific photographs therein. These can be accessed via the ML website, followed by the catalogue number (excluding the 'ML'), e.g., https://macaulaylibrary.org/

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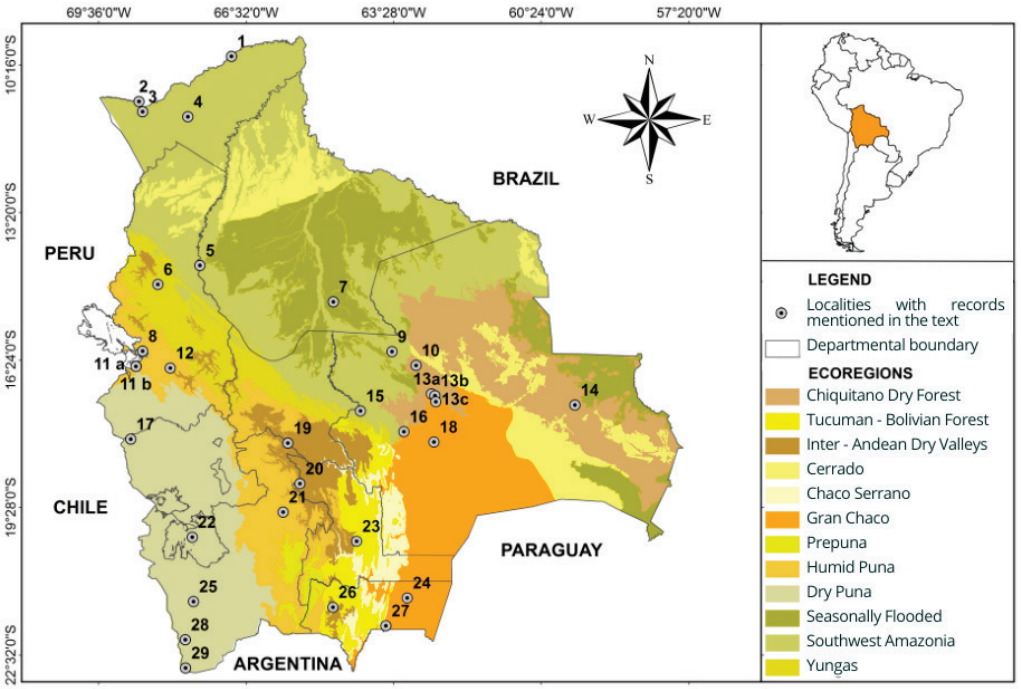

Figure 1. Sites mentioned in the text with records from the period 2005–24: 1a. Estación Biológica Abuná 'A' (10°05'08"S, 66°50'15"W; 125 m) and 1b Estación Biológica Abuná 'B' (10°07'57.60"S, 66°49'04"W; 149 m), municipality of Ingavi, Abuná province, Pando; 2. Estadio Roberto Jordán Cuéllar (11°01'28.46"S, 68°45'34.73"W; 224 m), municipality of Cobija, Nicolás Suárez province, Pando; 3. Río Tahuamanu (11°14'19.0"S, 68°41'09.6"W; 219 m), municipality of Porvenir, Nicolás Suárez province, Pando; 4. Barraca Puerto Cárdenas (11°20'26.9"S, 67°44'38.7"W; 180 m), Reserva Nacional de Vida Silvestre Amazónica Manuripi, municipality of Puerto Rico, Manuripi province, Pando; 5. Aeropuerto Capitán Selin Zeitun López (14°25'55.39"S, 67°29'42.73"W; 216 m), municipality of Rurrenabaque, José Ballivián province, Beni; 6. Camino a Atén (14°49'40.6"S, 68°22'03.9"W; 1,440 m), municipality of Apolo, Franz Tamayo province, La Paz; 7. Reserva Natural Laney Rickman (15°11'27.19"S, 64°43'12.96"W; 149 m), municipality of Loreto, Marbán province, Beni; 8. Inti Raymi, Lago Titicaca (16°12'54.0"S, 68°41'03.6"W; 3,283 m), municipality of Huatajata, Omasuyos province, La Paz; 9. Laguna La Pistola (16°13'31"S, 63°13'01"W; 199 m), municipality of El Puente, Guarayos province, Santa Cruz; 10a. Humamarca (16°31'56"S, 68°49'16"W; 3,831 m) and 10b. Río Tiahuanaco (16°32'3.65"S, 68°49'30.35"W; 3,381 m), municipality of Tiahuanaco, Ingavi province, La Paz; 11. Club de Golf La Paz (16°34'0.86"S, 68°06'37.19"W; 3,335 m), municipality of La Paz, Murillo province, La Paz; 12a. Humedal Fortín Libertad (17°06'09.75"S, 62°40'43.67"W; 259 m), 12b. Campos Felicias Ecological Refuge (17°08'32.50"S, 62°36'17.20"W; 259 m) and 12c. Área Natural Playón Garcero (17°15'51.81"S, 62°34'55.92"W; 274 m), municipality of Cuatro Cañadas, Ñuflo de Chávez province, Santa Cruz; 13. Laguna Mina Don Mario (17°20'11"S, 59°41'45"W; 248 m), Santa Cruz; 14. Cataratas El Cóndor (17°27'30.9"S, 64°09'20.9"W; 382 m), municipality of Yapacaní, Ichilo province, Santa Cruz; 15. Laguna Sofía (17°53'26.4"S, 63°15'11.2"W; 459 m), municipality of La Guardia, Andrés Ibáñez province, Santa Cruz, 16. Laguna Huayñacota (18°02'48.18"S, 68°55'59.46"W; 4,358 m), municipality of Curahuara de Carangas, Sajama province, Oruro; 17. Agripac Palmas Reales (18°06'16.7"S, 62°37'37.9"W; 327 m), municipality of Charagua, Cordillera province, Santa Cruz; 18. Cañón Jala Jala (18°07'40.25"S, 65°39'52.31"W; 1,898 m), municipality of Torotoro, Charcas province, Potosí; 19. Cordillera Los Frailes (18°58'17.06"S, 65°24'55.42"W; 3,335 m), municipality of Sucre, Oropeza province, Chuquisaca; 20. Yamparaéz (19°11'25"S, 65°06'46"W; 3,143 m), municipality of Yamparaéz, Yamparaéz province, Sucre; 21. Parque Recreacional Los Pinos (19°33'44.07"S, 65°45'46.12"W; 3,802 m), municipality of Potosí, Tomás Frías province, Potosí; 22. Salar de Uyuni (20°04'58.62"S, 67°39'11.39"W; 3,665 m), Potosí; 23. El Rodeo (20°08'17.33"S, 64°22'16.49"W; 1,442 m), municipality of Azurduy, Hernando Siles province, Chuquisaca; 24. Villamontes (21°20'51.80"S, 63°11'03.59"W; 348 m), Gran Chaco province, Tarija; 25. Bofedal Alota (21°25'20.6"S, 67°37'37"W; 3,828 m), municipality of San Agustín, Enrique Baldivieso province, Potosí; 26. Complejo Deportivo García Agreda (21°32'27.4"S, 64°43'48.0"W; 1,858 m), municipality of Tarija, Cercado province, Tarija; 27. Laguna Santa Martha (21°55'39"S, 63°37'38"W; 621 m), municipality of Yacuiba, Gran Chaco province, Tarija; 28. Laguna Colorada (22°13'02.92"S, 67°47'49.30"W; 4,296 m), municipality of San Pablo, Sud Lípez province, Potosí; 29. Laguna Blanca (22°48'10.52"S, 67°47'29.05"W; 4,328 m), municipality of San Pablo, Sud Lípez province, Potosí.

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asset/615715068. It should be noted that other records mentioned are indicated by their checklist number 'S', which can be accessed via the eBird website, followed by the checklist number, e.g., 'S120272280' can be accessed at www.ebird.org/checklist/S120272280. For coordinates of all our localities, and more complete details of their whereabouts, see the legend to Fig. 1.

COSCOROBA SWAN *Coscoroba coscoroba*

On 20 July 2017, JP saw one at Laguna Mina Don Mario, 112 km north of Roboré, Santa Cruz (Fig. 2). Recent years have seen a very marked increase in knowledge of the species in Bolivia. Initially documented at three sites (Tobias & Seddon 2007b, Herzog *et al*. 2017, Aponte *et al*. 2022), further field work has added an additional locality (Pantoja *et al*. 2022, van Els *et al*. 2024b) and proved that the species breeds in the country (Pantoja *et al*. 2023). Additionally, it has been reported at Laguna Taputarenda, municipality of Lagunillas (R. Hoyer, S119518874), making the present report the sixth documented locality and confirming that the species is not as rare as previously believed in Bolivia (Herzog *et al*. 2017). Its potential distribution in Bolivia may encompass central Santa Cruz, eastern Chuquisaca and Tarija, in the Chaco and Chiquitanía ecoregions.

Figure 2. Coscoroba Swan *Coscoroba coscoroba*, Laguna Mina Don Mario, Santa Cruz, Bolivia, 20 July 2017 (Javier Padilla)

SILVER TEAL *Spatula versicolor*

On 19 June 2022, LAG, WSP & J. Whittaker saw two adults at Laguna Sofía, Santa Cruz. Additionally, on 2 January 2023, JLM observed four in Campos Felicias Ecological Refuge, on 11 February 2023, JLM photographed five at Área Natural Playón Garcero (Fig. 3) and, on 4 February 2024, JLM saw one at Humedal Fortín Libertad, all in Santa Cruz. The

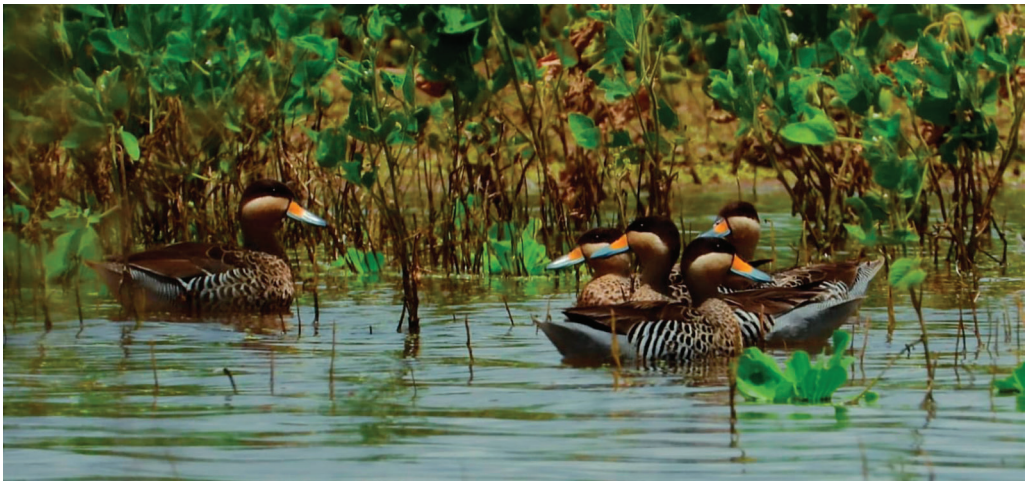

Figure 3. Silver Teal *Spatula versicolor*, Área Natural Playón Garcero, Cuatro Cañadas, Santa Cruz, Bolivia, 11 February 2023 (J. Luis Martínez)

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three last-named localities, all in the municipality of Cuatro Cañadas, possess analogous vegetation characteristics. These records are the northernmost for Santa Cruz, 154 km north-west and 366 km north-east from the two previously published departmental records (Herzog *et al*. 2017, van Els *et al*. 2024b), thereby substantiating the species' presence in the north, along with a 2017 report (S. Herzog, S38866393). The species exhibits partial migrations, breeding in the Southern Cone and wintering as far north as Rio de Janeiro, south-east Brazil (Sick 1997, Macarrão-Montanhini & Andrade-Figueiredo 2007, Rupp *et al*. 2008). It has also been recorded at sea off southern Argentina (Seco Pon & Bastida 2015). For Bolivia, until very recently records were available only from Tarija and Cochabamba and these suggested that the species was only a migrant to the country (Lane 2014). Since then, however, an apparently resident population has been discovered in southern Santa Cruz (van Els *et al*. 2024b) and a population that breeds in the austral winter has been found in the Cochabamba Basin (Herzog *et al*. 2017). Our records in northern Santa Cruz suggest dispersive or seasonal movements, but further field work will be necessary to more accurately determine the species' temporal presence and status in different parts of the country.

WHITE-CHEEKED PINTAIL *Anas bahamensis*

On 13 February 2023, MAAJ saw two at Camino a Atén, 13 km south-east of Apolo, La Paz. Subsequently, on 23 May 2023, TW & JW observed two at Bofedal Alota (ML 581150681), 4 km south-west of Alota, Potosí. On 10 June 2023, MM-A & NAA photographed one at Laguna Huayñacota, Parque Nacional Sajama, Oruro (Fig. 4). The record in Potosí is the first for the department, whilst that in Oruro is the second and is 195 km west of Lake Poopó, Oruro (Herzog *et al*. 2017); at 4,358 m it is also the highest-elevation record ever (Carboneras *et al*. 2024). Subspecies *rubrirostris* is mainly resident over its distribution, which encompasses coastal areas of South America, with records in the Andes up to 2,500 m; however, it exhibits some seasonal and dispersive movements (Carboneras *et al*. 2024, Begazo 2025). In Bolivia, recent sightings including ours indicate the species moves to higher elevations during the austral winter (Herzog *et al*. 2017). Sightings in Potosí and Oruro suggest that those on the Bolivian altiplano may disperse, contrasting with historical records indicating year-round presence in south-east Bolivia. The species is not known to migrate latitudinally but also makes elevational movements to high-Andean lakes in Peru (Begazo 2025) and Ecuador (Cisneros-Heredia *et al*. 2022).

Figure 4. White-cheeked Pintail *Anas bahamensis*, Laguna Huayñacota, Parque Nacional Sajama, Oruro, Bolivia, 10 June 2023 (Miguel Montenegro-Avila)

YELLOW-BILLED PINTAIL *Anas georgica*

On 28 January 2019, MAAJ & MAM observed one at Camino a Atén, La Paz. Subsequently, on 13 February 2023, MAAJ & DAP saw four at another lagoon, 1.5 km north of this at 1,440 m. Other records from the same area during 2022 and 2023 are available on eBird. Based on Herzog *et al*. (2017), these records are the northernmost in Bolivia for the species

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to date, as well as the lowest elevation for the species in the country (previously recorded at 2,550–4,550+ m; Herzog *et al*. 2017).

HORNED CURASSOW *Pauxi unicornis*

On 27 September 2017, MM-A saw one at Cataratas El Cóndor, 29 km west of Yapacaní, Santa Cruz, at 382 m. The bird ascended *c*.15 m in a tree, whereupon it initiated a series of tail-wagging behaviours accompanied by vocalisations (Fig. 5). Records of this globally threatened species are exceedingly few, with the majority of documented occurrences from the period 1997–2008 (https://ebird.org/). Recent reports are from Territorio Indígena y Parque Nacional Isiboro Sécure (TIPNIS), Cochabamba (e.g., T. Boorsma & T. Camacho, S120272280), made during a project led by Asociación Civil Armonía. Our record is the first for Santa Cruz since that reported by Maillard (2006). It was previously known from elevations of 400–1,400 m (Herzog *et al*. 2017).

Figure 5. Horned Curassow *Pauxi unicornis*, Cataratas El Cóndor, Santa Cruz, Bolivia, 27 September 2017 (Miguel Montenegro-Avila)

SCALED DOVE *Columbina squammata*

On 20 March 2023, CV saw one foraging on the ground at Aeropuerto Capitán Selin Zeitun López, Beni. On 28 June 2023, TC recorded one vocalising at Reserva Natural Laney Rickman, 4 km west of Loreto, Beni (Fig. 6). On 6 April 2023, JLM observed an adult vocalising in Campos Felicias Ecological Refuge, Santa Cruz (ML 554389071). The species is resident in north-east Argentina, Paraguay and south-east Brazil, whereas in Bolivia it was considered to be either an occasional visitor or a poorly known resident (Baptista *et al*. 2020). The persistent presence of the species in eastern Santa Cruz suggests it is resident there (Herzog *et al*. 2017). In contrast, records in Beni may concern vagrant individuals.

Figure 6. Scaled Dove *Columbina squammata*, Reserva Natural Laney Rickman, Beni, Bolivia, 28 June 2023 (Teodoro Camacho)

PAINT-BILLED CRAKE *Mustelirallus erythrops*

On 13 December 2021, CT found a dead individual 30 km east of Villamontes (Fig. 7), the first record in Tarija. It was not collected. On 16 November 2014, ES found a dead adult male at Agripac-Palma Reales, 47 km

Figure 7. Paint-billed Crake *Mustelirallus erythrops*, Villamontes, Tarija, Bolivia, 13 December 2021 (Cristhian Trigo)

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south-east of Pailón, the fifth record in Santa Cruz; it is now at the Noel Kempff Mercado Natural History Museum (MNK.AV 5922, left testis 4 × 5 mm, skull 100% ossified, high fat content, 78 g). The species could perhaps occur in any region of Bolivia, as evidenced by records in neighbouring countries (Taylor *et al*. 2020). In Bolivia, it is considered a migrant with few records, mainly in Santa Cruz but also in Beni and La Paz (Herzog *et al*. 2017).

SEMIPALMATED PLOVER *Charadrius semipalmatus*

On 19 March 2023, MM photographed one at Laguna Blanca, Potosí (Fig. 8). Subsequently, on 27 May 2023, AE saw another on the south side of Laguna Colorada, Potosí. The species is a boreal migrant in South America, spending its non-breeding season in the Southern Hemisphere. Most sightings in South America are on coasts (Hilty & Brown 1986), but there are reports far inland, including at Manaus (Stotz *et al*. 1992) and in Rondônia (Kirwan & Shirihai 2008). High-Andean records were thought to be extremely rare (Fjeldså & Krabbe 1990) but in recent years more have been made, including at Laguna Brava, Argentina (Allende & Marano 2017), Laguna Huaypo, Peru (N. Ccacya, ML 40646201) and Surire, Chile (C. Gherardi, ML 559977841). In Bolivia, only two historical records exist (Herzog *et al*. 2017). For now, it is impossible to be sure whether the species is a regular visitor or a only vagrant to the country.

Figure 8. Semipalmated Plover *Charadrius semipalmatus*, Laguna Blanca, Potosí, Bolivia, 19 March 2023 (Miglė Montrimaitė)

UPLAND SANDPIPER *Bartramia longicauda*

On 15 April 2023, GV saw two at Salar de Uyuni (Fig. 9), the first documented record in Potosí. Previously reported in Bolivia in Santa Cruz, Beni, Pando, Cochabamba, La Paz and Oruro (Herzog *et al*. 2017). The species undertakes long-distance migrations of 5,000–10,000 km (Hill *et al*. 2019) moving south between July and November, and north in February–May (Hill *et al*. 2019). This bird was presumably on return migration, as some wintering in Argentina and Uruguay follow a western route to North America through Chile, Peru and Ecuador (Medrano *et al*. 2018, Hill *et al*. 2019). In Chile, recent records indicate regular migration through the Andes in Antofagasta, with sightings in March–April between sea level and 4,000 m (Jaramillo 2003, Capllonch 2011). Blanco & López-Lanús (2008) posited that records in the Andes of Bolivia, Peru, Ecuador and Colombia evidence a western migratory route, which is reinforced by recent observations in Chile and Argentina (Capllonch 2011, Barros 2014). This suggests that migratory patterns in South America are

Figure 9. Upland Sandpipers *Bartramia longicauda*, Salar de Uyuni, Potosí, Bolivia, 15 April 2023 (Gabriela Villanueva)

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more complex than previously thought, with populations potentially following additional routes or using sites in the Andes as possible stopovers during their return to the Northern Hemisphere. Although the species is a habitat specialist of grasslands and savannas, it is occasionally found in deforested parts of Amazonia or elsewhere (Houston *et al*. 2023). The record at Salar de Uyuni suggests that south-west Bolivia may also be part of its route northwards, adding to previous records on nearby salt flats, such as Salar de Pedernales (Araya & Millie 2000) and reinforcing the hypothesis that these areas may serve as stopover sites on migration.

HUDSONIAN GODWIT *Limosa haemastica*

On 13 April 2023 AE photographed one in partial breeding plumage at the Río Tiahuanaco, La Paz (Fig. 10). The species breeds in Alaska and Canada, and spends the non-breeding season in southern South America (Walker *et al*. 2024). Southbound migration commences in July with individuals departing their breeding grounds and crossing the Caribbean to Venezuela and Colombia (Blanco *et al*. 1995). Records in the high Andes are considered to involve vagrants, including at Lake Uru Uru in Oruro (Pearson 1975, Aponte *et al*. 2022), the Atacama Desert in Chile (V. Araya, ML617336926), Peru (D. Samata, ML 77634961) and Argentina (F. Moschione, ML 619666586). Further field work is needed to determine the importance of the high-Andean zone during the species' migration.

Figure 10. Hudsonian Godwit *Limosa haemastica*, Río Tiahuanaco, La Paz, Bolivia, 13 April 2023 (Alberto Espinoza)

BUFF-BREASTED SANDPIPER *Calidris subruficollis*

On 10 October 2023, MM-A & NAA observed 27 foraging at Estadio Roberto Jordán Cuéllar (Fig. 11; ML 615660782) in the centre of Cobija, Pando. On 14 October 2023, MM-A & NAA saw one at the Río Tahuamanu, La Paz. Previous records in Bolivia were in Beni, Cochabamba and Santa Cruz (Herzog *et al*. 2017). A review of these records indicates the presence of two principal areas: Llanos de Moxos (T. Camacho, ML382669611) and Lagunas de Cochabamba (Laguna Cotapachi, E. Zeballos, ML 389052011, Laguna Albarrancho, M. Bienert, ML 389052011). In the Bolivian Amazon, there is a single record on the Río Madre de Dios (T. & J. Wijpkema, ML 506248541). Ours are the first records in La Paz and Pando.

Figure 11. Buff-breasted Sandpiper *Calidris subruficollis*, Estadio Roberto Jordán Cuéllar, Cobija, Pando, Bolivia, 10 October 2023 (Nicole A. Avalos)

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SOUTH AMERICAN PAINTED SNIPE *Nycticryphes semicollaris*

On 9 July 2023, JLM photographed one in Área Natural Playón Garcero, 4.5 km west of Cuatro Cañadas (Fig. 12), at a shallow wetland with abundant *Ludwigia octovalvis*, *Hymenachne amplexicaulis*, *Cyperus odoratus* and *Typha domingensis*. This species is principally crepuscular and nocturnal, and has a limited distribution in the Southern Cone (Canevari *et al*. 2001, Gutiérrez & González 2022). It inhabits short vegetation interspersed with some emergent shrubs in shallow water. In Bolivia, the species was first documented in 2019 at Kaukaya Lagoon, Santa Cruz (255 km south of the present location; Aponte *et al*. 2022). This is the second documented record in the department and country. The species is possibly regular in the area, but its inconspicuous habits have obscured its precise status.

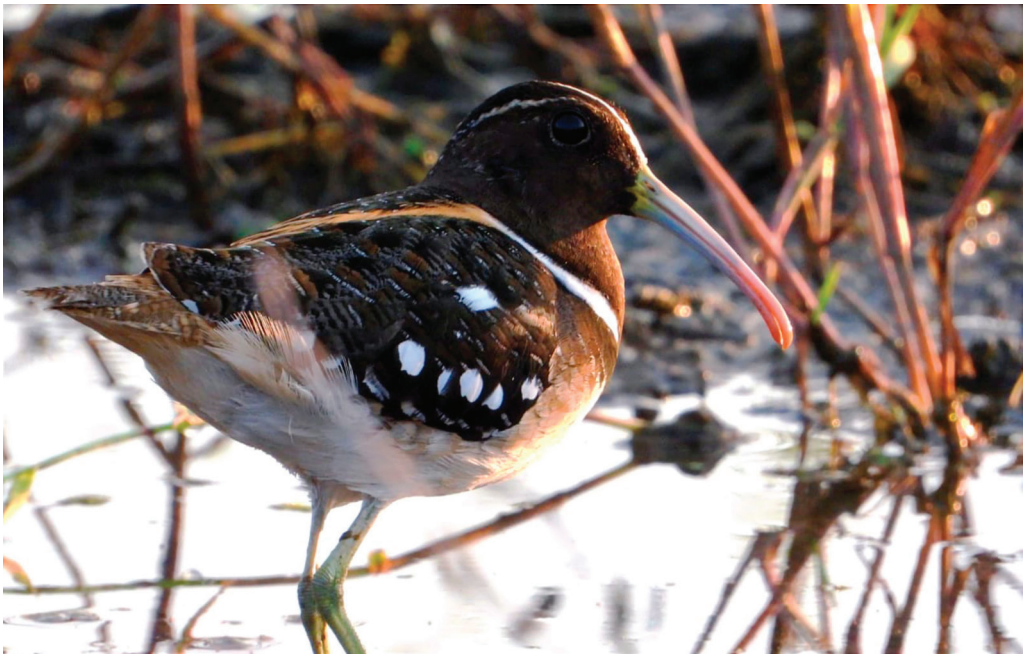

Figure 12. South American Painted Snipe *Nycticryphes semicollaris*, Área Natural Playón Garcero, Cuatro Cañadas, Santa Cruz, Bolivia, 9 July 2023 (J. Luis Martínez)

FRANKLIN'S GULL *Leucophaeus pipixcan*

On 16 July 2005, RSMS photographed one at Laguna La Pistola, municipality of El Puente, Santa Cruz (Fig. 13), feeding on fish scraps left by fishermen. The species' migrations along the Pacific coast of South America are well known (Burger & Gochfeld 2020) and in the boreal winter it is observed in large groups, primarily in coastal Chile and Peru (Jaramillo 2003). Records in the interior of the continent were considered rare (e.g., Hoogendoorn 1994, Hughes 1977), but recent observations have demonstrated more or less regular occurrence in locations such as the inter-Andean valley of Ecuador (Restall & Freile 2018; https://ebird.org/) and the lakes of Córdoba in north-west Argentina

Figure 13. Franklin's Gull *Leucophaeus pipixcan*, Laguna La Pistola, Santa Cruz, Bolivia, 16 July 2005 (Romer Miserendino)

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(Nores & Yzurieta 1980). Just one published record was previously available for Bolivia: at least 300 individuals at Lake Titicaca in March 1977 (Remsen & Ridgely 1980), but Herzog *et al*. (2017) mentioned other unpublished records, and mapped the species in Cochabamba, making this the second published country record and the first in Santa Cruz.

COMMON TERN *Sterna hirundo*

On 25 February 2024 SGI documented one at Inti Raymi, Lago Titicaca, La Paz (ML 615371060). Subsequently, on 8 May 2024, AE photographed another at the same location (ML 618686521). The species is mainly coastal in South America, although there are occasional inland records, mainly along rivers (Meyer de Schauensee 1966, Blake 1977, Di Costanzo 1978) including in Argentina (M. Minuet, S52440122; C. Rosso, S160460437) and Brazil (R. Andrade, S107638138; V. Vianna, S135462090). It has also been reported at high-Andean lakes in Colombia and Ecuador (Fjeldså & Krabbe 1990). In Bolivia, four records are available, three in the lowlands and one in the Cochabamba Andes (Herzog *et al*. 2017). Our records are the first in La Paz.

MAGUARI STORK *Ciconia maguari*

On 18 July 2023, AB photographed one at Humamarca, along the Río Tiahuanaco, La Paz (Fig. 14). Whilst the species is well known in Bolivia in the country's lowlands (except Pando; Herzog *et al*. 2017), there were no prior reports for the northern Andes, but in neighbouring Peru it is considered a vagrant (Schulenberg *et al*. 2007) with the nearest record at Lake Titicaca, Puno (García-Solsol *et al*. 2020). Our report is the first for La Paz and the third in Bolivia's highlands (Whitney *et al*. 1994; N. Wingert, S33035735). It is also the highest, at 3,831 m, above the previous record in Oruro at 3,700 m (Whitney *et al*. 1994).

Figure 14. Maguari Stork *Ciconia maguari*, Humamarca, Lago Titicaca, La Paz, Bolivia, 18 July 2023 (Alberto Espinoza)

WOOD STORK *Mycteria americana*

On 24 November 2023, TC observed four by the River Caine, near Cañón Jala Jala, 11 km east of Torotoro, Potosí (Fig. 15). In Bolivia the species primarily inhabits the lowlands, inter-Andean dry valleys, the Cerrado and Chaco regions (Herzog *et al*. 2017). Our record is the first in Potosí.

Figure 15. Wood Stork *Mycteria americana*, Cañón Jala Jala, Parque Nacional Torotoro, Potosí, Bolivia, 24 November 2023 (Tomás Calahuma)

ANDEAN IBIS *Theristicus branickii*

On 6 August 2022, CVI photographed at least ten at El Rodeo, Chuquisaca, in a paddock (Fig. 16). This site, in the basin of the upper River Parapetí, is characterised by Bolivian-Tucuman forests and a moderate degree of human disturbance (Herzog *et al*. 2017). The species' main range encompasses central Ecuador, southern Peru, western Bolivia and northern Chile (Medrano & Pyle 2023). However, recently extralimital reports have become available from elsewhere in Bolivia and far north-western Argentina (GBIF 2020, Müller *et*

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al. 2021, Medrano & Pyle 2023). This is the first record in Chuquisaca.

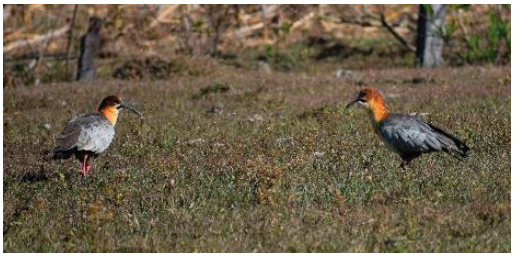

Figure 16. Andean Ibis *Theristicus branickii*, El Rodeo, Chuquisaca, Bolivia, 6 August 2022 (Claribel Villarroel)

CHESTNUT-CAPPED PUFFBIRD *Bucco macrodactylus*

On 22 October 2015, MM-A & MH saw one at Estación Biológica Abuná 'A', 47 km north-east of Puerto Evo, Santa Rosa del Abuná. It was foraging in the canopy at the edge of riparian forest near the River Abuná (ML 630231049). In Bolivia, the species occurs in north-east Cochabamba, northern La Paz, northern and western Beni, and Pando (Herzog *et al*. 2017) but there were no previous reports from eastern Pando, making this the first record there.

COLLARED PUFFBIRD *Bucco capensis*

On 29 October 2015, MM-A & MH observed one at Estación Biológica Abuná 'B', 47 km north-east of Puerto Evo, Santa Rosa del Abuná (ML 615715068). First documented in Bolivia in 2007, with sightings at two locations *c*.35 km apart in eastern Pando (Tobias & Seddon 2007a) and in 2023 sightings were made at three sites in central Pando (van Els *et al*. 2023). Until now, the species had not been reported on the Bolivian side of the River Abuná; this locality becomes the sixth known in Bolivia.

CRESTED CARACARA *Caracara plancus*

On 29 September 2023, EIT photographed one at the Club de Golf La Paz, in the Mallasa neighbourhood of the city of La Paz at 3,335 m, feeding with Andean Flickers *Colaptes rupicola* (Fig. 17). Widely distributed in Bolivia, where it is reported up to 2,900 m (Herzog *et al*. 2017). Elsewhere, there are a few records above 3,000 m, most notably in Cuzco, Peru, at 3,900 m (e.g., L. Rosas, S146109601). The species is notable for its environmental plasticity, yet its distribution is declining due to habitat loss and persecution in some areas (Ortiz-Crespo 1986). Conversely, in other regions its range is expanding, e.g., in Amazonia (van Els *et al*. 2023) and, recently, in the highland valleys of southern Peru and Bolivia. Ours is the southernmost record for La Paz and extends its elevational range by *c*.400 m.

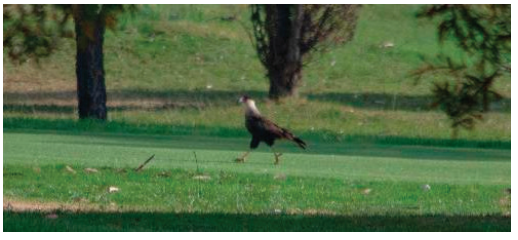

Figure 17. Crested Caracara *Caracara plancus*, Club de Golf La Paz, La Paz, Bolivia, 29 September 2023 (Estela I. Torrez)

Figure 18. Cobalt-rumped Parrotlet *Forpus xanthopterygius*, Laguna Santa Martha, Yacuiba, Tarija, Bolivia, 2 March 2022 (W. Sergio Pantoja)

COBALT-RUMPED PARROTLET *Forpus xanthopterygius*

On 30 April 2021 MTV saw two at the Complejo Deportivo García Agreda, 300 m from the River Guadalquivir, Tarija; their

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calls were sound recorded (ML 463927881). On 2 March 2022, WSP observed three near Laguna Santa Martha, Tarija, in a *Eucalyptus* tree in a patch of disturbed forest (Fig. 18). These are the first records in Tarija, the southernmost sightings in country, the highest elevation on record for the species (1,858 m) and the first indication of its presence in the inter-Andean dry valleys (Herzog *et al*. 2017).

PURPLE-THROATED COTINGA *Porphyrolaema porphyrolaema*

On 19 October 2015, MM-A encountered one at Campamento 2, Estación Biológica Abuná 'B', 6 km south of the River Abuná in Pando (Fig. 19, ML 630100564). Its plumage suggested the bird was a female, as juveniles have paler buff coloration compared to adult females, with buff not whitish fringes to the mantle and back feathers, and a different pattern to the rectrices (Kirwan & Green 2011). Distributed in western and southern Amazonia, the species is uncommon or rare, although it is probably overlooked due to its preference for the canopy (Schulenberg *et al*. 2007, Kirwan & Green 2011). In Bolivia, just two previous records were available, in northern La Paz, although it is expected to also occur in western Pando (Herzog *et al*. 2017). Our record is the first for Pando and the third for Bolivia, and suggests the species may be more widespread than was thought.

Figure 19. Purple-throated Cotinga *Porphyrolaema porphyrolaema*, Estación Biológica Abuná 'B', Pando, Bolivia, 19 October 2015 (Miguel Montenegro-Avila)

PEARLY-VENTED TODY-TYRANT *Hemitriccus margaritaceiventer*

On 2 December 2023, MM-A & NAA photographed one at Cañón Jala Jala, 11 km east of Torotoro, Potosí (Fig. 20). The species occurs in Beni, Cochabamba, La Paz, Santa Cruz, Chuquisaca and Tarija (Herzog *et al*. 2017). This record is 50 km west of known localities in Cochabamba and is the first in Potosí.

Figure 20. Pearly-vented Tody-Tyrant *Hemitriccus margaritaceiventer*, Cañón Jala Jala, Parque Nacional Torotoro, Potosí, Bolivia, 2 December 2023 (Nicole A. Avalos)

YELLOWISH PIPIT *Anthus chii*

On 26 and 27 June 2023, MAAJ photographed a pair at Barraca Puerto Cárdenas, Reserva Nacional de Vida Silvestre Amazónica Manuripi, Pando (Fig. 21). Herzog *et al*. (2017) knew of just one documented record in Pando but additional records are now available on eBird (e.g., T. & J. Wijpkema, S59579561; K. Rosenberg, S51617558). The species inhabits damp short grassland, pastures, agricultural land and Cerrado, often near

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rivers, lakes and marshes (Tyler *et al*. 2023). Given an increase in artificial pastures in central Pando, the species could become more widespread in the department.

SHORT-BILLED PIPIT *Anthus furcatus*

On 16 November 2022, DD observed one at Yamparáez, Chuquisaca (19°11′25″S, 65°06′46″W; Fig. 22). The species inhabits high-elevation areas in La Paz, Cochabamba, Oruro, Potosí and Tarija, at 2,650–4,000 m (Herzog *et al*. 2017). This record is the first in Chuquisaca.

BOBOLINK *Dolichonyx oryzivorus*

On 1 January 2023 MAC photographed an adult male at Parque Recreacional Los Pinos, Potosí (Fig. 23), *c*.180 km south of a previous record in Cochabamba (Herzog *et al*. 2017). Outside its known non-breeding range (Renfrew *et al*. 2020), there are documented reports in Argentina (F. de Grotte, S28464080), Chile (F. Moschione, S155938708) and Peru (G. Bautista, S123147028). Our report is the first in Potosí. In Bolivia, the species is primarily recorded in lowlands of the east and south (Herzog *et al*. 2017, Renfrew *et al*. 2020).

GLACIER FINCH *Idiopsar brachyurus*

On 9 September 2020, DD photographed two adults in the Cordillera Los Frailes, Chuquisaca (Fig. 24). In Bolivia, it was previously known from western and southern La Paz, central Cochabamba and south-west Tarija. This record is the first in Chuquisaca.

Figure 21. Yellowish Pipit *Anthus chii*, Barraca Puerto Cárdenas, Pando, Bolivia, 26 June 2023 (Miguel Angel Aponte)

Figure 22. Short-billed Pipit *Anthus furcatus*, Yamparáez, Chuquisaca, Bolivia, 16 November 2022 (Dirk Dekker)

Figure 23. Bobolink *Dolichonyx oryzivorus*, Parque Recreacional Los Pinos, Potosí, Bolivia, 1 January 2023 (Miguel Clavijo)

Figure 24. Glacier Finch *Idiopsar brachyurus*, Cordillera Los Frailes, Chuquisaca, Bolivia, 9 September 2020 (Dirk Dekker)

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Description of the Tamá-Santurbán subspecies of Slate-crowned Antpitta *Grallaricula nana*

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Summary.—We describe the population of Slate-crowned Antpitta *Grallaricula nana* in the northern section of the main East Andean range in Colombia and Venezuela (from Tamá to Páramo de Santurbán) as a new subspecies. Vocally, this population is differentiated from the previously consubspecific *G. n. nanitaea* of the Mérida Andes in Venezuela above the traditional 75% threshold for subspecies, with on average fewer notes, shorter song length, slower song speed, reduced change in acoustic frequency, lower max. acoustic frequency of the highest note and longer note length at the start of the song. Recently published molecular studies are also consistent with its treatment as a separate subspecies. Morphological differentiation is slight, but the Tamá-Santurbán population appears to have a paler breast in females, more extensive white feathering on the belly in males and a slightly broader bill than Mérida birds. The new subspecies is separated by the Chicamocha, Suárez and Sogamoso Valleys from the nominate subspecies of the southern East Andes and *hallsi* of the Serranía de los Yariguíes, both of which are more clearly differentiated in both voice and plumage.

Slate-crowned Antpitta *Grallaricula nana* (generally referred to as Grallariidae but Myrmotheridae is senior: see Gaudin *et al*. 2021, Gregory *et al*. 2024, 2025) is a small, nearly flightless understorey bird of high-Andean forests. A previous taxonomic revision (Donegan 2008) was driven by the discovery of a distinctive new subspecies in the Serranía de los Yariguíes, Santander, Colombia (*G. n. hallsi*). In the same study, taken together birds from the Mérida Andes in Venezuela and Tamá-Santurbán part of the northern East Andes in Colombia were clearly distinct from other populations and were described as *G. n. nanitaea*; type locality in the Mérida Andes. This subspecies comprises two geographically separated populations, for which vocal and mensural data were presented separately by Donegan (2008). The two populations showed some non-diagnosable phenotypic differentiation in bill width and four vocal characters. The geographically isolated Tamá-Santurbán population and its vocal differentiation have been noted by, e.g., Córdoba-Córdoba & Sierra (2018), Donegan (2018), Greeney (2018) and Van Doren *et al*. (2018). In particular, Donegan (2018), who measured differentiation in numerous undescribed populations of birds in the Andes, considered this population to be among of the most differentiated; furthermore, in the Van Doren *et al*. (2018) molecular study samples from Tamá-Santurbán and Mérida did not form a monophyletic group.

The sample sizes (n = 9–18 for the Tamá-Santurbán population in some vocal variables) and n = 24–25 for Mérida in Donegan's (2008) original study (reanalysed in Donegan 2018) were moderate. Fifteen years later, with the growth in bird sound libraries (xeno-canto.org and Macaulay Library), a larger vocal sample had been digitised or was now available from both populations. The statistical test in Donegan (2018) controlled for sample size using t-distribution values, which at 97.5% confidence is 2.28 when n = 10, but tends towards 2 as

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the sample size increases. As a result, samples with the same mean and standard deviation but based on a larger sample size will be measured as 'more differentiated' as confidence increases. Moreover, with a larger sample, the effect of any outliers is reduced. Critically, a larger sample produces more accurate results. As noted by Remsen (2010), the question of whether a population is a diagnosable unit can be reassessed with more data, sometimes producing different outcomes. It is therefore appropriate to re-run analyses with a larger sample of sound recordings and re-assess the taxonomic status of the Tamá-Santurbán population of *G. nana*.

The East Andes is a well-known centre of avian endemism (Stattersfield *et al*. 1998) and its northernmost part, the Perijá, has numerous endemic birds. In the East Andes, especially at high elevations, additional regions of endemism have been identified. The northern or Tamá-Santurbán region of the main East Andes lies largely in Colombia, north of the Chicamocha Valley and south of the Perijá (see Fig. 1), with a small extension in Venezuela. The Tamá is a national park straddling the border of both countries. Various high-elevation avian subspecies are restricted to this region (Donegan 2008, Avendaño & Donegan 2015).

The first specimen of *G. nana* from the Tamá-Santurbán region was collected in Colombia (at 07°25'W, 72°26'W, 2,450 m: Paynter 1997) in 1911 by W. H. Osgood, and is in the Field Museum of Natural History, Chicago (FMNH 43602) (Donegan 2008: 171). According to Chapman (1917: 651), Osgood and Jewell collected in the 'extreme headwaters', where 'higher up there is a small area of open rocky mountaintop with only narrow tongues of trees … too limited to support a true 'paramo' fauna so the life is mostly that of a forest

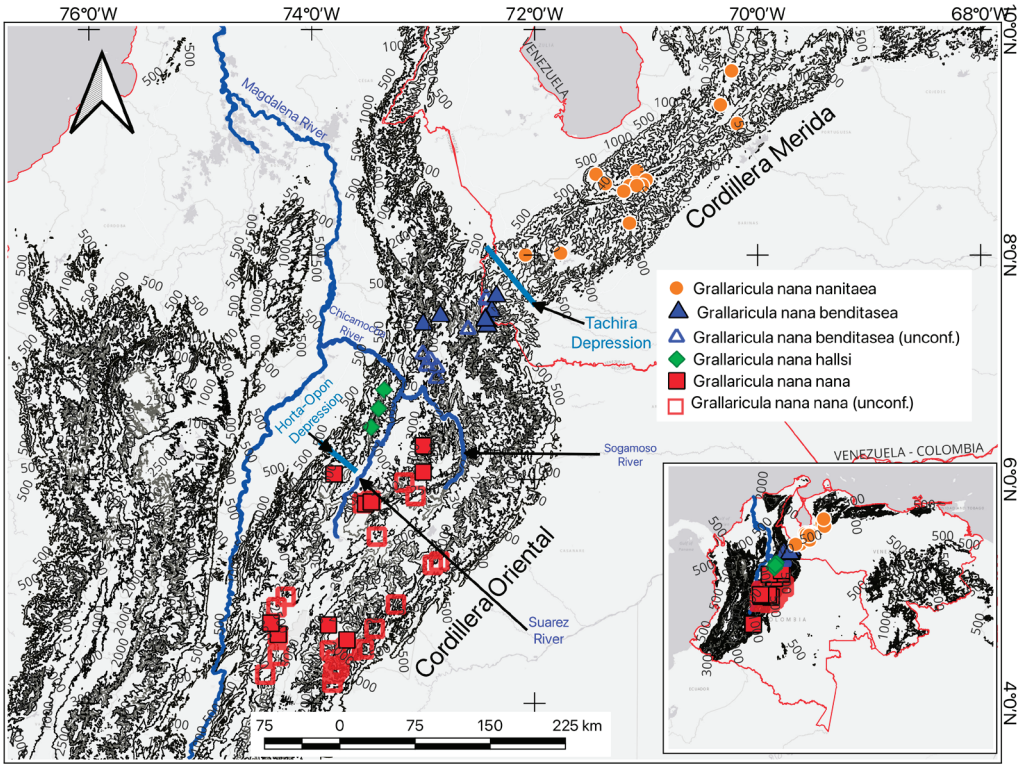

Figure 1. Map displaying localities for Slate-crowned Antpitta *Grallaricula nana* subspecies in the Colombian East Andes and Mérida (Venezuela) Andes, showing major rivers and other geographical features that define distributional limits. Unconfirmed records shown for the East Andes alone in the form of hollow shapes, with confirmed records being filled.

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region', a perfect description of *G. nana* habitat. Cory (1913, 1916) described numerous new taxa from Osgood's collections, but without commenting on this specimen.

On the Venezuelan side, R. Urbano first collected *G. nana* at Hacienda La Providencia, Río Chiquito (probably at *c*.07°38'N, 72°21'W; not 07°19'N, 71°37'W, as per Paynter 1982) in 1956 (Figs. 3–4). The species was not recorded during expeditions to the region led by the Phelps family in the 1940s. Phelps & Phelps (1956) published a detailed study of birds collected in the Venezuelan Tamá, including new subspecies descriptions (see Paynter 1982: 42). However, Urbano's collections at Hacienda La Providencia the same year occurred too late for that publication. Some of his specimens were mentioned by Phelps & Phelps (1959: 123; 1961: 246), but his *G. nana* series essentially went without further comment. M. Lastro and M. Costro collected additional specimens at Hacienda La Providencia in 1974–78 (Fig. 3).

On the basis of these records, *G. nana* was stated or mapped as occurring in the Tamá region by Cory & Hellmayr (1924), Meyer de Schauensee (1964), Hilty & Brown (1986), Fjeldså & Krabbe (1990), Ridgely & Tudor (1994), Restall *et al*. (2006), Krabbe & Schulenberg (2003) and others, in each case citing the nominate subspecies (which was considered more widespread prior to the revision by Donegan 2008).

In September 1999, M. Álvarez, S. Sierra and A. M. Umaña from the Instituto Alexander von Humboldt, Villa de Leyva (IAVH) conducted field work in Parque Nacional Natural (PNN) Tamá (e.g. Córdoba-Córdoba & Alvarez-M. 2003, Córdoba-Córdoba & Echeverry-Galvis 2006) and, in March 2002, SC made additional sound recordings; apparently the first vocal recordings of *G. nana* from this region were published by Córdoba-Córdoba & Alvarez (2003) and Álvarez *et al*. (2007). Further collections were made during an IAVH expedition on 3 September 2008 (eBird 2025, checklist S29528459) and Socolar & Peña (2022) reported various new bird records from PNN Tamá, but without mentioning *G. nana*.

More recently, LAP & JBS have studied birds in the Tamá region of Norte de Santander (Socolar & Peña 2022, Peña *et al*. 2022, 2024a,b). LAP first heard a *Grallaricula*, presumably the local population of *nana*, on 19 October 2019 at Páramo de Tierra Negra, Pamplona, Norte de Santander (07°20'29"N, 72°35'55"W, 3,000 m). On 19 March 2024, he visited PNN Tamá, including two localities where he sound recorded *G. nana*: at 07°21'51"N, 72°25'32"W, 2,450 m, in Andean forest; and 07°22'12"N, 72°25'17"W, 2,730 m at the páramo/forest ecotone. Both localities are in Vereda Samaria, Toledo municipality, dpto. Norte de Santander, which has been visited by various other ornithologists, including J. D. Ramírez, who accompanied LAP during one of these visits. Ramírez, who was familiar with *G. nana* from other localities and was aware of the work of Donegan (2008) and Van Doren *et al*. (2018), noted differences in song versus other Colombian populations of *G. nana* and made several sound recordings. In April 2019, JBS visited several localities in PNN Tamá and its buffer zone and conducted point counts as part of a larger study. During these, he sound recorded continuously using an omnidirectional Sennheiser ME-62 microphone. During one point count he heard *G. nana*, which is audible on the associated recording.

LAP uploaded sound recordings from these studies in March 2024. These included one confirming an interesting range extension for Undulated Antpitta *Grallaria squamigera*, which attracted TMD's attention. TMD contacted JS and LAP to ask if they had more recordings of *G. nana* from the same locality, and it was decided to combine our information and materials.

Methods

The same dataset originally used by Donegan (2008) to study the voice of *G. nana* was employed. All recordings in Macaulay Library and xeno-canto from localities in the

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Mérida and Tamá-Santurbán regions (and adjacent northern East Andes) were re-examined. Recordings by JS & LAP (held privately at the time but now archived) were also analysed. Previously studied recordings were initially discarded to avoid repeating their inclusion and cross-database duplicates were removed, as were recordings on the same day or next day at the same locality by the same recordist, whose vocal parameters were sufficiently similar as to appear to involve the same individual. Two recordings were considered misidentified and one had incorrect locality data; these were discarded and highlighted with the relevant website administrator. The rest of the sound recordings were identified as 'new' and up to three songs from each of them (or a combination of recordings considered to involve the same individual) were measured using Raven Lite for the same ten vocal variables studied by Donegan (2008): (i) number of notes in song; (ii) total song duration (seconds); (iii) song speed (i ÷ ii); (iv) max. acoustic frequency of highest note (kHz); (v) max. acoustic frequency of lowest note (kHz); (vi) variation in acoustic frequency (kHz) (iv minus v); (vii) position of peak (time of peak frequency measured from the start of the song divided by song length); (viii) note length at start (time from start of second note to start of third); (ix) note length at end (timed from the start of the penultimate note to the start of the last); and (x) change of pace (viii ÷ ix). Acoustic frequencies from the original dataset were remeasured to four significant figures. Once the larger database was compiled, max. and minimum recorded values for both populations for each variable were remeasured and verified (or corrected, in which case any newly identified lowest or highest data point was identified and checked) until the minimum and max. bounds for both populations were established.

Statistical tests were then applied on a pairwise and total population basis, using the methods in Donegan (2018), with a Microsoft Excel spreadsheet devised for rapid measurement of multiple pairwise statistical tests across multiple populations (Donegan 2021).

First, vocal data for *G. nana* from Mérida and Tamá-Santurbán were combined in a Microsoft Excel spreadsheet and Pearson's correlation coefficient was calculated on a matrix basis between all ten vocal variables. Where $r > 0.80$, one of the variables was eliminated, resulting in song duration being excluded (correlates with number of notes, $r = 0.82$). Next, a Welch's *t*-test at $p < 0.05$ was applied, but applying a Bonferroni correction. For this study, which involved ten variables, $p < (0.05 / 9) = 0.00556$ was the corrected confidence interval for statistical significance. The unequal variance (Welch's) *t*-test was applied as this makes no assumptions concerning the standard deviations of each population tested. For song speed, the two-sample Kolmogorov-Smirnov test was applied to account for the possibility of a non-normal distribution. These tests were used as a gateway for measuring the extent of differentiation in any variable. If these tests were passed for a variable between the two populations under study, then the next test, which measured differentiation, was scored. If not, then the variable was scored as having zero difference.

'Diagnosability coefficients' or 'controlled effect sizes' (following Donegan 2018) were calculated on a pairwise and then cross-population basis between all comparisons which passed the test of statistical significance for each variable, as follows. This test measures the differences between the means of two populations for each variable, expressed in terms of average standard deviations, but controlled for the sample size of both populations.

In the formula below, $\bar{x}_1$ and s_1 are the sample mean and SD of population 1; $\bar{x}_2$ and s_2 refer to the same parameters in population 2; and the *t* value uses a one-sided confidence interval at the percentage specified for the relevant population and variable, with t_1 referring to population 1 and t_2 referring to population 2.

$$p<0.05/n_v \rightarrow |(\bar{x}_1 - \bar{x}_2)| \; / \; ¼[\, s_1\,(t_{1\,@\,97.5\%}) + s_2\,(t_{2\,@\,97.5\%})]$$

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These scores for each variable were then subject to Euclidian summation using Donegan's (2018) proposed scoring system, as follows:

$$\sqrt{\left(\sum [p<0.05/n_v \rightarrow |(\bar{x}_1 - \bar{x}_2)| \,/\, ¼[\, s_1 (t_{1\,@\,97.5\%}) + s_2 (t_{2\,@\,97.5\%})\,]\,]^2\right)}$$

Where:

p: the probability using Welch's unequal variance t-test (supplemented by Kolmogorov-Smirnov test for song speed), as set out above.

n_v: the number of continuous variables used in the study, i.e. applying a Bonferroni correction.

n_1 or n_2 refer to sample sizes for the relevant variable of the two populations under study.

$\bar{x}_1$ and $\bar{x}_2$ are the sample means of population 1 and population 2, respectively.

s_1 and s_2 are the standard deviations of population 1 and population 2, respectively.

The t value uses a one-sided confidence interval at the percentage specified for the relevant population and variable, with t_1 and t_2, referring to population 1 and population 2, respectively.

This method can be preferable to more widely known subjective approaches or those involving hard cut-offs (i.e. only applying weightings above particular thresholds) (e.g. Isler *et al.* 1998, Tobias *et al.* 2010). Instead, measured differentiation takes into account all statistically significant variation between two populations and discards all non-statistically significant variation. Differentiation is scored based on the unit of standard deviations (so-called 'effect size') and controlled for sample size using t-distributions. The scored differentiation measurements for each variable showing statistically significant differences are then subject to a Euclidean summation, to produce a measure of total differentiation between the two populations in multi-dimensional space, measured in controlled effect sizes. Diagnosability is demonstrated in multi-dimensional space if the populations attain a score of 4 or more. Whether a population or variable achieves a score of 4 is essentially equal to Isler *et al.*'s (1998) diagnosability test, but based on the whole dataset. The traditional 75% test for subspecies (Patten & Unitt 2002) is broadly equivalent to a score of 2 on this scale, which reflects the point where the mean of one population falls outside the range of the other population (Donegan 2018).

To assess species rank, measured differentiation must be compared with differentiation among closely related sympatric species. An appropriate benchmark in the present case would be that between *G. nana nanitaea* and Rusty-breasted Antpitta *G. ferrugineipectus* in the Mérida Andes of Venezuela (Donegan 2008, 2018). These scored 7.90 for vocal variation (Donegan 2018), which is here treated as an appropriate proxy for species rank.

Plumage and biometrics were previously studied by Donegan (2008) based on specimens and photographs of both populations. Plumage can be used to identify *G. nana nanitaea* (*sensu lato*) from all other described subspecies. No plumage differences between the Tamá-Santurbán and Mérida populations were identified by Donegan (2008). They are very similar and comparisons are not easy because Tamá-Santurbán specimens are scarce and Colombian collections lack material from Mérida for comparison. The Colección Ornitológica Phelps (COP), Caracas, has examples of both populations but few Mérida specimens, with all of the males being juveniles. Adult females were compared directly (see Fig. 4).

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Results

For vocal variation between, and scoring of, the Tamá-Santurbán and Mérida populations of *G. nana nanitaea* see Appendix 2. Acoustic frequency variation was the most differentiated vocal variable, achieving a score above 2. An overall score of 3.42 was recorded in multidimensional space, marginally short of diagnosability (4) but establishing a reasonable basis for subspecies diagnosis under traditional concepts, supporting the description of:

Grallaricula nana benditasea subsp. nov.

Holotype.—Adult male at the Instituto Alexander von Humboldt, Villa de Leyva, Colombia, IAVH-A-10714, collected at PNN Tamá, Sector Orocué, municipality Herrán, Norte de Santander, Colombia (07°25′31″N, 72°26′38″W, 2,430 m) on 27 June 1999 by M. Álvarez, A. M. Umaña and S. Sierra (field no. MAR 681). Habitat stated as 'bosque Andino. Sotobosque denso dominado por *Rhipidocladium* sp'. Also bears the code 152 in pencil on the label. See Fig. 2.

Diagnosis.—Similar to *G. n. nanitaea* of the Mérida Andes, but song is near-diagnosable in multidimensional space (score 3.42 using Donegan 2018). Each measured vocal variable overlaps, but songs of the new subspecies have reduced change in max. acoustic frequency (2.08), fewer notes (1.93), shorter length (1.37), longer note length at the start (1.25), lower max. acoustic frequency of the highest note (0.94) and slower speed (0.79). For each of these variables the differences are both statistically significant and involve material effect size differentiation (Appendix 2; Figs. 5A–C; see sonograms in figs. 10–11 of Donegan 2008). The bill is slightly broader on average (barely visible in Fig. 4; see also Donegan 2008: 174). Based on the COP series, females are slightly darker rufous on the belly (Fig. 4) and have marginally more extensive white feathering on the belly and vent (see Fig. 4; compare Figs. 2–4 with Donegan 2008: fig. 7). A greater sample size is needed to confirm the nature (morphological vs. individual) and extent of these variations.

Van Doren *et al.* (2018) studied two mitochondrial genes (NADH ND2, 1,041 bp; and NADH ND3, 351 bp) and three autosomal nuclear introns (TGFb2, 629 bp; MUSK, 651 bp; bF5, 568 bp). They found *G. n. nanitaea* and *G. n. benditasea* not to be mutually monophyletic.

Differs from other *G. nana* subspecies as discussed by Donegan (2008) in the diagnosis of *G. nana nanitaea*. Compared to nominate *G. n. nana* of the adjacent East Andes (south of the Chicamocha Valley and depression) *G. n. benditasea* has paler (more orange, less rufous) underparts and a more olivaceous (less brownish) back and mantle, and diagnosably different voice (overall score 5.50). The best-differentiated character is its lower max. acoustic frequency, which is close to diagnosable (3.75); max. frequency of the lowest note (3.11) and slower song speed (1.75) are also rather differentiated (see Fig. 5D). *G. n. hallsi* of Serranía de los Yariguíes is considered distinct genetically (Van Doren *et al*. 2018) and is diagnosably distinct in max. acoustic frequency of songs (4.98), with differences also in number of notes (3.48) and acoustic frequency variation (3.01) (Donegan 2008: 177; see also Fig. 5D). An overall measured differentiation of 7.14 from *hallsi* approaches the minimum score for species rank in *Grallaricula* in multi-dimensional vocal space. The latter subspecies differs further in lacking white feathers on the throat. *G. n. occidentalis* of the Central and West Andes of Colombia south into Ecuador and Peru has no visible white on the throat or upper breast and a browner mantle and wings. Molecular work suggests that these are not so closely related to *benditasea* (Van Doren *et al*. 2018). Surprisingly, these more southern and western populations, split into three groups for analytical purposes, differ non-diagnosably in voice from the new subspecies (Donegan 2008: 175–177), scoring 2.04 overall

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Figure 2. The holotype of *Grallaricula nana benditasea* and two paratypes. in ventral (above) and dorsal views, showing bottom to top and left to right (left-hand three individuals alone), respectively: (i) IAVH-A-10714 (holotype), (ii) IAVH-A-10702 (paratype) and (iii) IAVH-A-10722 (paratype), all collected in Parque Nacional Natural Tamá, Colombia, see full details under 'Holotype' (Thomas M. Donegan)

for Ecuador–Peru, 3.89 for West Andes and 2.56 for Central Andes. A 'leapfrog' reversion to a similar vocal pattern in a more geographically distant and less closely related population

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is therefore evident. The most consistently differentiated variable for these populations is their slower song compared to the new subspecies (1.16–1.61, depending on population).

Eastern Venezuelan populations are all diagnosable vocally. *G. n. olivascens* of the Coastal Cordillera (5.53 overall) is most different in song speed (3.44). Sucre Antpitta *G. cumanensis* has a very different voice, biometrics and plumage coloration, and is now usually split following Donegan (2008). The Tepui endemic *G. n. kukenamensis*, for which species rank has also been proposed, has a very different song, diagnosably distinct biometrics and more triangular bill, as well as differences in plumage coloration (Donegan 2008).

Description of the holotype.—Colour nomenclature follows Munsell Color (1977, 2000). Lores, central forehead and crown dark grey (Gley 1 3/N). Mantle and tail generally brown (10YR 3/3), becoming richer brown (less olive) over upperwing, particularly on the primary-coverts and outer webs of the flight feathers, and rectrices. Large loral spot, eye-ring, throat, breast, flanks, underwing-coverts, tip of largest alula and tip of outermost primary orange-rufous (7.5YR 5/8 or 5YR 5/8 but more rufous). Central belly to vent white, becoming broader white to vent. Small and indistinct patch of feathering on throat is white. Breast feathers dark grey basally with rufous tips (most of flanks and breast), white basally with rufous tips (throat) or dark basally with white tips (white of breast and lower belly). Trailing edge of primaries pale grey distally. Rictal bristles black. Wing chord 68 mm; tail 33 mm; tarsus 27.5 mm; bill to skull 15 mm; specimen label states mass as 23 g.

Paratypes.—See specimens listed and some illustrated in Donegan (2008: 150–151, 171; also Figs. 2–4 herein). Venezuela: Colección Ornitológica Phelps (COP) 73941–943 (Cumbres Cerro Retiro, Rebancha (= Revancha), Táchira, 07°30′N, 72°23′W, 2,800 m), 74419–420 (Copas La Rebancha (= Revancha), Táchira, 07°30′N, 72°23′W, 2,800 m), 62203–206 (Hacienda La Providencia, Río Chiquito, Táchira, 07°19′N, 71°37′W, 2,100–2,300 m) (Figs. 2–3). Colombia: IAVH-A-10702, 10722 (locality as holotype); Instituto de Ciencias Naturales, Universidad Nacional, Bogotá, Colombia (ICN-UN) 33933 (locality as holotype, formerly IAVH-A-10645; see Donegan 2008: 151, fig. 5, where referred to as *nanitaea*), 36125 (Vereda El Monsalve, Suratá, Santander, 07°23′N, 73°00′W, 3,000 m; see also Donegan 2008: 151, fig. 2, referred to as *nanitaea*); FMNH 43602 (Páramo de Tamá, Norte de Santander, 07°25′N, 72°26′W). Immature photographed by J. E. Avendaño-C. at Suratá, dpto. Santander, Colombia, and illustrated in Donegan (2008: 151, fig. 2). See Appendix 3 for a list of previous references to the new subspecies in the periodical and some other literature.

Variation in the series.—As reported in Donegan (2008: 160, fig. 2) and shown in Fig. 2 (left-hand three specimens), some females have less white in the throat than others. IAVH-A-10722 is a female with such markings. Juveniles or immatures have asymmetrical rufous patches on the crown and elsewhere (Donegan 2008, fig. 2; other examples here in Figs. 3–4, second from left in both). There is some variation in the shade of the olivaceous-brown dorsal coloration, which also appears to be sex- and age-related (Fig. 3).

Etymology.—The name *G. n. nanitaea* was originally chosen recalling the Spanish advent carol or *villancico*, which starts '*A la nanita nana nanita ea*' (Donegan 2008). The name has proven memorable, even giving rise to at least two memes on social media, in which a Slate-crowned Antpitta illustration from Quiñones (2019) was juxtaposed with Christmas decorations and festive clothing, with the *villancico* as a soundtrack. The same *villancico* continues '*El niño tiene sueño, bendito sea, bendito sea*'. 'Bendito' as an adjective agrees with a masculine noun, referring to a male child. Here, feminine 'bendita' is used to promote gender agreement in modern Spanish ('nana' being an informal feminine noun meaning nanny'; in the carol it may refer to a lullaby). '¡Bendita sea!' means 'blessed be [her or it]'. Often said in isolation, this is a modern colloquialism in Colombia, equivalent to 'Goodness me!' or 'Thank goodness for that!' in English. As a combination of two Spanish-language

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Figure 3. Series of *Grallaricula nana benditasea* at Colección Ornitológica Phelps, Caracas; three females (left) and six males (right) (all paratypes). From left to right: (i) COP 73941, (ii) COP 73942, (iii) COP 73943, (iv) COP 74419, (v) COP 74420 (all Cerro El Retiro, La Rebancha (= Revancha), Táchira, 2,800 m, 4 August–13 September 1978, collected by M. Castro), (vi) COP 62206, (vii) COP 62205, (viii) COP 62204, (ix) COP 62203 (all Hacienda La Providencia, Río Chiquito, Táchira, 2,100–2,300 m, collected by R. Urbano) (Thomas M. Donegan)

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Figure 4. Two female specimens of *Grallaricula nana benditasea* (left, middle) and female of *G. n. nanitaea* (right) at Colección Ornitológica Phelps, Caracas; left to right: (i) COP 79343, (ii) COP 73942 (both paratypes), (iii) COP 65392 (La Azulita, Mérida, 2,300 m, collected 25 November 1959 by R. Urbano) (© Margarita Martínez)

words, the name is non-variable with respect to gender of the Latin genus in which it is placed.

Distribution and ecology.—See Fig. 1. The new subspecies occurs in the northern section of the East Andes. Its elevational range and habitat appear similar to those of the recently described Tamá-Santurbán endemic tapaculo, *Scytalopus griseicollis morenoi* (Avendaño & Donegan 2015). The northern distributional limit of *G. nana benditasea* is marked by the Ocaña (Serranía de los Motilones) depression (*c*.1,200 m). No member of the *G. nana* species-group has been recorded in the Perijá Mountains. To the north-east, the new subspecies is replaced by *G. n. nanitaea* on the opposite side of the Táchira depression, a well-known barrier for high-elevation birds (Stattersfield *et al*. 1998). To the south-west, the rivers Chicamocha, Suárez and Sogamoso are associated with a deep, dry valley that deeply bifurcates the western section of the East Andes and also separates the Yariguíes Mountains from the main range. These are formidable geographic barriers for near-flightless understorey birds such as these antpittas; moreover, they are associated with changes in environmental conditions (Graham *et al*. 2010).

The southern limit of the new subspecies' distribution on the east slope is less certain. In Donegan (2008: fig. 9), modelling based on then-known localities considered *G. nana* unlikely to occur on the east slope north of PNN Chingaza, near Bogotá (*c*.04°40′N); climatic conditions appeared unfavourable in the environs of PNN Pisba (*c*.05°52′N) and PNN Cocuy (*c*.06°50′N), where no high-elevation *Grallaricula* has been reported. There are now unconfirmed sight records, presumably of the nominate subspecies, on the east slope to around the latitude of Yopál (*c*.05°20′N) (eBird 2025) but not further north (Fig. 1). Ornithological visits to PNN Pisba and PNN Cocuy tend to start on the more accessible west side; montane forest on the east slope in this region is largely inaccessible. Given that the nominate subspecies is diagnosably distinct in song from *G. n. benditasea* and exhibits notable plumage differences for the genus, it seems unlikely that variation is clinal.

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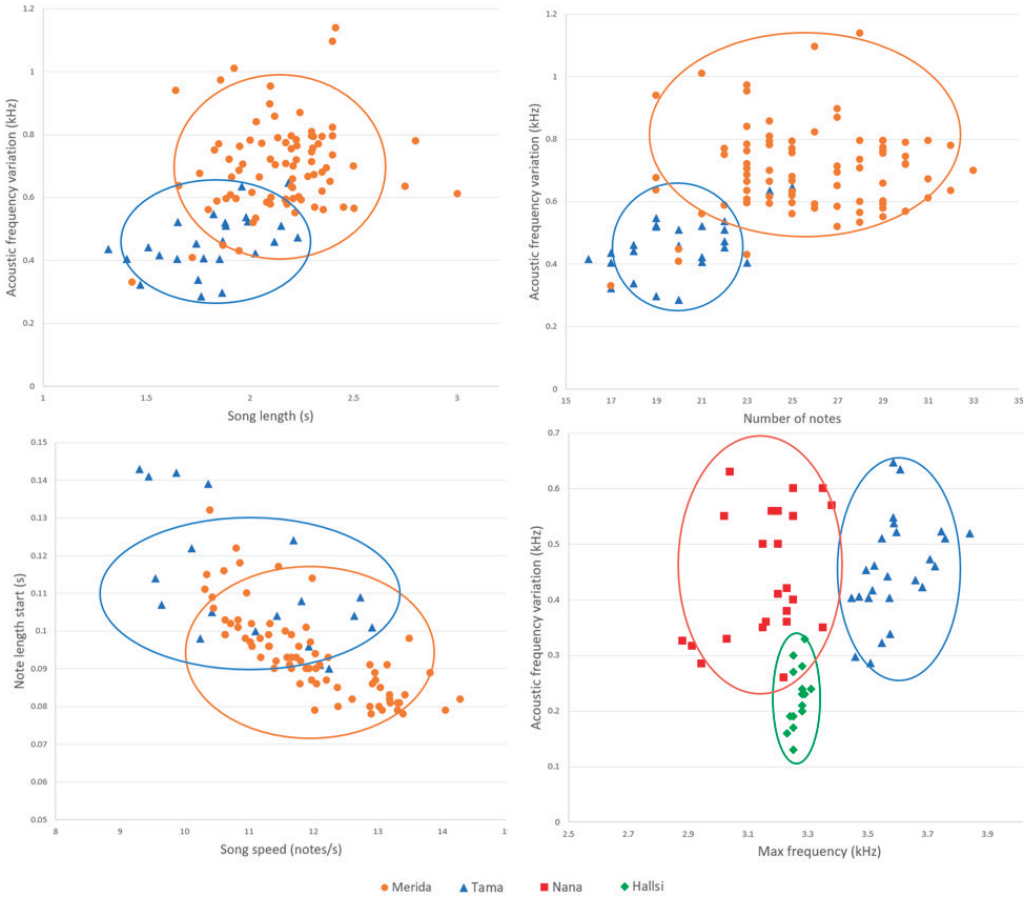

Figure 5A–C. Plots comparing certain vocal variables of the Mérida (*Grallaricula nana nanitaea*) and Tamá-Santurbán (*G. n. benditasea*) populations, demonstrating differentiation in (A) song length (seconds) (*x*) and acoustic frequency variation in kHz (*y*); (B) number of notes (*x*) and acoustic frequency variation (kHz) (*y*); (C) song speed (notes/second) (*x*) and note length at start (seconds) (*y*); and (D) plot comparing Tamá-Santurbán (*G. n. benditasea*), main East Andes (nominate *G. n. nana*) and Yariguíes (*G. n. hallsi*) songs for max. frequency (*x*) and acoustic frequency variation (*y*). Ellipses are placed two standard deviations from each centroid.

On the west slope of the East Andes, there are recent records of *G. nana* by Córdoba-Córdoba & Sierra (2018) from El Peñon, Santander (06°03'N, 73°48'W, 2,856 m) and Arbeláez-Cortés *et al*. (2023) from Finca Fontibón, vereda Guadual, Coromoro, Santander (06°18'N, 73°00'W, 3,000 m) (B. Arenas Vega: XC 740586), both at the northern limits of the range of the nominate subspecies. Neither record was identified to subspecies. These localities lie south or west of the Chicamocha Valley and are considered to involve nominate *G. n. nana* (being mapped as such in Fig. 1). The bird illustrated by Córdoba-Córdoba & Sierra (2018) has a relatively rufous breast, with no visible white on the throat, consistent with the nominate. The recording by B. Arenas-Vega is relatively short, of relatively low frequency and of low within-song frequency variation compared to Tamá-Santurbán recordings. In those features, it is consistent with the nominate. 'Main' East Andes subspecies (as opposed to Tamá-Santurbán endemic subspecies) have been confirmed for *Scytalopus* tapaculos at nearby localities (e.g., Donegan & Avendaño 2008, Avendaño & Donegan 2015).

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The habitat of the new subspecies is similar to that of *G. n. hallsi*, in the highest belt of Andean forest, especially at the páramo/forest ecotone. Páramo de Tierra Negra has bushy areas and stunted or elfin forest where the species was heard, as well as tree frailejones and bamboo clusters. One of LAP's study sites in Tamá National Park was in high-elevation Andean forest and had vegetation typical of remnant patches of this region, including frailejones of the genus *Libanothamnus* or *Espeletia*. Two *G. n. benditasea* were sound recorded at *c*.08.45 h. Another was heard *c*.100 m away. The second site was in the páramo/forest ecotone, with bamboo and other bushy vegetation prevalent, and an individual was heard just 200 m from the páramo. Both localities experienced rainfall during the study with ground-level clouds or fog.

Vocalisations.—See Donegan (2008: 156, fig. 10(g)) for a sonogram of the song of the new subspecies alongside those of all other *G. nana* subspecies including Mérida birds. Donegan (2008: fig. 12(g)) included a sonogram of a weak recording of its apparent call, alongside those of other *G. nana* subspecies. Vocal parameters for the new subspecies are elucidated in full in Appendix 2. Vocal differentiation is illustrated between the Tamá-Santurbán and Mérida populations and among East Andes subspecies in Fig. 5.

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Appendix 1: sound recordings inspected

G. n. nanitaea (all Venezuela)

Parque Nacional Guaramacal, Trujillo (09°10′N, 70°11′W, 1,600–3,000 m) (XC 223754 = ML 285673 = Boesman 2007*).

Ramal de Calderas, Camino Real Niquitao–El Bambú, Barinas (RAP Calderas project ref. CI-MHNLS AF2) (08°58′N, 70°26′W) (D. Ascanio: ML 387407441).

La Azulita, Mérida (08°43′N, 71°27′W) (R. Behrstock uncatalogued*; C. Jones: ML 314014141).

La Carbonera, Mérida (08°38′N, 71°22′W, 2,300 m) (P. Schwarz: ML 62191*).

Parque Nacional Sierra Nevada (most, La Mucuy or Pico Humboldt trail), Mérida (08°37′N, 71°02′W, 2,400–2,500 m) (N. Athanas: XC 6858*; A. Spencer: XC 9895*; B. M. Whitney uncatalogued*; B. López-Lanús: XC 50628; J. Klaiber: XC 43323 [XC 43324 is same recording], XC 43325, XC 42940; H. Matheve: XC 202967; D. Edwards: XC 27919; N. Athanas: XC 6883, XC 6885; C. Jones: ML 314013941; D. Ascanio: ML 304208561, ML 309065291, ML 309065301 [treated as same individual as previous], ML 309065311, ML 309065341 [treated as same individual as ML 309065291], ML 309065351, ML 309065381; D. Beadle: ML 204021871 = IBC 1130975; L. Macaulay: ML 102523).

Tabay, Mérida (08°37′N, 71°05′W) (T. H. Davis: ML 182405).

Universidad de Los Andes, Mérida (08°37′N, 71°09′W) (K. J. Zimmer uncatalogued*; G. Rosenberg: ML 305918351).

Jají, Mérida (08°34′N, 71°12′W) (T. H. Davis: ML 182417).

El Morro–Aricagua road, Mérida (08°17′N, 71°09′W) (XC 223756 = ML 289146 = Boesman 2007*).

Páramo Zumbador, Táchira (08°00′N, 72°05′W, 2,450–2,800 m) (P. Schwarz: ML 62189*–190*, 62192*–193*).

Parque Nacional Juan Pablo Peñaloza, Páramos El Batallón y La Negra, Táchira (08°00′N, 71°57′W) (B. C. Quintero: ML 484154001, ML 560771771, ML 560771591) [treated as same individual as previous], ML 617724732).

Parque Nacional Juan Pablo Peñaloza, vía La Palma, Táchira (07°52′N, 71°53′W) (B. C. Quintero: ML 358966611, ML 358968281, ML 358968341, ML 361772261 [all four treated as same individual], ML 361780641, ML 361780791 [treated as same individual as previous]).

G. n. benditasea (all Colombia)

Sisavita, Cucutilla, Norte de Santander (07°28′N, 72°51′W, 2,400 m) (S. Córdoba: IAVH-CSA-8660*, 8662*, 8813*).

Parque Nacional Natural Tamá, Herrán, Norte de Santander (07°26′N, 72°27′W, 2,430 m) (M. Álvarez *in* Córdoba & Álvarez 2003, track 19*, Álvarez *et al*. 2007, disc 4, track 26b = IAVH-CSA-11722*, 11727*).

Parque Nacional Natural Tamá, Vereda Samaria, Toledo municipality, dpto. Norte de Santander. Point 1 (07°21′51″N, 72°25′32″W, 2,450 m) (L. A. Peña: ML 630434230, ML 630434231). Point 2 (07°22′12″N, 72°25′17″W, 2,730 m) (L. A. Peña: ML 630491034, ML 630491035). ORF1, Orocué, PNN Tamá, dpto. Norte de Santander (07°25′08″N, 72°26′34″W, 2,538 m) (J. Socolar: ML 621265271).

Note: * = recording originally included in Donegan (2008). A lack of such denotation signifies a 'new' recording included in this study.

Appendix 2: vocal data

For each taxon/variable, data are presented as follows: mean ± standard deviation (lowest recorded value–highest recorded value) (n = no. of songs analysed). In the final column, differentiation is measured in diagnosability coefficients based on Donegan (2018), which equate to a measure of differentiation in units of standard deviations, controlling for sample size (i.e. 4 is 'full' diagnosability). Variables that are non-statistically significant (using a t-test, subject to Bonferroni correction at p <0.05/9 = p <0.00556) were scored as zero. The score for song duration shown in italics was excluded from Euclidean summation due to a correlation of r = 0.82 with number of notes.

Taxon	No. of notes	Song duration (s)	Song speed (notes/s)	Max. acoustic frequency of highest note (kHz)	Max. acoustic frequency of lowest note (kHz)	Acoustic frequency variation (kHz)
G. n. benditasea Tamá-Santurbán, Colombia/Venezuela	20.00 ± 2.36 (16–25) (n = 24)	1.82 ± 0.24 (1.32–2.23) (n = 25)	11.06 ± 1.15 (9.30–12.91) (n = 24)	3.59 ± 0.10 (3.45–3.84) (n = 25)	3.14 ± 0.10 (2.94–3.32) (n = 25)	0.46 ± 0.09 (0.29–0.65) (n = 25)

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G. n. nanitaea Mérida, Venezuela	25.67 ± 3.46 (17–33) (*n* = 81)	2.16 ± 0.25 (1.43–3.00) (*n* = 85)	11.92 ± 0.99 (10.32–14.29)(*n* = 81)	3.73 ± 0.19 (3.24–4.30) (*n* = 85)	3.03 ± 0.19 (2.46–3.41) (*n* = 85)	0.70 ± 0.14 (0.33–1.14) (*n* = 84)
Statistical significance (t-test)	$p < 1 \times 10^{-12}$	$p < 3 \times 10^{-7}$	$p = 0.0021$	$p < 9 \times 10^{-6}$	$p = 0.00045$	$p < 1 \times 10^{-14}$
Diagnosability coefficient (controlled effect sizes)	**1.93**	***1.37***	**0.79**	**0.94**	**0.73**	**2.08**

Taxon	**Note length at start (s)**	**Note length at end (s)**	**Change of speed**	**Position of peak**	
G. n. benditasea Tamá-Santurbán, Colombia/ Venezuela	0.11 ± 0.02 (0.09–0.14) (*n* = 19)	0.07 ± 0.02 (0.05–0.12) (*n* = 18)	1.58 ± 0.31 (1.18–2.24) (*n* = 17)	0.18 ± 0.05 (0.08–0.27) (*n* = 25)	
G. n. nanitaea Mérida, Venezuela	0.09 ± 0.01 (0.08–0.13) (*n* = 80)	0.07 ± 0.02 (0.04–0.12) (*n* = 74)	1.45 ± 0.47 (0.83–2.51) (*n* = 74)	0.19 ± 0.05 (0.11–0.36) (*n* = 84)	
Statistical significance (t-test)	$p = 0.00022$	$p = 0.50$	$p = 0.18$	$p = 0.53$	
Diagnosability coefficient (controlled effect sizes)	**1.25**	**0**	**0**	**0**	**Euclidean summation of diagnosability coefficients (excluding items in italics) 3.42**

Appendix 3: references to the new subspecies in the mainly periodical literature

Córdoba-Córdoba & Álvarez (2003, track 19), '*G. nana*'.

Álvarez *et al*. (2007, Disc 4, track 26b and p. 28), '*G. nana nana*'.

Donegan (2008) 'immature *G. n. nanitaea*' (p. 150 and fig. 2 on p. 151), '*G. n. nanitaea* Tamá' (p. 150 and fig. 5(vi) on p. 151; fig. 10(g) on p. 156; fig. 12(g) on p. 158; pp. 174–178); 'TAMÁ-SANTANDER' (p. 160), 'Those on the other side of the Táchira depression…' (p. 164), 'Specimens from the Tamá region…' (p. 164), 'Tamá specimens…' (p. 165), '*G. n. nanitaea* SANTANDER-TAMÁ' (pp. 171–173).

Salaman *et al*. (2008: 48, 2009: 44, 2010: 44) '*Grallaricula nana* subsp. (Ae: Tamá)'.

Donegan *et al*. (2009: 80) '*Grallaricula nana nanitaea*'.

Greeney (2018: 429) '*nanitaea* of the Andes on the Colombia/Venezuela border', 'records from north-east Colombia...' (p. 432).

Donegan (2018: 59) 'Tamá population of *Grallaricula nana*'.

Van Doren *et al*. (2018: 159) '*Grallaricula nana nanitaea* COL Norte de Santander'.

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Firewood-gatherer *Anumbius annumbi*: a new species and genus in Bolivia

by W. Sergio Pantoja

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Summary.—Firewood gatherer *Anumbius annumbi* is a furnariid endemic to southern South America that occurs in grassland, agricultural areas, shrubland, savanna, and open woodland. I report the first record of the species for Bolivia in Parque Nacional y Área Natural de Manejo Integrado Otuquis in September 2024.

Firewood-gatherer *Anumbius annumbi* is a medium-sized furnariid with pale brown upperparts, a sparsely black-streaked back, rufous forehead and whitish supercilium, and a long, graduated and pointed tail with broad white tips. This distinctive feature differentiates it from superficially similar and sympatric species such as Wedge-tailed Grass Finch *Emberizoides herbicola* and Chotoy Spinetail *Schoeniophylax phryganophilus* (Ridgely & Tudor 1994). It is distributed across southern South America, in south-east Brazil, central and eastern Paraguay, and northern and eastern Argentina to Uruguay. It is common in grassland, agricultural areas, scrubland, savanna and at the edges of open forest, from sea level up to 1,000 m (Remsen 2020).

On 10 September 2024, I was conducting an avifaunal assessment for the Parque Nacional y Área Natural de Manejo Integrado (PN & ANMI) Otuquis management plan, Santa Cruz, Bolivia, conducted by the Museo de Historia Natural Noel Kempff Mercado and Fundación Amigos de la Naturaleza. During the survey, I photographed a Firewood-gatherer perched on a *Sesbania virgata* (Fig. 1) near the Servicio Nacional de Áreas Protegidas

Figure 1. (A–B) Firewood-gatherer *Anumbius annumbi*, Puerto Busch, PN & ANMI Otuquis, Santa Cruz, Bolivia, 10 September 2024; (C) habitat where the Firewood-gatherer was recorded; and (D) the same area after it was burned (W. Sergio Pantoja)

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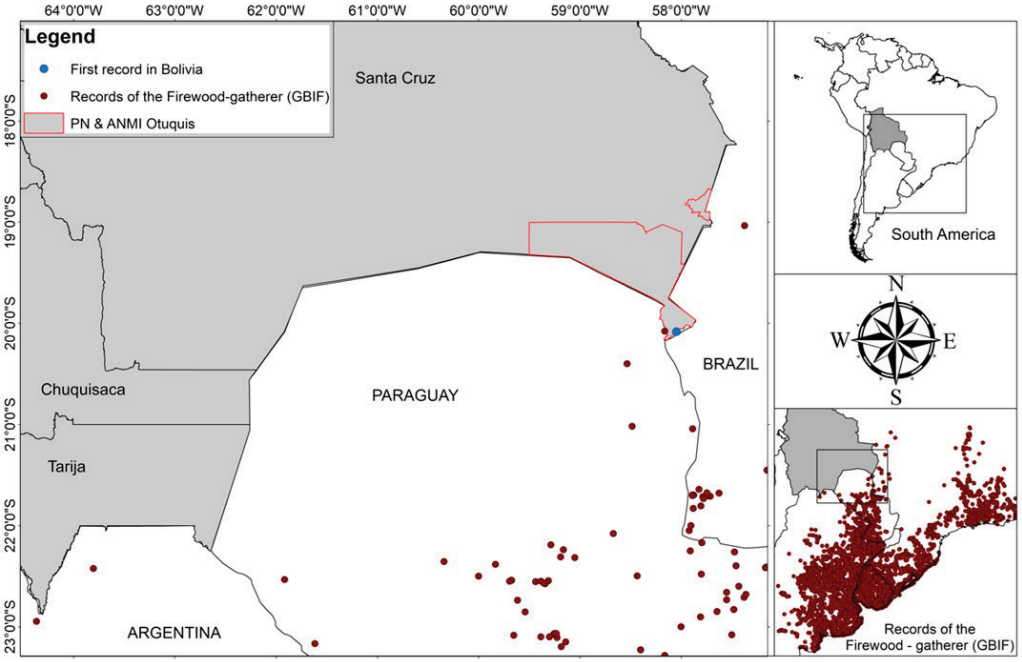

Figure 2. Location of the Firewood-gatherer *Anumbius annumbi* record in PN & ANMI Otuquis, Santa Cruz, Bolivia, along with the geographically closest records available in the GBIF (2025) platform.

Puerto Busch camp (20°04′58″S, 58°02′44″W; 80 m) in dry grassland with shrubs and a few young trees. The area belongs to the seasonally flooded marsh formation (Navarro 2011), close to riparian forest along the Paraguay River. This part of the protected area frequently experiences fires during the dry season and these have become increasingly common in recent years. Two days later the area burned and I could not relocate the Firewood-gatherer.

My record in Parque Nacional y Área Natural de Manejo Integrado Otuquis (Fig. 2) is the first documented sighting of the species in Bolivia. PN & ANMI Otuquis is a relatively understudied protected area, as research has been confined to specific sectors due to its vast size. Studies include technical documents (Rebolledo & Flores 1997, Quiroga & Malo 2006) and a small number of checklists on the eBird platform (eBird 2025). Therefore, it is possible that the species has been overlooked in the region.

On the eBird platform, the closest records to the Bolivian borders of this species are 35 km away on the Brazilian side (by J. Raven), 9 km away in Argentina (by F. N. Moschione) and less than 1 km away in Paraguay (by K. Gardiner and N. Cantero). The latter is 13 km from my record in PN & ANMI Otuquis.

Comparing the species' potential distribution polygon (BirdLife International & Handbook of the Birds of the World 2007) and records on the eBird platform shows that part of the northern population in south-west Brazil and north-east Paraguay extends beyond this polygon. All of these records are in the second half of the year, suggesting the possibility of some seasonal shifts in its distribution. The PN & ANMI Otuquis appears to function as a corridor for this so, to more accurately determine the species' status in Bolivia, more studies are needed to assess its presence or absence in the area.

Seasonally flooded marsh formations, where the species was recorded, extends across south-east and eastern Bolivia, thus Firewood-gatherer seems likely to occur in other areas with similar vegetation. I recommend additional surveys in the general region to confirm

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the presence of a population there, as well as elsewhere in Bolivia close to records in neighbouring countries. It seems likely that the species has been overlooked in Bolivia.

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Nest, eggs and nestlings of Spot-backed Puffbird *Nystalus maculatus* from Maranhão, north-eastern Brazil

by Hilda Raianne Silva de Melo, Januário da Conceição Júnior & Flávio Kulaif Ubaid

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Summary.—Spot-backed Puffbird *Nystalus maculatus* is widely distributed across eastern South America but its breeding biology is poorly known. We present the first detailed observations on the nest, eggs, nestlings and their development, made in Maranhão, Brazil. Nests are tunnel-shaped, averaging 7.0 ± 1.0 cm wide and 111.0 ± 26.8 cm long (n = 11), excavated in sandy soil in sloping terrain, ending in an egg chamber. Clutches comprise 2–4 unmarked white eggs, mean 25.36 ± 12.36 × 20.82 ± 10.17 mm, mass 5.55 ± 2.74 g (n = 7). Nestlings hatch naked with closed eyes and the nestling period occupies 21–22 days. Nest predators included Crab-eating Fox *Cerdocyon thous*, domestic dog *Canis lupus familiaris* and Common Tegu *Salvator merianae*.

The Neotropical family Bucconidae (puffbirds) is distributed from southern Mexico to northern Argentina. The 38 puffbird species are classified into ten genera (Winkler *et al*. 2020, Pacheco *et al*. 2021), with the greatest species richness in northern South America, especially Amazonia (Rasmussen & Collar 2018). It is one of the least-known families of Neotropical birds, with many aspects of breeding being poorly documented. In some cases, no data are available even on the nest characteristics for a given species. Puffbirds are known to be monogamous and exhibit biparental chick care (Sick 1997); they nest in holes dug in either level ground or raised banks, with some species constructing their nests in arboreal termitaria (Winkler *et al*. 2020).

Spot-backed Puffbird *Nystalus maculatus* occurs predominantly in the Caatinga dry forest and Cerrado biomes of the 'dry diagonal' of Brazil. It is found in various types of savanna, dry shrubby and semi-deciduous forest, forest edge and farmland (Rasmussen & Collar 2020). We review breeding data for the genus *Nystalus* and present the first detailed description of the nest, eggs and nestling development of *N. maculatus* based on observations made in Maranhão, Brazil.

Materials and Methods

The descriptions presented here are based on observations made at two sites in eastern Maranhão state, north-east Brazil: (i) Inhamum Environmental Protection Area (APA do Inhamum) in the municipality of Caxias (04°53′30″S, 43°24′53″W) and (ii) Piquizeiro II rural community, municipality of São João do Sóter (04°49′20″S, 43°48′53″W). The study region lies in the Cerrado biome, with vegetation varying from *cerrado sensu stricto* (true savanna) to *cerradão* woodland. The local climate is dry subhumid, with a mean annual temperature of 27°C, relative humidity of 70–73% and annual rainfall of 1,600–2,000 mm. Local substrates are dominated by red-yellow latosols and red-yellow podzolic sand and alluvial soils, with a medium to deep layer of leaf litter (Albuquerque 2012).

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Searches for nests were based on the approach proposed by Martin & Geupel (1993), which involves meticulous inspection of the vegetation, combined with any observations of adults carrying nesting material or food for nestlings. Our searches were conducted within known *N. maculatus* territories during the austral spring and summer (September–March); the breeding period of most Cerrado species occurs mainly in September, October and December (Marini *et al*. 2012). Nests were examined using an endoscopic camera mounted on a semi-rigid 3-m cable with LED lighting at the tip. Images were visualised in real time using a smartphone.

Eggs and nestlings were extracted from nests by hand or by using a long-handled spoon, and were measured using analogue metal callipers (precision 0.5 mm) and a metal ruler (1 mm), and weighed on a portable balance accurate to 1 g. The following nest measurements were taken: height and breadth of the entrance, total length of the nest (from the entrance to the posterior wall of the incubatory chamber) and the distance from the entrance to the eggs. The length of the tunnel and the distance to the eggs were initially determined by the length of the camera cable that was inserted, measured using a surveyor's tape (accurate to 1 cm). Nest type was classified according to Simon & Pacheco (2005).

Clutch size was determined as the max. number of eggs during two consecutive visits (Auer *et al*. 2007). The period during which chicks remained in the nest was defined as that between the hatching of the first egg and the fledging of the last chick from the nest (Robinson *et al*. 2000). Bushnell Trophy Cam camera traps were installed near the entrance of active nests in an attempt to register and identify any predators.

Growth curves were compiled for the nestlings and were adjusted using a second-degree polynomial regression, based on wing measurements, the total length of the bird, the total length of the head, culmen, tarsus, and mass. A polynomial equation and the respective coefficient of determination (R^2) were generated for each parameter. Mensural data obtained from three adult *N. maculatus* trapped at different times in the states of Maranhão and Piauí were used as a reference for comparisons. Analyses were run in the R program (R Core Team 2022), using the packages 'ggplot2' (Wickham 2016), 'ggpmisc' (Aphalo 2021) and 'dplyr' (Wickham *et al*. 2020).

We conducted a comprehensive analysis of breeding data for species in the genus *Nystalus* including key aspects such as nesting period, nesting sites, tunnel length, tunnel entrance size, clutch size and incubation period. To update previous information, we provide a compilation of published data for each of the seven recognised species (del Hoyo *et al*. 2013, Pacheco *et al*. 2021).

Results

Eleven active nests of *N. maculatus* were found between September and February, four at APA do Inhamum and seven at Piquizeiro II. All were classified as the cavity type, with a tunnel (*sensu* Simon & Pacheco 2005), which was either simple or in the form of a platform.

All the tunnels were ovoid in shape and had been excavated either at ground level, in slightly sloping terrain, or in raised banks. On average (± SD), the tunnel entrance was 7.0 ± 1.0 cm (range 5.5–9.1 cm) in breadth and 6.9 ± 0.8 cm (range 5.8–8.9 cm) in height (n = 11). The mean length of the tunnels, measured from the entrance to the posterior wall of the nesting chamber, was 111.0 ± 26.8 cm (range 76–163 cm; n = 11), whilst the mean distance between the entrance and the eggs was 97.2 ± 47.0 cm (range 67–150 cm; n = 11). Identification of some nests was facilitated by the presence of a small pile of sand next to the entrance, derived from the excavation of the tunnel (Figs. 1a–b).

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Figure 1. Examples of Spot-backed Puffbird *Nystalus maculatus* nests and eggs in eastern Maranhão, Brazil: (a) nest excavated in flat ground, (b) nest constructed in a bank, and (c) a clutch of three eggs (Hilda Raianne Silva de Melo)

Figure 2. Spot-backed Puffbird *Nystalus maculatus* nestlings at (a) one day, (b) five days, (c) ten days, (d) 15 days, (e) 20 days, and (f) 22 days old (Hilda Raianne Silva de Melo)

All clutches comprised two (n = 6), three (n = 4) or four (n = 1) eggs or nestlings (2.54 ± 0.68). Eggs were oval and white with no markings (Fig. 1c). They measured 20.82 ± 10.17 mm by 25.36 ± 12.36 mm; mass 5.55 ± 2.74 g (n = 7).

Nestlings hatched completely naked with the eyes fully closed (Fig. 2). The skin was pinkish, whilst the bill was whitish pink and the claws black. On the fifth day of life, the pterylan zones were well defined, with feather quills visible in the capital, humeral, alar, ventral, spinal, femoral, crural and caudal pterylae. On day ten, nestlings had open eyes and well-developed feathers and quills on the wings, tail, back and belly. At this age, the nestlings already had a discreet yellowish collar and the belly was covered with black spots, contrasting with the pale grey ground colour. By day 20 the plumage was well developed and similar to that of the adult. The nestling period lasted 21 or 22 days.

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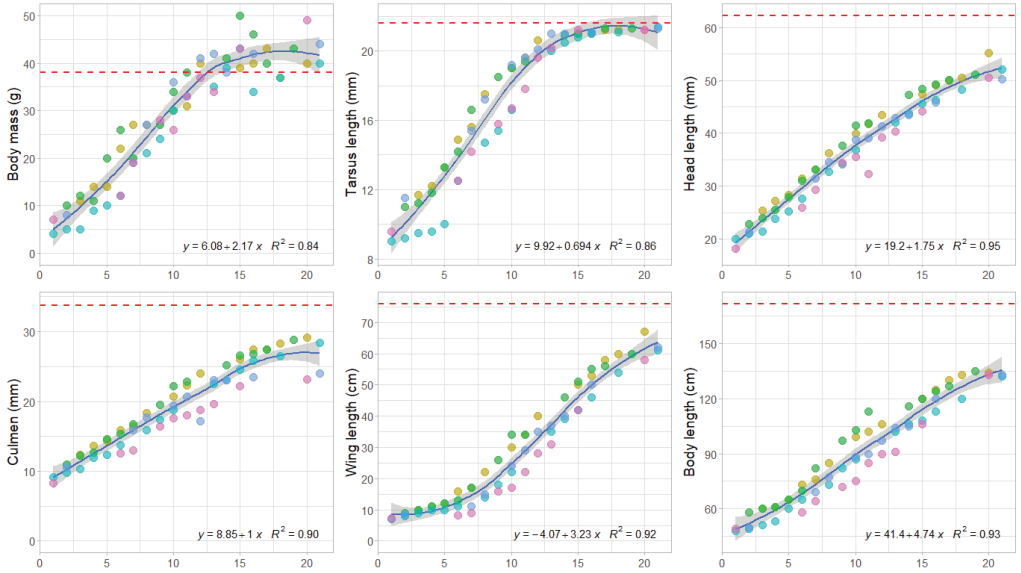

Figure 3. Growth curves of Spot-backed Puffbird *Nystalus maculatus* nestlings monitored during the present study (n = 4), adjusted by second-degree polynomial regression. The dashed red lines indicate adult means. The different-coloured data points represent different nestlings.

Growth curves indicated that the birds abandon the nest before reaching adult body size, based on the majority of the parameters measured here (Fig. 3). The mean length of the tarsus, for example, had reached only 86% of adult length, although mean body mass of the nestlings exceeded that of the adult by day 13, and remained above the adult mean until they fledged. The best-adjusted growth curves were obtained for head length (R^2 = 0.95), body length (R^2 = 0.93) and wing length (R^2 = 0.92).

Overall, only five (45.5%) of the 11 nests monitored were successful. Three species of predator were identified: Crab-eating Fox *Cerdocyon thous*, domestic dog *Canis lupus familiaris* and Common Tegu *Salvator merianae*.

A summary of published breeding data for this and other *Nystalus* species is presented in Table 1. No data on the breeding of Natterer's Striolated Puffbird *N. striolatus* and Eastern Striolated Puffbird *N. torridus* were found.

Discussion

The breeding season of *N. maculatus* in eastern Maranhão matched the local rainy season (September–April) and was similar to patterns observed for other bucconids (e.g., Marini *et al*. 2007, 2012, Cockle *et al*. 2015, Ubaid & Melo 2018, Cockle *et al*. 2020, Melo *et al*. 2021). While few data are available on nesting systems for most puffbirds, the available information indicates they are monogamous and nest in holes excavated in the ground or in arboreal termitaria (Skutch 1957). It also demonstrates that species in the genera *Notharchus*, *Bucco* and *Hypnelus* typically but not obligatorily nest in arboreal termitaria, whilst *Nystalus*, *Monasa*, *Chelidoptera*, *Micromonacha* and *Malacoptila* invariably use tunnels excavated in the ground, whether in flat terrain or in raised banks (Freile & Endara 2000, Greeney *et al*. 2004, Aracil & Londoño 2016). Members of the genus *Nonnula* nest in both termitaria and the ground (Winkler *et al*. 2020).

The tunnel entrance in *N. maculatus* is not camouflaged, as has been observed in other bucconids, e.g., Swallow-wing *Chelidoptera tenebrosa*, which leave a characteristic mound

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TABLE 1
Published data on basic nesting parameters for members of the genus *Nystalus*. No data on the breeding of Natterer's Striolated Puffbird *N. striolatus* and Eastern Striolated Puffbird *N. torridus* were found.

Species	Breeding season	Nest site	Mean tunnel length (cm)	Mean size of nest entrance (cm)	Clutch size (no. of eggs)	Nestling period (days)	References
Barred Puffbird *N. radiatus*	January	Tunnel excavated in ground	105	7.0 across	2	unknown	Greeney *et al*. (2004)
Spot-backed Puffbird *N. maculatus*	September–February	Tunnel excavated in ground or in a raised bank	111	7.0 × 6.9	1–4	21–22	Present study
Chaco Puffbird *N. striatipectus*	February	Tunnel excavated in ground or bank	100	8.0 across	2–3	unknown	Martínez *et al*. (2020)
Western Striolated Puffbird *N. obamai*	September–October	Tunnel excavated in ground	104	7.6 × 8.0	3	unknown	López-Ordóñez *et al*. (2017)
White-eared Puffbird *N. chacuru*	September–February	Tunnel excavated in ground or bank	75–120	unknown	2–4	25	Marini *et al*. (2012), Nascimento *et al*. (2016)

of earth at the entrance to their tunnels (Haverschmidt 1950). However, Lesser Crescent-chested Puffbird *Malacoptila minor* and Chaco Puffbird *N. striatipectus* camouflage their nest entrances using plant debris and earth (Ubaid & Melo 2018, Veneciano & Veneciano 2016, Martínez *et al*. 2020). The size and shape of the nest entrance recorded here for *N. maculatus* were similar to other *Nystalus* species (Table 1) namely Barred Puffbird *N. radiatus*, *N. striatipectus* and Western Striolated Puffbird *N. obamai* (Greeney *et al*. 2004, de la Peña 2013, López-Ordóñez *et al*. 2017, Martínez *et al*. 2020).

The eggs of *N. maculatus* are white, like those of all other bucconids which have been described (Rasmussen & Collar 2018). Clutch sizes of 2–4 eggs were recorded here, similar to White-eared Puffbird *N. chacuru* (Table 1), and Greater Crescent-chested Puffbird *Malacoptila striata*, for which clutches of up to four eggs have been reported (Marini *et al*. 2007).

The characteristics of the *N. maculatus* nestlings during their first few days of life, including the coloration of their skin, bill and claws, and the fact they are born naked with their eyes closed, are shared with other bucconids, e.g., Lanceolated Monklet *Micromonacha lanceolata* and species of *Monasa* and *Malacoptila* (Aracil & Londoño 2016). Similarly, the duration of the nestling period in *N. maculatus* is similar to that of White-whiskered Puffbird *Malacoptila panamensis* (20 days) (Skutch 1958) and *M. minor* (16–23 days) (Melo *et al*. 2021). The nestling period of *Micromonacha lanceolata* is 22–23 days (Aracil & Londoño 2016), whereas that of one of the larger bucconids (White-fronted Nunbird *Monasa morphoeus*) is considerably longer, at 29–31 days (Skutch 1972).

All of the unsuccessful nests during the present study were predated. Melo *et al*. (2021) recorded *Cerdocyon thous* and *Salvator merianae* also predating nests of *Malacoptila minor*.

The reproductive biology of the bucconids is still poorly known, and even the nests of some species have never been described in any detail. The results of the present study constitute the first detailed data on the breeding biology of *N. maculatus*, thereby filling a prominent knowledge gap in the species' natural history.

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Composite figures in the intaglio plates of Wilson's *American ornithology* (1808–14)

by Matthew R. Halley

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Summary.—The 'plates' (intaglio prints) of Alexander Wilson's nine-volume work, *American ornithology* (1808–14), collectively depicted hundreds of individual bird specimens including the types of many new species—or so scholars have long assumed. Here, by reconstructing the modified intaglio process used by Wilson and his team, I demonstrate that many (probably most) of his figures were composite in nature, combining anatomical details copied from multiple specimens, sometimes even multiple species. This phenomenon has been universally overlooked by historians and ornithologists, despite its critical implications for understanding Wilson's taxonomy and nomenclature.

American ornithology (1808–14), the first colour-plate book devoted to the enumeration and description of American birds, was illustrated and authored by Alexander Wilson (1766–1813) and published in Philadelphia, Pennsylvania, almost entirely using local materials and labour (Wilson 1810: vi, Burns 1908, Halley in press). Seventy-six 'plates' (intaglio prints)—an auspicious number in post-revolutionary Philadelphia—were interleaved with a charming and scientific letterpress, bound in nine volumes. Because of its consistent use of binomial nomenclature, *American ornithology* became a foundational taxonomic work, containing the original descriptions of at least 25 species and four subspecies of American birds (Gill *et al*. 2024).

However, for more than a century, ornithologists seeking to identify the material basis of Wilson's descriptions (e.g., Faxon 1915, Bangs 1930, Burtt & Davis 2013) have generally assumed that each of the 319 published figures in his plates was a depiction of a single specimen; that Wilson collected the specimen himself, in most cases; that the 'Peale numbers' cited in his synonym lists were 'in all cases the [same] subjects that he drew and described' (Faxon 1915: 125); and that those numbers had been uniquely assigned when Wilson deposited the specimens in the 'Philadelphia Museum' of Charles Willson Peale (1741–1827). New research suggests that these assumptions were unfounded and consequently many errors have been perpetuated in the scientific literature (Halley 2022, 2024a).

Peale's contributions to American ornithology (*c*.1786–1804), although known to Wilson and his contemporaries, were overlooked by historians and broadly misattributed to Wilson by the late 19th century (Halley 2022, 2024a, but see Burns 1932). In fact, Wilson deposited relatively few (*c*.30) study skins in the Philadelphia Museum, not '279' as asserted by Burtt & Davis (2013: 310), who overlooked critical sources including Peale's diaries and correspondence (Miller 1983, 1988), unpublished ornithology lectures (Halley 2024b), the Philadelphia Museum Accessions Book (Halley 2022), and many other primary materials in the Academy of Natural Sciences of Drexel University Archives (ANSP), American Philosophical Society Library (APS) and Historical Society of Pennsylvania (HSP). A digital inventory of Peale's bird collection, assembled using primary sources, shows that *c*.90% of the species in *American ornithology* were already mounted in the Philadelphia Museum,

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and arranged according to the Linnaean system, by the summer of 1804, when Wilson first visited the collection. This includes most of Wilson's 'new' species, which Peale had already described in his lectures (1799–1802), often with more detail (Halley 2024a).

Wilson was not 'unquestionably, the first American ornithologist' (Burtt & Davis 2013: 331), nor the 'first American ornithologist to adopt the Linnaean system' (Burtt & Davis 2013: 289, Burtt 2017); nor did he '[believe] that he had discovered fifty-one species of North American birds' that were unknown to Peale and other American ornithologists (Burtt & Davis 2013: 304). These errors stem from a misinterpretation of the 'Peale numbers' cited in Wilson's accounts (Halley 2022). Wilson cited 'Peale's Museum' for the same reason that he cited Linnaeus (1766), Latham (1790), Bartram (1791) and other authors, to give the Peale family due credit for having previous knowledge (and specimens) of the species. Wilson considered Peale's mounted collection to be the scholarly equivalent of those printed works, and cited it as such. Except in a few cases, the citations did not document Wilson's own specimen deposits (*contra* Burtt & Davis 2013), but specimens that pre-dated *American ornithology*. This misunderstanding has effectively erased Peale's legacy despite Wilson's effort to preserve it.

Furthermore, the 'Peale numbers' were not uniquely assigned to specimens as assumed by Faxon (1915), Bangs (1930), Burtt & Davis (2013) and others. Rather, they were copied from a simplified list of 'species' and 'varieties' (loosely and inconsistently defined) which was devised and painted on the frames of the display cases in 1803, before Wilson's arrival, apparently as an alternative to the cumbersome (specimen-based) numbering scheme that Peale had used in his lectures (Halley 2022, 2024a). A pamphlet entitled *A guide to the Philadelphia Museum*, printed and distributed to visitors in 1804—the same year Wilson first visited—contained the following statement (my italics): 'in frames over each case, the genus is first noted, then their species and names in Latin, English, and French, referring to the numbers which are *attached to each species*' (Miller 1988: 761–762).

Thus, each number cited by Wilson was evidently not assigned to one specimen, although some species and varieties were represented by only one specimen in the display cases, and some later proved to be merely different plumages of a single species (Halley 2022). This explains why, for example, Wilson (1810: 48) cited only one number ('Peale's Museum, No. 6026') for the sexually dimorphic Bobolink *Dolichonyx oryzivorus* (Linnaeus, 1758), despite figuring both sexes (Wilson 1810, Pl. 12); and only one number ('No. 5970') in separate accounts (Wilson 1810: 35, 1812b: 90, respectively) of the sexually dichromatic male and female Eastern Towhee *Pipilo erythropthalmus* (Linnaeus, 1758). Duplicates were usually dismounted and stored separately in boxes, for use as currency in specimen exchanges with foreign correspondents, or as replacements for when the displayed specimens became damaged by insects. There were exceptions to this normal practice, like when Peale included duplicates in the display because they helped illustrate something interesting about the natural history of the species, but generally he did not have interest or space to display duplicates (e.g., Miller 1988, Halley 2024a).

Here, I explore yet another point of long-standing confusion, which bears on Wilson's taxonomy and nomenclature: each of his published figures was not a faithful depiction of a single specimen, as widely assumed, except when only one specimen was available—and even then, there is uncertainty. This is because Wilson made deliberate modifications to the intaglio process (see below), which rendered many or most of his published figures composite in nature, bearing details copied from multiple specimens of the same species, and sometimes of multiple species that he incorrectly assumed were the same. This phenomenon has broad implications for Wilson's taxonomy and nomenclature. In the following sections, I reconstruct the intaglio process to reveal the composite elements and their causes.

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The artists

Intaglio printmaking is a multi-step process that involves the transfer of a drawing to a hard surface, the cutting of grooves into that hard surface (in Wilson's case, a copper plate) with sharp tools and/or corrosive chemicals; the inking and subsequent cleaning of the surface, until the ink is contained only within the grooves; and finally the transfer of the inked pattern to a sheet of dampened paper, by means of a mechanical press (Green 1810). Fifty copper plates (66%) for *American ornithology* were engraved by Alexander Lawson (*c*.1773–1846, Fig. 1), who lived with Wilson during the early years of their collaboration (Halley in press); 20 plates (27%) were engraved by John G. Warnicke (*c*.1780–1819), who joined Wilson's team during the production of the fifth volume (Wilson 1812a); five plates (7%) in the first three volumes (Wilson 1808, 1810, 1811a) were engraved by George Murray (*c*.1766–1822); and one plate in volume four (Wilson 1811b) was engraved by Benjamin Tanner (1775–1848). Relatively few details about these men are known.[1]

Proof-sheets were occasionally printed for Wilson to review, until he deemed the engraving complete. Then, the plates were 'lettered' by John Vallance (1770–1823), who was 'noted for the excellence of his script' (Burns 1929: 20), and delivered to the printer, Joseph Brown (?–1816), who alone pressed the monochrome prints for all nine volumes. During production, Brown moved his workshop on several occasions, mostly within the Southwark neighbourhood, from '23 Church alley' (Robinson 1807, 1808) to '8 Pear [St.]'

Figure 1. (left) Oil portrait of Alexander Lawson (*c*.1773–1846), primary engraver of *American ornithology* (1808–14) and its extended editions, executed by Bass Otis (1784–1861) by 1824, reproduced courtesy of the Pennsylvania Academy of the Fine Arts (PAFA 1898.12); (right) cropped and angled view of Lawson's copperplate engraving of the American Robin *Turdus migratorius* Linnaeus, 1766, used to press the intaglio prints for Wilson (1808, Pl. 3), reproduced courtesy of the Academy of Natural Sciences of Drexel University Library and Archives (coll. 427).

[1] Lawson, like Wilson, was an immigrant from Scotland. He was profiled by Dunlap (1834) and posthumously by his daughter, Malvina (Christy 1937), but primary sources give conflicting dates of birth and arrival (Halley in press). Warnicke's burial record is dated 30 December 1818: 'John G. Warnock, [aged] 38 years; native of Denmark; for many years [resided] in or near [Philadelphia]; engraver of renown; married, leaving his wife & children indigent. He had a disorder in the liver. [Resided] in New 2d. St. by Federal [St.]. Some pronounce the name Warnicke.' (Gloria Dei Church). Murray was 'Born in Scotland. Engraver in London. Emigrated to Philadelphia [*c*.1800 and] Died there on 2 July 1822' (Dobson 1984: 161). His burial record states that he was 'aged 56 years' (First Unitarian Church). Tanner was 'born in the city of New York' on 27 March 1775 (Baker 1875: 167) and died on 14 October 1848: 'Benjamin Tanner aged 74 years. Died in Baltimore' (Gloria Dei). All burial records were accessed at https://philadelphiacongregations.org/, 20 July 2024.

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(Robinson 1809, 1810) to '80 Union [St.]', now called Delancey St. (Robinson 1811, Paxton 1813), to '11 Cypress alley' (Kite & Kite 1814). A book of receipts, preserved in the Museum of Comparative Zoology, Harvard University (MCZ), with entries dated January 1810–January 1811, reveals the magnitude and pace of the printing operation (Christy 1937); and a separate inventory of Brown's property dated 14 October 1816, filed with the City of Philadelphia after his death, listed five 'copper pl[ate] printers press[es]' valued between $50–100 each (Administration Files no. 317–328, 1–63, 1818–19, Book M, p. 132).

Wilson picked up the monochrome prints from Brown in batches, then coloured them by hand with a rotating team of at least seven hired 'colourists', whose names appeared in the aforementioned receipt book (Christy 1937). One was Alexander Rider (*fl*. 1808–25), '[who] spoiled a great many copies by using opaque colors' according to Malvina Lawson (*c*.1806–84), eldest daughter of Wilson's engraver, who was a colourist of the second edition (Burns 1917: 279). Peale's niece, Anna Claypoole Peale (1791–1878), assisted Wilson in 1810, but the extent of her involvement is unknown because her name appears on only one extant receipt. Another colourist was Eliza Leslie (1787–1858), elder sister of Charles Robert Leslie (1794–1859), the English painter, who also assisted Wilson according to his retrospective memoir (Taylor 1860, see below). Eliza's receipts were signed by her father ('Thos. Leslie for E. Leslie'), so we may assume that Charles, who was seven years her junior, did not begin working with Wilson until 1811 at the earliest. The last colourist, of whom some certain biographical information is known, was John H. Hopkins (1792–1868), who became a bishop in the Episcopal church (Hopkins 1873). Recollections from Charles Leslie and Hopkins are discussed below.

Composite figures

In its basic form, intaglio is a process in which details are gradually lost during production. The artist's drawing only captures a portion of the specimen's detail, and the engraving captures a portion of the drawing's detail. To combat this problem, whenever possible, Wilson modified the intaglio process such that new details were added to his figures at each stage, copied directly from specimens. Wilson brought fresh (even live) specimens to the engravers and encouraged them to add fine anatomical details, which he had failed to render in his original drawings. Accordingly, the resulting figures were often composite but gave the appearance of a single specimen. Wilson (1808: 7), whose general aim was to depict the species, not one particular specimen, defended the practice:

> 'Every person who is acquainted with the extreme accuracy of eminent engravers, must likewise be sensible of the advantage of having the imperfections of the pencil corrected by the excellence of the graver. Every improvement of this kind the author has studiously availed himself of; and has frequently furnished the artist with the living or newly-killed subject itself to assist his ideas.'

Take note of Wilson's use of the word 'artist' and his seemingly genuine concern that Lawson's ideas (not merely his own) be realised in the final image. Malvina Lawson recalled that 'Wilson never painted birds, he drew them in watercolors, and more frequently in outline, either with pencil or pen, and my father finished them from the birds themselves' (Burns 1917: 278). Compare most of Wilson's extant drawings, to their engraved figures, and the truth of this assertion is obvious. For example, compare the original drawings of Saltmarsh Sparrow *Ammospiza caudacuta* (J. F. Gmelin, 1788) and Savannah Sparrow *Passerculus sandwichensis* (J. F. Gmelin, 1789)—executed on a single sheet of paper (HSP coll. 0175)—to the same figures, printed from the engraved plate (Wilson 1811b, Pl. 34), and

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it is clear that Lawson copied the outlines and general features of Wilson's drawings, but then added a plethora of new (fine) details including individual feather barbs and clearly defined leg scales (Fig. 2). The extra details were apparently copied directly from specimens, as Wilson (1808: 7) stated, but we cannot be certain they were the same ones that served as the models for Wilson's drawings.

This is because the colourists also used specimens for colour reference, and here we find evidence that the specimens they used were not Wilson's models. Hopkins (1873: 29), son of Wilson's colourist of that name, heard from his father that 'Mr. Wilson always shot a fresh bird for his colorist, so that there should be no chance of the fading or changing of the brilliant tints of life.' This second-hand testimony may be somewhat exaggerated, but it is consistent with Charles Leslie's first-hand account: 'I assisted [Wilson] to colour some of [his] first plates. We worked from birds which he had shot and stuffed, and I well remember the extreme accuracy of his drawings, and how carefully he had counted the number of scales on the tiny legs and feet of his subject' (Taylor 1860: 245).

Faxon (1915: 119), who overlooked Hopkins (1873), cited Leslie's account as evidence that Wilson 'found it expedient to draw a bird [only] after it had assumed a definite form and attitude by being stuffed and mounted, often by his own hands.' However, Wilson (1810: viii) clearly stated that 'no drawings have been, or will be made for this work, from any stuffed subjects, where living specimens of the same can be procured.' Leslie's testimony does confirm that stuffed specimens were used as colour references, but it does not prove that they were the models for Wilson's drawings, or that Wilson (contrary to his own testimony) actually drew from stuffed specimens, when living or freshly killed birds

Figure 2. (left) Wilson's original drawing of Saltmarsh Sparrow *Ammospiza caudacuta* and Savannah Sparrow *Passerculus sandwichensis* and (right) three close-up comparisons between the drawing and the published figures in Pl. 34, which were engraved by Lawson (Wilson 1811b). Spots of glue residue (denoted by black arrows) show where the tracing paper was attached to the front of the drawing (see text), reproduced courtesy of the Historical Society of Pennsylvania (HSP coll. 175, box 308, folder 44). The printed images are from the second edition (Wilson 1824a), pressed from the original plate and coloured by Lawson's daughters (see Burns 1917: 276), preserved at the Delaware Museum of Nature & Science; the colours of the first and second editions match (Matthew R. Halley)

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were available. The 'drawings' of Leslie's memory were probably the monochrome prints that he and his sister had been hired to colour—images imbued with extra (potentially composite) details, added by the engravers. Indeed, it was evidently Lawson who 'counted the number of scales on the tiny legs' of the Savannah and Saltmarsh Sparrows, where Wilson had placed some non-committal squiggles (Fig. 2).

Wilson's drawing of the Fox Sparrow *Passerella iliaca* (Merrem, 1786), preserved in the ANSP (coll. 79), provides a similar example of Lawson's artistry and positive evidence that Hopkins (1873) was correct: the specimen used for colour reference (after the engraving was complete) was not the model for Wilson's drawing (Fig. 3). The sparrow in Wilson's drawing has extensive gray on the head, and a yellowish cutting edge on the maxilla, whereas the published figure (in the first and later editions) has a uniform rusty head (no gray) and a black cutting edge. These characters are variable in *P. iliaca* in the Mid-Atlantic region during the non-breeding season (winter); as such, it seems likely that two different specimens were used to produce the figure (i.e., the colourists, and perhaps Lawson, used a specimen reference that was not Wilson's original model).

Figure 3. Comparison between Wilson's original drawing (left) of Fox Sparrow *Passerella iliaca* and the figure in Pl. 22 (right), which was engraved by Lawson (Wilson 1811a). Lawson's engraving is enriched with fine details, absent in the original drawing, and the birds differ in colour, which suggests that the specimen reference used by the colourists was not the same as Wilson's model. The drawing is reproduced courtesy of the Academy of Natural Sciences of Drexel University Archives (coll. 79, box 2, folder 17). The printed image is reproduced from a presentation copy of the first edition, 1809 reissue (Wilson '1808') in the American Philosophical Society Library (APS 598.2 W69).

A similar example is the figure of the Northern Shrike *Lanius borealis* Vieillot, 1808. Comparison of the original drawing (MCZ 869.15a) and published figure (Wilson 1808, Pl. 5) reveals that Lawson copied the general outline and features, then added many fine details to the copper plate, which were absent in Wilson's drawing (Fig. 4). The drawing appears to have been based on a bird in first-cycle formative plumage, as evidenced by the brownish wash on the dorsal surface and indistinct facial mask (Pyle 2022: 304), but the published figure has uniform grey upperparts and a black mask that extends across the forecrown, both characters of the second-cycle (adult) plumage. There is another, more rudimentary drawing of *L. borealis* in the ANSP (coll. 79), that has the extended facial mask of the adult but is otherwise quite unlike the published figure. This confirms that Wilson had specimens (or at least drawings) of both age classes; and he described both in his text account, mistaking them for different sexes: '[In the male] the upper part of the head, neck and back is pale cinereous; sides of the head nearly white, crossed with a bar of black that passes from the nostril thro the eye to the middle of the neck … The female is easily distinguished by being ferruginous on the back and head; and having the band of black extending only *behind* the eye, and of a dirty brown or burnt color' (Wilson 1808: 78–79). However, the published figure in Pl. 5 (Wilson 1808) was a composite because it combined details from both specimens (Fig. 4).

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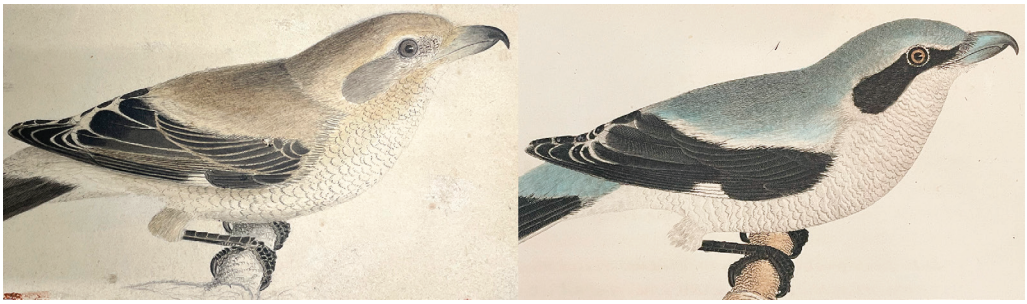

Figure 4. Comparison between Wilson's original drawing (left) of Northern Shrike *Lanius borealis*, which was apparently based on an immature (first-winter) specimen, and the figure in Pl. 5 (right), engraved by Lawson (Wilson 1808), which was apparently coloured from an adult male specimen. Lawson's engraving is also enriched with fine details, absent in the original drawing. The drawing is reproduced courtesy of the Ernst Mayr Library, Museum of Comparative Zoology, Harvard University (MCZ 869.15a, f. 54). The printed image is reproduced from a presentation copy of the first edition, 1809 reissue (Wilson '1808') in the American Philosophical Society Library (APS 598.2 W69).

In another example, Wilson (1808: 39) stated that his figure of American Robin *Turdus migratorius* Linnaeus, 1766, depicted a 'full grown bird, in his most perfect dress', collected in 'the depth of winter'. In this case, his drawing (HSP coll. 0175) was more detailed than usual, but a careful comparison of the plumage on the nape reveals that Lawson still added fine details when engraving the copper plate, which are lacking in the drawing (Figs. 1, 5). Wilson's drawing and published figure (Pl. 2) are also coloured quite differently despite having nearly identical outlines (Fig. 5). In the drawing the crown is brown (vs. black in Pl. 2), the bill has black edges (vs. completely yellow), the throat is streaked black for its entire length (vs. converging in a black band) and the nape is uniform with the back (vs. contrasting). Obviously, the specimen reference used by the colourists was not Wilson's original model—the figure is a composite.

The two thrushes on Pl. 43 (Wilson 1812a) demonstrate that some of Wilson's composites combined the characters of multiple species, which he assumed were the same (Fig. 6). Wilson's 'Hermit Thrush / *Turdus solitarius*' was based on an original drawing (MCZ 869.5) likely of the 'eastern' Hermit Thrush *Catharus* [*guttatus*] *faxoni* (Bangs & Penard, 1921), as evidenced by the exaggerated rusty colour on the tail and uppertail-

Figure 5. Comparison between Wilson's original drawing (right) of American Robin *Turdus migratorius* and the figure in Pl. 2 (left), as engraved by Lawson (Wilson 1811b). The drawing is reproduced courtesy of the Historical Society of Pennsylvania (HSP coll. 175, box 308, folder 44). The printed image is reproduced from a presentation copy of the first edition, 1809 reissue (Wilson '1808') in the American Philosophical Society Library (APS 598.2 W69).

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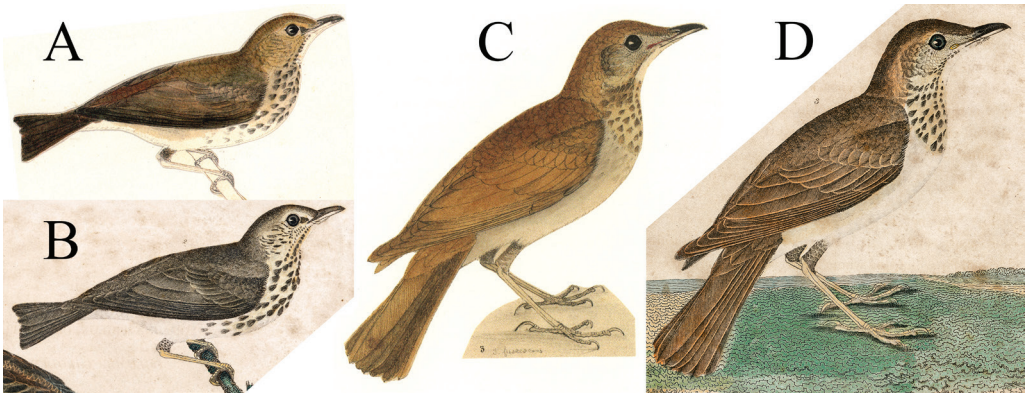

Figure 6. Comparisons between Wilson's (A) original drawing of 'Hermit Thrush / *Turdus solitarius*' and (B) its published figure, printed from Lawson's engraved plate (Wilson 1812a, Pl. 43); and his (C) original drawing of 'Tawny Thrush / *Turdus mustelinus*' and (D) its published figure, printed from Lawson's engraved plate (Wilson 1812a, Pl. 43). Both published figures are probably interspecific composites (see text). The drawings are reproduced courtesy of the Ernst Mayr Library, Museum of Comparative Zoology, Harvard University (MCZ 869.5, 869.15a), and the printed images are reproduced from William Bartram's personal copy of Wilson (1812a), preserved at Bartram's Garden, Philadelphia.

coverts, but the printed figure (Pl. 43) has a uniform olive dorsal aspect, which is a better match to Swainson's Thrush *C.* [*ustulatus*] *swainsoni* (Cabanis *in* Tschudi, 1845; see Halley 2019 for neotype designation), or the 'grey' or 'olive' morph of Grey-cheeked Thrush *C. minimus* (Lafresnaye, 1848), than *C.* [*g.*] *faxoni*.[2] Thus, the published figure is an interspecific composite. Coues (1878: 24) noticed the discrepancy between Wilson's text and plate but failed to identify its cause or taxonomic implications. In a similar case discussed by Halley (2018), Wilson's drawing of 'Tawny Thrush / *Turdus mustelinus*' (MCZ 869.15a) resembles a Veery *C. fuscescens* (Stephens, 1817; see Halley 2018 for neotype designation), but again the colourists' model for the published figure was apparently a different species—probably a brown morph *C. minimus*, as evidenced by its darker (less warm) colours and bolder ventral spots (Halley 2018). Coues (1878: 27), overlooking the composite, incorrectly concluded that *C. fuscescens* was 'first adequately described' by Wilson (1812a).

Finally, but not exhaustively, consider Clark's Nutcracker *Nucifraga columbiana* (Wilson, 1811a), which was unambiguously based on a single specimen (holotype). Wilson (1811a: 29) wrote: 'The figure in [Pl. 20] was drawn with particular care, after a minute examination and measurement of the only preserved skin that was saved; and which is now deposited in Mr. Peale's Museum.' Meriwether Lewis (1774–1809) had carried the specimen to Philadelphia in 1807, upon returning from the Lewis and Clark expedition, and Wilson likely drew it between 1 December 1809 and 20 February 1810, before he departed for the southern USA (Halley 2023a: 341). Wilson's drawing (ANSP coll. 79) has more detail than usual, especially on the foot, nape and wings; but the opposite is true for the plumage of the back, breast, belly and flanks, which lack any detail at all (Fig. 3.24 *in* Burtt & Davis 2013: 104). How then do we explain the intricate details on the back, breast, belly and flanks of Wilson's (1811a, Pl. 20) published figure? Did Lawson also examine the holotype at the Philadelphia Museum and faithfully copy the details that Wilson had neglected, before engraving them into the copper plate? Or did he simply copy those details from a specimen of some other species, closer to hand, to produce the desired effect?

[2] Because of a transcription error, the coordinates of the *C.* [*u.*] *swainsoni* type locality, where the neotype (ANSP 207077) was collected, were incorrectly given by Halley (2019). The correct DMS coordinates are: 41°41′25.36″N, 79°14′23.28″W.

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To summarise, the evidence shows that, to produce a single figure, Wilson used multiple reference models during three different stages of production (drawing, engraving, colouring). Usually the reference models were of the same species, but sometimes (inadvertently) they were of different species. This rendered many or most of his figures composite. This is not a phenomenon affecting one or a few species; most of Wilson's extant drawings are missing details found in their respective published figures, which is compelling evidence that the engravers added details directly from specimens, as Wilson (1808: 7) explained, and the confirmed composites include common species that Wilson encountered in multiple years, seasons and locations (e.g., *Turdus migratorius*). There are many examples of mismatched colour phenotypes, which provide unambiguous evidence that the colourists (including Wilson himself) often did not use the same specimens that were the models for Wilson's drawings, but different (presumably fresh) specimens that he 'shot and stuffed' for subsequent reference (Taylor 1860: 245, Hopkins 1873: 29). Therefore, we cannot safely assume that the engravers used Wilson's original models either.

The composite figures in *American ornithology* have been hiding in plain sight, overlooked by ornithologists and historians alike, for two centuries. Notwithstanding, the evidence suggests that they were a natural, perhaps even intended, outcome of Wilson's methodology and creative process. Wilson (1808: 7) acknowledged, even defended, the engravers' creative role in his work; and this was corroborated by Malvina Lawson's eyewitness (albeit retrospective) testimony that her father copied details 'from the birds themselves' (Burns 1917: 278). In the next section, to bring further clarity to Wilson's methods, I reconstruct the mechanical processes that Lawson and the other engravers used to transfer Wilson's drawings (outlines) to the copper plate, before the engraving began.

Transferring drawings to plates

Coues (1880: 198) noted that 'Some [drawings] show the rubbing process by which they were transferred', after examining drawings now in the MCZ collection (869.15a). More than a century later, Burtt & Davis (2013: 67–69) studied the same collection of drawings and proposed the following technical hypothesis of the image transfer process:

> 'The back of each sketch was dusted with iron oxide … daubs of glue were applied to the back of the drawings and the drawings were positioned on the copper plate. (The small, brown spots visible in the [periphery of the sketches] show where the glue has soaked through the paper as the glue and paper aged.) The lines of the drawings were redrawn, thereby transferring the orange iron oxide powder from the back of the drawing to the surface of the copper plate. Finally, the drawing was removed and Lawson used his tools to cut into the surface of the copper plate along the orange lines transferred from the back of the drawing.'

There are fundamental problems with this explanation. Except for the American Robin (see above), which lacks iron oxide residue on any surface, the birds in Wilson's extant drawings face the same direction as their respective figures in *American ornithology*. Thus, in most cases, the engravers transferred the *mirror* images of the drawings to the copper plates, not the forward-facing images that the iron oxide method would produce; otherwise, the published birds would have faced the opposite direction (Fig. 7). Also, it would have been counterproductive to allow iron oxide or any other corrosive substance to touch the 'ground' (prepared surface) of the copper plate, after it had been cleaned and polished in preparation for engraving (see Ord *in* Wilson 1814a: xxix). The available evidence suggests (*contra* Burtt & Davis 2013) that iron oxide was used only to transfer images between

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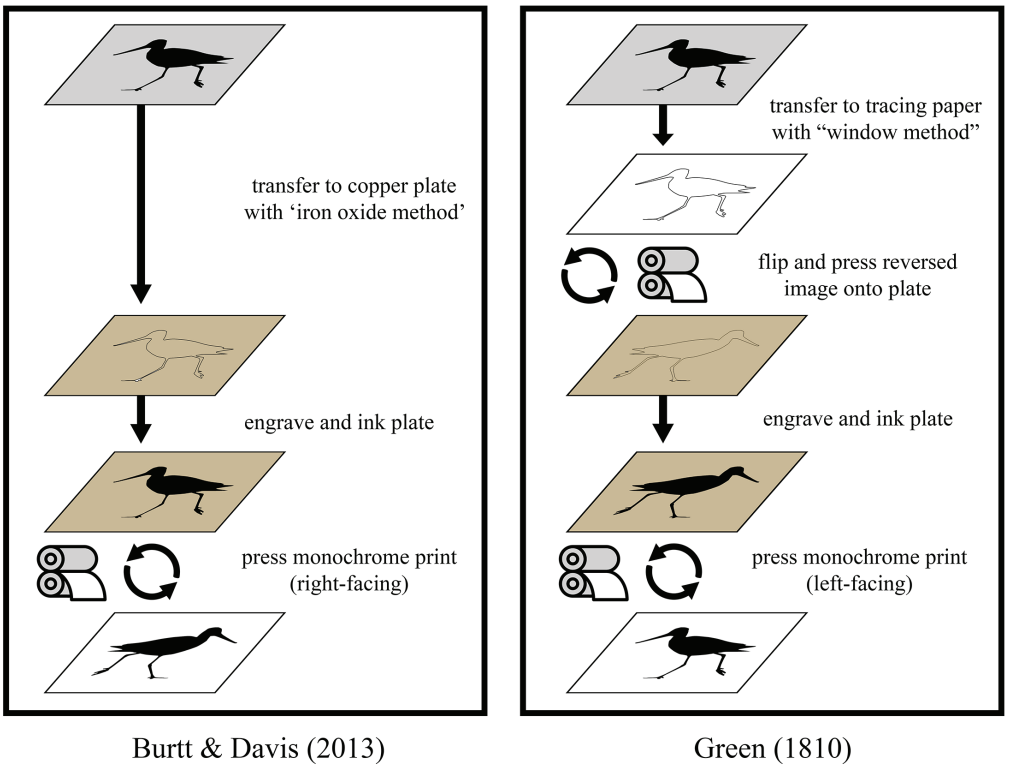

Figure 7. Hypothetical reconstructions of the intaglio process as proposed by Burtt & Davis (2013) and Green (1810). In both scenarios, Wilson's drawing (top, grey) is transferred to the copper plate (beige), which is engraved and inked, then passed through a roller press to produce the print (white). Notably, the method proposed by Burtt & Davis (2013) would produce printed birds that face the wrong direction.

pieces of paper (without reversal), whereas transfers from paper to copper plate (with reversal) were apparently accomplished with disposable (non-extant) tracing paper, which was attached to the front of the drawing with a temporary adhesive—probably a ball of wax, which left behind an oily 'glue spot'. This common technique was described by John Hippisley Green (1775–1820), an English contemporary of Wilson and Lawson, in a popular printing manual:

> '…take some thin paper and paste it to the [front] of the drawing … then hold it against the window to the light, and with a black lead pencil, trace all the outlines pretty strongly that you wish to etch, then take the tracing from the drawing and cut it to the size of the intended work, next wet the back with a sponge, turn the face to the etching ground, and run the plate through the copper-plate rolling press, which may be as tight as they generally use it for printing, and you will have all the outlines reversed on the ground' (Green 1810: 17)

I examined most of Wilson's drawings in the ANSP, HSP and MCZ collections, and found that Burtt & Davis's (2013) assertion that the 'back of each sketch was dusted with iron oxide' is not true. In fact, most drawings have no trace of iron oxide residue on any surface, and the 'daubs of glue' (glue spots) are located on the *front* (recto) surfaces, not the back (verso) as they contended. The preponderance of primary evidence is consistent with Green's (1810) 'window tracing' method (e.g., Figs. 8–10). The occasional iron oxide residue

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Figure 8. Verso and recto views of Wilson's original drawings of (top) Eastern Screech Owl *Megascops asio* (Linnaeus, 1758) and (bottom) Black-and-white Warbler *Mniotilta varia* (Linnaeus, 1766), which were both engraved by Lawson for Wilson (1810, Pl. 19). Neither drawing has iron oxide residue on the verso (*contra* Burtt & Davis 2013: 67–69). Black arrows denote brown 'glue spots' on the recto (absent from the verso) where Lawson evidently used an oily adhesive (possibly wax) to temporarily attach the tracing paper to the drawing paper, consistent with Green's (1810) 'window tracing' method (Matthew R. Halley, reproduced courtesy of the Ernst Mayr Library, Museum of Comparative Zoology, Harvard University [MCZ 869.15a, f. 6])

on the verso of some drawings can be explained as a byproduct of transferring images between pieces of paper (without reversal)—not from paper to the copper plate, as Burtt & Davis (2013) hypothesised.

The oldest drawing with iron oxide residue, by order of appearance in *American ornithology*, is the juvenile Eastern Whip-poor-will *Antrostomus vociferus* (Wilson, 1812a) in the MCZ collection (869.15a), which was engraved by Warnicke for Pl. 41 (Fig. 9). It appears that Warnicke (or possibly Wilson) used iron oxide to transfer (without reversal) the outlines of Wilson's field sketch to a larger composite drawing of two adults; but the composite (engraved) drawing lacks residue, which means that iron oxide was not used to transfer the final (reversed) image to the copper plate (*contra* Burtt & Davis 2013). The only other examples with iron oxide residue are the preliminary drawings used for the final plate of the eighth volume (Wilson 1814a, Pl. 72) and the plates of the ninth volume (Wilson 1814b, Pl. 73–76). These images were published posthumously. According to George Ord (1781–1866), editor of the final volumes, 'all the plates [of Vol. 8], except one, were engraved' at the time of Wilson's death (Wilson 1814a: iii). Thus, the MCZ collection (869.15a) includes both preliminary (with residue) and composite drawings (without residue), the latter being the source of the engraved images for Pl. 72–75 (*contra* Burtt & Davis 2013: 69).

Finally, it must be noted that Wilson sometimes drew birds on both sides of the same leaf of paper, and consequently one drawing was mutilated in favour of the other, during or after the engraving process. For example, the outlined heads of Turkey Vulture *Cathartes*

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Figure 9. Wilson's preparatory drawings for Pl. 41, depicting Eastern Whip-poor-will *Antrostomus vociferus* (not to scale). An original field sketch (left, top and bottom) bears the following inscription in Wilson's hand: 'Stump feathers bluish / down nearly color of the […] of the Humming Bird's nest / found July 17th 1809'. The verso of the sketch was evidently coated with iron oxide powder (red residue), which was used to transfer the image to a larger composite drawing (right). However, there is no iron oxide residue on the verso of the composite drawing, and there are 'glue spots' on the upper corners of the recto (black arrows), which suggest that the composite image was transferred via Green's (1810) 'window tracing' method (*contra* Burtt & Davis 2013) (Matthew R. Halley, reproduced courtesy of the Ernst Mayr Library, Museum of Comparative Zoology, Harvard University [MCZ 869.15a, f. 54])

aura (Linnaeus, 1758) and Black Vulture *Coragyps atratus* (Bechstein, 1793), which appeared in Pl. 75 (Wilson 1814b), were originally drawn on the backsides of his original (engraved) drawings of Red-winged Blackbird *Agelaius phoeniceus* (Linnaeus, 1766) and Carolina Parakeet *Conuropsis carolinensis* (Linnaeus, 1758), respectively (Fig. 10). The blackbird and parakeet engravings had already been published in the third and fourth volumes, respectively (Wilson 1811a, 1811b), when the drawings (MCZ 869.15a) were mutilated during the production of the ninth volume (Wilson 1814b).

This example seems to have occurred after Wilson's death, but there are also examples from his lifetime. A coloured drawing (ANSP coll. 79) of Blue Jay *Cyanocitta cristata* (Linnaeus, 1758), probably the one engraved for Pl. 1 (Wilson 1808), was mutilated in favour of a verso sketch of Rusty Blackbird *Euphagus carolinus* (Statius Müller, 1776), but in this case there was no iron oxide residue (Fig. 11). Although the extent of these destructive methods is unknown, they provide a relatively simple (partial) explanation for why so many of Wilson's original drawings are unknown to scholars. Of the 319 figures depicted in Wilson's plates (i.e., 'individual' birds in the foreground), the original (engraved) drawings of only 155 (49%) are known to me, not counting the three mutilated drawings (1%) and about 50 preparatory (unengraved) drawings. This further complicates the process of evaluating Wilson's published figures for composite characters.

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Figure 10. Wilson's original drawings of Red-winged Blackbird *Agelaius phoeniceus* and Carolina Parakeet *Conuropsis carolinensis*, which were respectively engraved by Murray for Pl. 26 (Wilson 1811a) and Lawson for Pl. 30 (Wilson 1811b), were evidently mutilated during the production of Pl. 75, which was engraved by Lawson (Wilson 1814b). 'Glue spots' (black arrows) show where the tracing paper was attached during the engraving process for Pl. 26 and 30, consistent with Green's (1810) 'window tracing' method. Presumably after Wilson's death, iron oxide was used to transfer the vulture drawings to a composite drawing (extant but not shown), which was engraved for the posthumous ninth volume (Matthew R. Halley, reproduced courtesy of the Ernst Mayr Library, Museum of Comparative Zoology, Harvard University [MCZ 869.15a, f. 8, 10])

The 'alternate' (original) woodpecker

In the autograph collection of Ferdinand J. Dreer (1812–1902) at the HSP (coll. 0175) there is a partial (torn) monochrome proof-sheet of Pl. 7 (Wilson 1808) that is noteworthy (Fig. 12). After two centuries, the plate marks are still crisp along its top and sides, impressed into the high-quality (wove) paper. Like the typical Pl. 7, the proof-sheet shows the printed image of Cedar Waxwing *Bombycilla cedrorum* Vieillot, 1808, and partial images of Yellow-throated Vireo *Vireo flavifrons* Vieillot, 1808, and Red-bellied Woodpecker *Melanerpes carolinus* (Linnaeus, 1758). However, there are some critical differences—the woodpecker in the proof-sheet faces to the right (vs. upward to the left) and the beetle is missing from the overhead branch. Before it was donated to HSP, the proof-sheet was examined by Grosart (1876: vii), who received it in Scotland from an anonymous correspondent: 'As I write these

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Figure 11. A mutilated fragment of Wilson's original drawing of Blue Jay *Cyanocitta cristata*, presumably the one that was engraved for Pl. 1 (Wilson 1808), found on the verso of his drawing of Rusty Blackbird *Euphagus carolinus*, which was engraved for Pl. 21 (Wilson 1811a) (Matthew R. Halley, reproduced courtesy of the Academy of Natural Sciences of Drexel University Library and Archives, coll. 79, scrapbook vol. 2: 12a)

Figure 12. Partial monochrome proof-sheet of Pl. 7 (Wilson 1808), with the 'alternate' (original) woodpecker and notes in Wilson's handwriting. The verso is signed and dated, 28 August 1808, coincident with the initial printing (200 copies) of Wilson (1808) (Matthew R. Halley, reproduced courtesy of the Historical Society of Pennsylvania, Dreer Collection)

words, there reaches me, from America, a fly-leaf note by Wilson on a fragment or proof-sheet.' Hunter (1983: 272) examined it in the HSP collection. Both apparently overlooked the 'alternate' (original) woodpecker and evidence of Wilson's composite figures.

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The bottom half of the proof-sheet was neatly torn off, apparently by Wilson himself, on or before 28 August 1808, three days (or one month, see below) before he signed the preface to his first volume (Wilson 1808: iv). This is because the verso contains a signed and dated memorandum that fills the page, right up to the torn edge (Hunter 1983: 272). At this time, Wilson was preparing for another long journey to seek subscribers and new information about the American avifauna. Faxon (1901: 216) wrote:

> 'Two hundred copies of Vol. I were published in September, 1808. On the 21st of that month Wilson started on a tour through the New England States to exhibit his book and solicit subscribers, and soon afterward he travelled south on the same mission as far as Savannah, Ga. On his return to Philadelphia, in [March] 1809, the subscription list was large enough to warrant the publication of three hundred additional copies of the first volume.'

I personally studied five first edition copies of *American ornithology* in the ANSP (n = 2), APS (n = 1) and Library Company of Philadelphia (LCP, n = 2) collections, in addition to the scanned copy from the Smithsonian Institution Libraries and Archives available online at Biodiversity Heritage Library (BHL). Except one (LCP 985.F), all had the updated (1809) letterpress. Even an inscribed copy (APS 598.2 W69) that was 'presented by [the] author & publishers [to the APS]. Philad. Sep 21. 1810' has the reissued (1809) letterpress in volume 1. The BHL copy is the only 'first edition' scan of *American ornithology* currently available to researchers online, but it also contains the 1809 letterpress. The only copy that I have examined with the 1808 letterpress is LCP 985.F, which is conspicuously 'wanting plate 7' (LCP database).

The critical text variant used to identify the 1808 edition appears on p. 33, in the account of the Wood Thrush *Hylocichla mustelina* (J. F. Gmelin, 1789) (Faxon 1901: 216). The original account, written before Wilson went on his tour of the Carolinas, contained the following sentence: 'Tho it is believed that some of our birds of passage, and among them the present species, winter in the Carolinas, yet they rarely breed there; and when they do, they are certainly vocal' (Wilson 1808: 33, original). After returning to Philadelphia in March 1809, Wilson ('1808': 33, reissue) replaced that sentence with the following anecdote: 'I have myself searched the woods of Carolina and Georgia, in winter, for this bird, in vain, nor do I believe that it ever winters in these states.'

Notably, the preface to the original (1808) edition is dated '*October* 1*st*, 1808', not '*September* 1*st*, 1808', as it appears in the 1809 reprint and all later editions. This fact may nullify some authors' arguments with respect to the priority of Wilson (1808) over Vieillot (1808). For example, *Bombycilla cedrorum* Vieillot, 1808, was evidently not antedated by Wilson (1808), as assumed by Browning & Banks (1996), who nevertheless successfully petitioned to have Wilson's name suppressed because it was in little use, having long been placed in the synonymy of *B. cedrorum*, owing to the incorrect assumption that Vieillot published his description in 1807 (ICZN 1998). The priority of *Vireo flavifrons* Vieillot, 1808, over *Muscicapa sylvicola* Wilson, 1808, is also reaffirmed.

A unique copy of vol. 1 in the ANSP (QL681.W732) contains the letterpress of the 1809 reissue, but a coloured print of the original Pl. 7 (Fig. 13). Digitally overlaying the original and updated prints reveals a plethora of subtle differences in every figure, confirming that an entirely new copper plate was engraved for the 1809 reissue. Comparing the right-facing woodpecker in the monochrome proof-sheet (HSP coll. 0175) to the coloured print is also revealing (Fig. 14). The copper plate engraved with the left-facing woodpecker is extant, although extremely worn (ANSP coll. 427), but the copper plate with the right-

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Figure 13. (left) The original Pl. 7 of Wilson (1808), with a right-facing Red-bellied Woodpecker *Melanerpes carolinus*, was presumably included in the first 200 copies of vol. 1 and evidently some copies of the 1809 edition. (right) The re-engraved Pl. 7 of Wilson (1808), with a left-facing woodpecker and beetle, was included in most 1809 copies of vol. 1 (first edition) and all editions thereafter. The left image is reproduced courtesy of the Academy of Natural Sciences of Drexel University Library and Archives (QL681.W732). The right image is provided by the Biodiversity Heritage Library, courtesy of Smithsonian Libraries and Archives.

facing woodpecker is unknown. To my knowledge, Pl. 7 was the only plate in *American ornithology* that was engraved multiple times, and this has apparently not been discussed in the literature heretofore.

Perhaps the original copper plate for Pl. 7 was damaged or lost, and if a new plate had to be engraved, why not take the opportunity to make some aesthetic changes? Or else, the changes may have been made for aesthetic reasons despite the added cost. According to the receipt book, in addition to the expense of the copper, Wilson was paying Lawson about

Figure 14. Cropped anterior views of the original figure of Red-bellied Woodpecker *Melanerpes carolinus*: (left) monochrome proof-sheet from the Dreer collection (HSP, coll. 0175), reproduced courtesy of the Historical Society of Pennsylvania; (right) published figure taken from a unique copy of the 1809 reissue of Wilson (1808), courtesy of the Academy of Natural Sciences of Drexel University Library and Archives (Matthew R. Halley)

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sixty dollars per plate, and he paid Murray (the engraver of Pl. 7) 'Twenty five dollars in full [for] etching & work done on the Carolina Parrot [Pl. 26] of Amer. Orn. Vol. 3d.' (Christy 1937). The lettering was a relatively minor cost because Wilson 'paid Vallance [only] 3.50 cts for letterg the Cuckoo plate Vol. 4.'

Digital alterations in Burtt & Davis (2013)

Finally, researchers should be wary of 'reproductions' of Wilson's drawings in Burtt & Davis (2013), which were digitally altered in subtle but significant ways that are practically impossible to detect. The authors, or someone on their production team, inexplicably used the 'clone' tool in Photoshop (Adobe, Inc.), or a similar digital tool, to 'repair' missing portions of Wilson's drawings in the digital images, falsely expanding the paper texture into areas where the paper was cut away. In some cases, this produced false 'glue spots' that do not appear on the original drawings (Fig. 15).

Burtt & Davis (2013) noted that 'Most of Wilson's drawings and draft plates [were] reproduced [in their book] for the first time', and their figures remain the only published reproductions available. Researchers who have not personally examined the MCZ drawings should not take for granted that the Burtt & Davis (2013) reproductions are faithful to the originals. For future reference, the manipulated images include Northern Saw-whet Owl (J. F. Gmelin, 1788), in the upper right of the figure (Fig. 3.35 *in* Burtt & Davis 2013: 131); Chuck-will's-widow *Antrostomus carolinensis* (J. F. Gmelin, 1789), in the lower half (Fig. 15); Dunlin *Calidris alpina* (Linnaeus, 1758), in the lower left (Fig. 3.55 *in* Burtt & Davis 2013: 182); and Sanderling *C. alba* (Pallas, 1764), in the upper right (Fig. 3.63 *in* Burtt & Davis 2013: 200). There may be other cases, yet undetected, so I encourage researchers to exercise caution. Ironically, like Wilson's figures, the 'reproductions' in Burtt & Davis (2013) are more than meets the eye.

Taxonomic implications

Interpreting the published figures and text accounts of *American ornithology* is not straightforward. Not only were the 'Peale numbers' cited by Wilson not 'in all cases the [same] subjects that he drew and described' (*contra* Faxon 1915: 120, Stone 1915: 512, Bangs 1930, Burtt & Davis 2013); many or most of Wilson's published figures were composites,

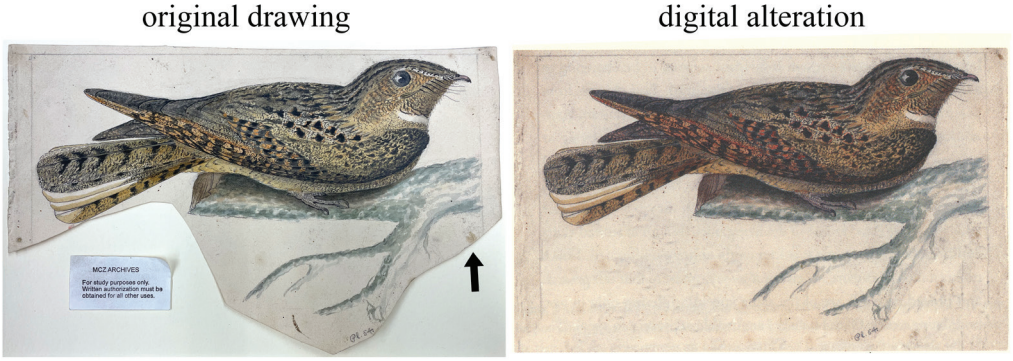

Figure 15. Comparison between (left) the original drawing of Chuck-wills-widow *Antrostomus carolinensis* (J. F. Gmelin, 1789) and (right) the digitally altered reproduction (Fig. 3.53b *in* Burtt & Davis 2013: 176). Fine details reveal that a 'clone' tool was used to 'expand' the paper texture into the missing areas of the drawing. On the left side of the image, this resulted in the erasure of a pin hole and false extension of the paper edge. On the right side, it resulted in the false triplication of a single front-facing glue spot (black arrow), where the tracing paper was attached during the engraving process (see text). The photo of the unmodified drawing is reproduced courtesy of the Ernst Mayr Library, Museum of Comparative Zoology, Harvard University (MCZ 869.15a) (Matthew R. Halley)

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created with details copied from multiple specimens, usually but not always of the same species. In general, the composites were a natural, perhaps even intended, outcome of Wilson's modified intaglio process. The interspecific composites (e.g., *Catharus* thrushes), which in retrospect reveal the limits of Wilson's knowledge, likely represent only a small fraction of the total number of composite figures. However, for various reasons including Wilson's destructive methods (see above), for most of his figures, the primary sources (drawings, specimens) needed to identify and disentangle the composite elements are no longer extant.

Dozens of data-deficient specimens in the MCZ collection, which were once preserved in the Boston Museum and have a circuitous but legitimate Pealean provenance, have been promoted as Wilson's types with no evidence other than a perceived similarity to Wilson's figures in structure or pose (Bangs 1930, Faxon 1915). After examining most of these specimens in November 2023, my general impression is that they are a 'trap' for confirmation bias. The believer's mind, primed by a misunderstanding of the 'Peale numbers' (see above), is naturally drawn to any similarity between the MCZ birds and Wilson's figures, however slight, even in the face of obvious dissimilarities. The specimens remain tantalising but inconclusive.

After Wilson's death, the Philadelphia Museum bird collection (then at the Pennsylvania State House, now called Independence Hall) continued to grow for three more decades and occasionally the exhibits were updated (e.g., damaged specimens were switched for fresh ones, or cabinets were rearranged to accommodate new acquisitions). In 1827, a few months after Peale's death, the collection was moved to the Philadelphia Arcade on Chestnut St., where it remained until 1838, when it moved to the 'Great Hall, built expressly for its accommodation, at the corner of Ninth and George [now Sansom] Streets' (M'Elroy 1840). However, the Philadelphia Museum was legally closed in *c*.1845, and the birds were purchased by Peale's nephew, Edward, and moved to the Masonic Hall (Chestnut St. between 7th and 8th streets). They remained there until December 1849, when they were purchased by Moses Kimball (1809–95) and P. T. Barnum (1810–91), who divided the collection into halves. No inventory of the two allotments is known. This complicated history makes it impossible to be certain, without original data, that any extant specimen at MCZ or elsewhere, was on display during Wilson's visits at Independence Hall, even if the specimen has an undisputed Philadelphia Museum provenance. If any extant specimen is to be considered as a potential syntype, under the assumption that it was indicated as such by a 'Peale number' citation in Wilson's work, there must be positive evidence that it was on display when he visited, or that he deposited the specimen himself, prior to his published description (e.g., Halley 2020). The MCZ specimens generally fail to meet this standard of evidence.

Here, I have identified several long-standing misconceptions about the production of *American ornithology*, which bear directly on the status of Wilson's taxonomy and nomenclature. A comprehensive review of Wilson's original descriptions, at least, based on an integrative analysis of primary sources, is warranted but beyond the scope of this study. The Code states that 'any evidence, published or unpublished, may be taken into account to determine what specimens constitute the type series' (ICZN 1999, Art. 72.4.1.1). To that end, I recommend that such work be focused on one or a few species at a time (e.g., Halley 2018, 2023b, 2024b), to accommodate a detailed and technical discussion and, if needed, appropriate actions to preserve nomenclatural stability.

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A 19th-century specimen of Black-bellied Storm Petrel *Fregetta tropica*, putatively from the seas off Port Essington, Cobourg Peninsula, Northern Territory, Australia

by Alexander L. Bond & Clemency T. Fisher

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Summary.—A 19th-century specimen of Black-bellied Storm Petrel *Fregetta tropica* in the collection of the Natural History Museum, Tring is putatively from Port Essington, an inlet on the Coburg Peninsula in Northern Territory, Australia, where there was a colonial-period settlement. There are no other records from the seas off northern Australia except east of the Torres Strait. Previous assessments of the avifauna of the Northern Territory have suggested that the identity or locality of the specimen should be questioned. We examined the specimen, verified that it is *F. tropica*, and determined that it was collected by the well-known natural historian John Gilbert, probably in 1840 or 1841, and probably in Northern Territory waters. This specimen therefore represents a notable vagrant and the first (and only) record of Black-bellied Storm Petrel for Northern Territory.

Black-bellied Storm Petrel *Fregetta tropica* is a relatively widespread seabird of the Southern Ocean, breeding on islands in Antarctica, and on subantarctic islands from Chile through the Falklands, Tristan da Cunha and Gough, South Georgia, the South Orkneys, South Shetlands, Kerguelen and the large seabird islands of New Zealand (Marchant & Higgins 1990, Medrano & David 2023). In Australia, it is a relatively common visitor off southern and eastern coasts, where it has been recorded as far as the northern Coral Sea (Marchant & Higgins 1990, Walbridge 2019). There are a few records from Papua New Guinea, all from the Coral Sea region (Cheshire 2010). It is easily confused with other *Fregetta* storm petrels, including White-bellied *F. grallaria* especially around Tristan da Cunha and Gough (Robertson *et al.* 2016), New Caledonia Storm Petrel *F. lineata* (Bretagnolle *et al.* 2022) and, rarely, New Zealand Storm Petrel *F. maoriana* (Harrison *et al.* 2021).

There are no verified records or specimens of Black-bellied Storm Petrel from the west coast of Western Australia north of Albany, or anywhere along the north coast west of the Torres Strait, including in the Timor and Arafura Seas (GBIF.org 2025). In Northern Territory, the only storm petrel (Hydrobatidae or Oceanitidae) known to occur is Wilson's Storm Petrel *Oceanites oceanicus*, which is a regular non-breeding visitor (Storr 1977, McCrie & Noske 2015). Here, we report on a 19th-century specimen of Black-bellied Storm Petrel in the Natural History Museum, Tring (NHMUK) purportedly collected at Port Essington, which has received passing mention in previous publications.

The specimen (NHMUK 1888.5.18.24) was collected by John Gilbert (1812–45) in 1840 or 1841 (Fisher & Calaby 2009) and still bears his original label (Fig. 1). At some point, the specimen was passed to the collection of Osbert Salvin (1835–98) and Frederick DuCane Godman (1834–1919), who in the 1880s donated their substantial collection to what is now the Natural History Museum (Sharpe 1906).

In the relevant volume of the *Catalogue of the birds in the British Museum*, Saunders & Salvin (1896) listed it as specimen '1', an adult skin, under *Cymodroma melanogaster*, noting

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Figure 1. Black-bellied Storm Petrel *Fregetta tropica* from Port Essington, Northern Territory, Australia, collected in 1840 or 1841 by John Gilbert and held at the Natural History Museum, Tring (NHMUK 1888.5.18.24); note the similarity in the handwriting of 'Port Essington' on the label compared to Figs. 2 and 3 (Jonathan Jackson, © Trustees of the Natural History Museum, London)

the location as 'Port Essington, N.W. Australia' and recorded that the specimen originates from the Salvin-Godman collection.

It was either overlooked or misidentified by Alexander (1920) in his summary of Procellariiformes in Australia, although he remarked on a Wilson's Storm Petrel in the NHMUK collection bearing a similar Gilbert label (NHMUK 1888.5.18.9; Fig. 2), questioning its origin and calling for further investigation. Black-bellied Storm Petrel is included in Appendix I of Storr (1967), who believed the details were doubtful, but presented no rationale for his conclusion.

In the 1970s, Serventy *et al.* (1971) indicated that there were no Black-belled Storm Petrel specimens from the Australian mainland and that this species was found mostly between 30 and 60°S, whilst Storr (1977) listed the species in square brackets, suggesting its status in Northern Territory is unknown, but referred to the specimen in NHMUK with little added detail. Marchant & Higgins (1990) mentioned the record and suggested further investigation was required.

Historically, Black-bellied Storm Petrel may have been more common north of Australia, and its current absence could be an effect of climate-related distributional change (Hazen *et al.* 2013), perhaps coupled with a decline affecting more tropical populations. The species' non-breeding movements and distribution remain poorly known, and putative vagrants (e.g., in the Atlantic and northern Indian Oceans) may in fact represent regular

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Figure 2. Wilson's Storm Petrel *Oceanites oceanicus* collected by John Gilbert at Port Essington in 1840 and held at the Natural History Museum, Tring (NHMUK 1888.5.18.9) showing the similar label and identical handwriting of the locality as in Fig. 1 (Jonathan Jackson, © Trustees of the Natural History Museum, London)

movements (Medrano & David 2023). However, the distance to the nearest definitive record is >1,100 km east to the Torres Strait, and multiple years of pelagic surveys this century have not detected the species in the adjacent Timor Sea (Lavers *et al.* 2014). A range shift of that spatial magnitude over 150 years would be exceptional.

Having examined the specimen, the identification is not in doubt. It lacks the strong streaking of New Caledonian or New Zealand Storm Petrel (Harrison *et al.* 2021, Roberts 2023), has a strong dark central belly stripe, precluding White-bellied Storm Petrel (Robertson *et al.* 2016, Harrison *et al.* 2021) (Fig. 1), and is morphologically similar to other Black-bellied Storm Petrel specimens in the NHMUK collection.

The question of its origins, however, is more complex. Gilbert arrived in the inlet of Port Essington from Sydney on HMS *Gilmore* on 12 July 1840, departing on 17 March 1841 (with a brief trip to Timor in October 1840) (Fisher & Calaby 2009, Noske 2017). No storm petrels are included in Gilbert's manuscript list of birds from the Cobourg Peninsula (Gilbert 1841–42), which he probably completed on his return to England (Fisher & Calaby 2009).

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Figure 3. Brown Booby *Sula leucogaster* collected by John Gilbert on 29 October 1840 off Melville Island, near Port Essington, Northern Territory, Australia (NMV B.17578) showing the similar label style (lower panel) and writing of 'Port Essington' (Clemency T. Fisher)

Gilbert made no mention of the species (and mentioned Wilson's Storm Petrel only from the Swan River Colony in present-day Western Australia) in his contemporary notebooks (Gilbert n.d.).

Black-bellied Storm Petrels of the South Pacific, Indian Ocean and Australian seas were described by John Gould (1844) as '*Thalassidroma melanogaster*' from specimens he and

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Gilbert collected en route to Australia in 1838, so the species would have been familiar to Gilbert. *Thalassidroma* [= *Fregetta*] *tropica* was also described by Gould in 1844 but on the basis of one or more specimens from the Atlantic Ocean (NHMUK 1841.6.1323, an adult male from off Sierra Leone) (Warren 1966). Gould (1844, 1848) noted that the bird was common in southern latitudes during their voyage between Cape Town and Tasmania, with particularly large numbers around the islands of Amsterdam and St Paul in the Indian Ocean, so he would have been likely to recognise that a tropical specimen was noteworthy. Neither Gould (1848) nor Gilbert (1841–42) refer to the specimen in the context of Port Essington or the Cobourg Peninsula, apart from on Gilbert's sparsely worded original label.

There are therefore two possible explanations as to the origin of the specimen. The first is that Gilbert collected it during his return from Timor in October 1840 on the schooner *Lulworth*. This vessel left Timor on 10 October 1840; a Brown Booby *Sula leucogaster* was collected on 29 October 1840 and bears a rectangular label, typical for Gilbert, giving the locality as 'off Melville Island, near Port Essington' (specimen now in Museums Victoria, Melbourne: NMV B.17578; Fig. 3) (Fisher & Calaby 2009). 'Port Essington' on both labels is in Gilbert's handwriting. The *Lulworth* arrived in Victoria, the colonial settlement at Port Essington, on 31 October 1840 (Cameron 1999).

A less plausible possibility, although it cannot be discounted fully, is that the specimen was collected on Gilbert's voyage from Sydney to Port Essington, between 15 June and 12 July 1840 on HMS *Gilmore*, a convict and supply transport ship (Bateson 1969) and that Gilbert labelled the specimen 'Port Essington' either on his arrival or as an indication of his destination. Though not a research vessel, the ship's master, Edward Thacker, may have permitted Gilbert to collect specimens during the month-long voyage north, as Gilbert and Gould had done aboard the *Parsee*, which transported them from London to Australia in 1838 (Fisher & Calaby 2009). This is a less plausible explanation as there are no other specimens known to have been collected during this voyage (CTF unpubl. data).

Regardless, we are confident that the specimen was collected by Gilbert and is from Northern Territory. In the austral winter, Black-bellied Storm Petrel is reasonably common on northbound migration through the Tasman and Coral Seas (Marchant & Higgins 1990, Comben *et al.* 2001) but this represents the first (and, as far as we are aware, only) record of the taxon in Northern Territory.

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Continental Asia's longest-lost bird? The taxonomic and conservation status of the Ayeyarwady Broadbill *Cymbirhynchus* [*macrorhynchos*] *affinis*

by Alex J. Berryman, Nigel J. Collar & Paul F. Donald

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Summary.—A recent proposal to treat Ayeyarwady Broadbill *Cymbirhynchus* [*macrorhynchos*] *affinis* of south-west Myanmar as a species separate from Black-and-red Broadbill *C. macrorhynchos* has failed to garner widespread support. Here we compare six specimens of *affinis* with a large series of *C. macrorhynchos* and glean what information we can from specimen data and the literature about this poorly known taxon's distribution and conservation status. *C. affinis* differs in being 10–17% smaller, with a 22% shallower bill, and having elongate crimson spots on the tertials, a much larger white wing spot, paler and brighter red on the underparts and rump, and broader and more extensive white subterminal tail tips. In our view these characters, which represent abrupt and profound differences across a trivial distance from the nearest population of the wide-ranging and (as we argue) probably monotypic *C. macrorhynchos*, uphold species rank for the taxon. However, we can find no record of it since 1874. It may once have occurred throughout the Ayeyarwady Delta, where it may now be extirpated due to the near-total loss of suitable habitat. It has also been recorded in the Rakhine Yoma (Arakan Hills) up to an elevation of at least 750 m, where suitable habitat remains, although recent (untargeted) field work has not found it there. However, the meagre evidence for its former range and status is disconcertingly inconsistent. We recommend that Ayeyarwady Broadbill be listed on the IUCN Red List as Data Deficient.

The Black-and-red Broadbill *Cymbirhynchus macrorhynchos* as generally recognised is endemic to South-East Asia, where it occurs in south-west and southern Myanmar, south-east and Peninsular Thailand, south and south-central Indochina, Peninsular Malaysia, Sumatra and Borneo (and islands between the two), occupying lowland waterside habitats in forest, plantations and mangroves (Lambert 1996, Bruce 2003). In the 20th century the subspecific taxonomy of the species was somewhat unsettled, largely owing to populations on Sumatra being designated as additional subspecies *tenebrosus* and/or *lemniscatus* (Meyer de Schauensee & Ripley 1939, Peters 1951, Lambert 1996; see also Mees 1986). Most recent major taxonomies now follow Bruce (2003) in recognising four subspecies, *affinis* in south-western Myanmar, *siamensis* in southern Myanmar, eastern and southern Thailand and Indochina, *malaccensis* in southern peninsular Thailand and Peninsular Malaysia, and nominate *macrorhynchos* in the Greater Sundas (Dickinson & Christidis 2014, Clements *et al*. 2024, Gill *et al*. 2024). However, one taxonomy (BirdLife International 2024) splits *affinis* as a separate species, Irrawaddy (better now Ayeyarwady) Broadbill, and assigns all remaining continental populations to *malaccensis* and the insular populations to nominate *macrorhynchos* (del Hoyo & Collar 2016).

Among authorities who have commented on the matter, all have acknowledged that *affinis* is the most differentiated of these various taxa. In the 19th century *affinis* was

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universally treated as a separate species (Blyth 1846, Oates 1875, 1882, 1883, Sclater 1888, Blanford 1895), as it was by Baker (1926) and Stanford & Ticehurst (1931: 915); when Meyer de Schauensee & Ripley (1939) considered the complex without access to specimens of *affinis* they remarked that 'from descriptions this seems to be a very distinct race'. Precisely how distinctive was shown by del Hoyo & Collar (2016) when they used criteria that assign the strength of diagnostic phenotypic characters to a class and score (major 3, medium 2 and minor 1, with a total score of 7 forming the threshold for species status: Tobias *et al*. 2010), as follows:

> 'differs in its smaller size (sample small, but at least 2); elongate crimson spots on wings (innermost secondary and outer web of next two) (3); much paler red underparts and especially rump, which also has narrow black edging (2); small but clear white flash in wing *vs* none or entirely vestigial (2); broader white tips to tail (ns[1–2]).'

The 1–2 score for the tail tips is placed in square brackets because the criteria permit only three differences in plumage coloration to be scored, but the character is still mentioned as further evidence of divergence. However, despite the total score (9) comfortably surpassing their threshold for species rank, indicating a significant discontinuity in characters, the split has failed to gain support from other taxonomic lists. The evidence is therefore worth revisiting for fuller consideration than the concise enumeration of points of divergence allowed in the text above. Indeed, given the apparent lack of recent documented sightings (Rutt *et al*. 2024), a review of the distribution and conservation status of *affinis*—which is currently assessed, perhaps surprisingly, as Least Concern by BirdLife International (2016)—seems appropriate.

Methods

Taxonomy.—Del Hoyo & Collar (2016) measured five specimens of *affinis* (one male, four unsexed) all held at the Natural History Museum, Tring (NHMUK). Three known syntypes are held in the Zoological Survey of India (ZSI) collection at the Indian Museum, Kolkata (Blyth 1846, 1849, 1875; G. Maheswaran *in litt*. 2025), of which only one was mentioned by Sakthivel *et al*. (2011). There is also one specimen in the University Museum of Zoology, Cambridge, UK (UMZC). VertNet/GBIF indications (at the time of writing) of two specimens in the Field Museum of Natural History (FMNH), Chicago, and one in the Muséum d'histoire naturelle de Bourges (MHNB), France, have proved to be in error. We can trace no other specimens in museums, although early texts imply that many more were once collected: Blyth (1846) referred to receiving 'a good series', and Oates (1882) mentioned having 'many specimens' from one particular locality, so it is possible that material exists elsewhere. For plumage comparisons, *affinis* specimens at NHMUK and UMZC were inspected by the authors, whilst photographs of the three ZSI specimens were sent to us. Only the six NHMUK and UMZC *affinis* specimens were measured. For comparison, we examined and measured the large series of specimens of other named taxa in NHMUK.

When the split of the species was proposed by del Hoyo & Collar (2016), the measurements of bill (skull to tip), wing (curved) and tail (point of insertion to tip) of the five NHMUK *affinis* were taken and considered against equivalent values of five male and five female *C. m. siamensis*. For this new analysis, bill depth (vertical distance at proximal end of the nareal slit, bill closed) was measured on this sample plus the UMZC bird, and five males and five females of both *C. m. malaccensis* and *C. m. macrorhynchos* (as assigned by all 21st century authorities) were also measured. Bill depth was missed as a character by del Hoyo & Collar (2016), but was added after direct comparisons of the material and

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discovery of various references in the literature, notably in the original description of *affinis* (Blyth 1846). All measurements were made by NJC. Checks were also carried out on the wider collection of material in NHMUK to assess whether the defining characters of *affinis* are ever present in other taxa in the complex.

We used linear discriminant analysis (LDA) in R (R Core Team 2022) to simultaneously compare the four biometric measurements between the four taxa, scaling each variable to account for their different ranges of measurement.

Distribution and conservation status.—We reviewed all available literature and specimen labels to ascertain as much information as possible on *affinis*, notably in relation to its distribution. This evidence was then examined in relation to habitat cover and other factors that might improve assessments of its conservation status.

Results

***Characters of* affinis**.—Taxon *affinis* differs consistently in a range of characters from all other *Cymbirhynchus* taxa, which are barely divergent from one another. Compared to neighbouring *siamensis*, *affinis* is markedly smaller (10–17%) in length of bill (19.8 vs. 23.7 mm), wing (89.3 vs. 99.7 mm) and tail (70.5 vs. 84.5 mm) (hence overall size), and bill depth averages 22% (9.3 vs. 11.9 mm) less (Table 1, Figs. 1–2). There was no overlap with any other taxon in measurements of *affinis* in bill length, bill depth or tail length, and only very minimal overlap in wing length (one female *malaccensis* 91 mm, one unsexed *affinis* 92 mm), whereas there was extensive overlap in all mensural characters between *siamensis*, *malaccensis* and *macrorhynchos* (Table 1, Fig. 3). The LDA plot showed complete separation of *affinis* from the other taxa, which intersected greatly in LDA space (Fig. 3).

Examination and comparison of specimens confirm the plumage differences in *affinis* as enumerated in del Hoyo & Collar (2016). The 'elongate crimson spots'—one on each of the three innermost secondaries (tertials) (Figs. 2 and 4)—are present on all six specimens examined personally and on the three ZSI specimens (based on photographs supplied), whereas a check of 93 specimens involving the other taxa found 91 to have no trace of them. Two nominate *macrorhynchos*, one from Sarawak (NHMUK 1969.33.17) and one from south-east Sumatra (NHMUK 1887.12.1.185), show a single tiny smudge of reddish in an equivalent position. Incidentally, Blyth (1846) specified that the 'oblong red spot' was 'margining the tip of the outer web of two of its tertiaries, and a third margining the inner web of the uppermost tertiary', but that 'in what appear to be the females' the first two are white and only the third red. All spots on all *affinis* in NHMUK and UMZC are red. Photographs of the three specimens in ZSI suggest that the colour on these spots has faded,

TABLE 1

Mensural data, in mm, of four commonly acknowledged taxa of Black-and-red Broadbill *Cymbirhynchus macrorhynchos s. l.* Samples of ten consisted of five males and five females. Values in **bold** represent the mean of each character with standard deviation; parenthetic values are the range. Sample of *affinis* consisted of one male and five unsexed. Measurements did not differ significantly between the sexes (see Fig. 3).

	n	Bill length	Bill depth	Wing	Tail
C. m. affinis	6	**19.8 ± 1.06** (18.4–21.3)	**9.3 ± 0.69** (8.2–10.0)	**89.3 ± 2.73** (85–92)	**70.5 ± 1.05** (69–72)
C. m. siamensis	10	**23.7 ± 0.96** (22.2–24.6)	**11.9 ± 0.65** (10.6–12.7)	**99.7 ± 3.92** (93–106)	**84.5 ± 3.41** (80–88)
C. m. malaccensis	10	**23.4 ± 0.56** (22.6–24.2)	**12.0 ± 0.39** (11.0–12.4)	**95.7 ± 3.06** (91–101)	**82.4 ± 3.44** (75–86)
C. m. macrorhynchos	10	**25.6 ± 1.05** (23.5–26.7)	**13.4 ± 1.04** (11.1–14.4)	**103.3 ± 3.56** (99–109)	**86.0 ± 3.02** (81–92)

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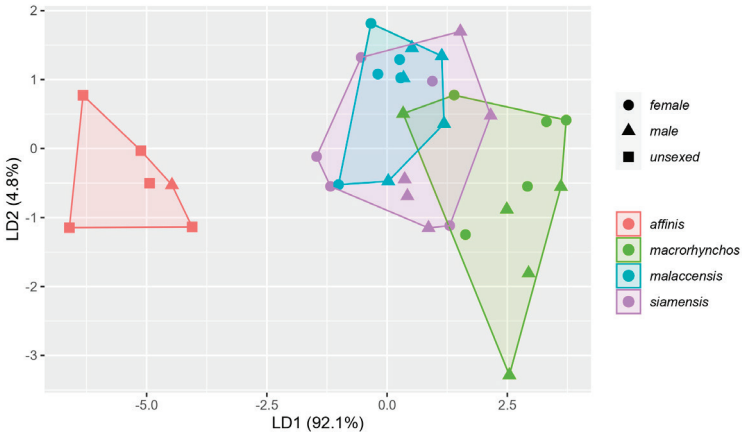
Figure 1 (above). Ventral view of five specimens each of *affinis* (left) and *siamensis* (right) from Tenasserim (Myanmar) at NHMUK; note overall smaller size of *affinis*, paler red underparts and more extensive white in undertail (Alex J. Berryman, © Trustees of the Natural History Museum, London)

Figure 2 (right). Lateral view of *affinis* (left) and *siamensis* (right) from Tenasserim (Myanmar) at NHMUK; note on *affinis* the presence of three crimson markings on the tertials (see also Fig. 4) and a conspicuous white wing spot; also the smaller size of *affinis*, particularly the much shallower bill (Alex J. Berryman, © Trustees of the Natural History Museum, London)

Figure 3 (below). LDA plot based on measurements of bill length, bill depth, wing length and tail length of four taxa in *C. macrorhynchos*. LD1 accounted for most of the variation between the four taxa and represents a scale of increasing overall size.



but it is apparent that one specimen, ZSI 35353, possesses the configuration that Blyth speculated as indicating a female (Fig. 5).

The white spot midway along the closed wing is far larger in *affinis* than in any of the specimens of the other taxa examined (Fig. 2). The brighter, paler red of the underparts and rump is obvious and consistent (Figs. 1, 2 and 4). Del Hoyo & Collar (2016) mentioned also that *affinis* has black transverse lines on the rump (these are, it should further be noted, vague and irregular; Fig. 4); but they are very occasionally also present in other taxa, albeit

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Figure 4 (left). Close-up of three crimson spots on the tertials and transverse black markings on the rump (Paul F. Donald, © Trustees of the Natural History Museum, London)

Figure 5 (right). Close-up of three spots on the tertials of ZSI 35353, showing the uppermost spot coloured faded red and the other two faded whitish (Anindya Naskar, Zoological Survey of India, Kolkata)

Figure 6. Undertail of *affinis* (left) and *siamensis* (right) from Tenasserim (Myanmar) at NHMUK (Paul F. Donald, © Trustees of the Natural History Museum, London)

much less obvious in part because they are less contrasting. The 'broader white tips to the tail' mentioned by del Hoyo & Collar (2016) are formed by white extending subterminally onto the outer web on at least the outer two rectrices, so that it spreads across the entire feather, isolating a small dark tip. In a point missed by del Hoyo & Collar (2016), this white occurs on all rectrices except the central pair (Fig. 6). In NHMUK specimens labelled or assigned to *siamensis* and *malaccensis* the white is restricted to the inner web, so there is no continuous white band across the feather, and even on the inner web the white is much less extensive, with a broad dark tip.

The synonymisation of *siamensis* with *malaccensis* in Lambert (1996) and del Hoyo & Collar (2016) appears justified. No consistent plumage differences between them could be found in our examination of a large series of both taxa. In morphometrics the bill of the two taxa is almost identical, and while mean wing and tail length are fractionally longer in *siamensis*, there is far too much overlap (Table 1) to consider the taxon diagnosable on the basis of either. We also agree with Mees (1986) that it is inappropriate to recognise any taxon endemic to Sumatra.

In our view the red on the underparts of *malaccensis* is no different from, and the orange spotting on those underparts no more prevalent than, that on nominate *macrorhynchos*,

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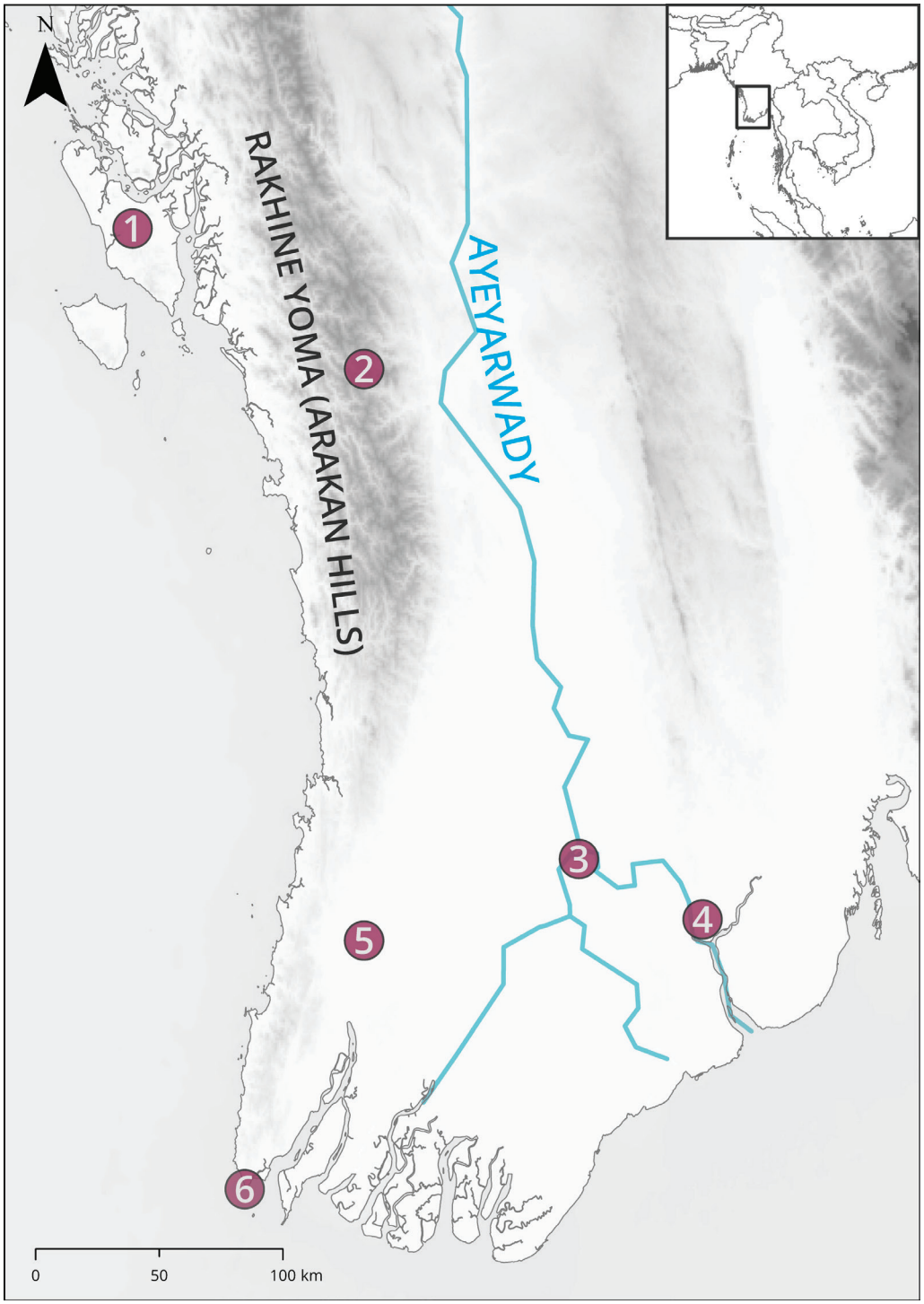

Figure 7. Localities of Ayeyarwady Broadbill *Cymbirhynchus* [*macrorhynchos*] *affinis* as discussed in Results. Shading represents elevation. Note that site 6 is not necessarily dependable (see Results).

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contra Lambert (1996). However, the separation of these taxa might be upheld on the basis of the former's slightly smaller size (Table 1) and greater amount of white in the tail tips. Nevertheless, it is possible that if the measurements of these characters were plotted by locality they would form a gentle northward cline in slightly diminishing size and increasing quantity of white in the tail, which then undergoes an abrupt change across the small geographical divide between *siamensis* (if recognised) and *affinis*. If the specific status of *affinis* were to be widely recognised, the result might therefore involve two monotypic species of *Cymbirhynchus*, an arrangement we would favour.

***Distribution of* affinis**.—Since the taxon's original description (Blyth 1846) the general area of distribution has repeatedly been given, in various spellings, as Arakan (in modern usage Rakhine, although not necessarily what is now Rakhine State). In due course this became 'Arakan hills' (Oates 1875, 1882, 1883), known now as the Rakhine Yoma. Four of the five NHMUK specimens are labelled imprecisely from these hills, two (1882.1.20.256, 1882.1.20.257) collected by 'Mr Raikes (ex. coll. E. W. Oates)' with no date, one (1882.1.20.259) by Oates dated 'Jan/72' and one (1887.5.1.665) dated 1874 (no collector; from the Hume Collection *fide* Sclater 1888). The fifth specimen (1887.5.1.666) is labelled as collected at Rangoon (now Yangon) on 12 March 1871 by J. Armstrong (see below). The specimen in UMZC (27/Eur/3/a/15), bequeathed by H. E. Strickland (1853) and said by Gould (1850–83), to whom it was loaned for illustration, to be 'the only one in this country' (i.e. England), is labelled 'Arracan 1847 procured by E. Blyth' (as also indicated in Salvin 1882). The three specimens in ZSI, reg. nos. 35353, 37646 and 37647, are all labelled 'Arakan' and two are dated 1844 (photographs taken by A. Naskar *per* G. Maheswaran *in litt*. 2025).

In addition, we find in published literature evidence for six relatively precise localities, presented below north to south (superscript numbers correspond to Fig. 7). In the late 1980s and early 1990s, spellings (in Roman script) of indigenous toponyms were widely changed in Myanmar to better reflect and standardise them in relation to modern Burmese pronunciation (as well as, to a lesser extent, to expunge colonial influence; see PCGN 2007). For each locality we place in parentheses variant historical spellings which have been cross-walked to their modern spellings using published maps (Oates 1883, Smythies 1986) and PCGN (2007). In the case of Nyaunggyo we use the evidently more modern spelling in Stanford & Ticehurst (1931), although the settlement itself seems no longer to exist, at least by that name.

[1]**Ramri Island** (Ramree).—The posthumous catalogue of Blyth (1875) identified Ramri as a locality for the species. Oates (1883) revealed that this information was based on specimens received by Blyth 'from the island of Ramree', and his earlier indication (Oates 1875) that the species reaches north at least to 19°N was presumably based on Ramri, which is precisely at that latitude. Enquiries of ZSI have, however, established that no other specimens of *affinis* are held there (G. Maheswaran *in litt.* 2025), so the location or fate of the specimens sent to Blyth from Ramri is unknown, unless any or all of the three syntypes (labelled 'Arakan') were taken there.

[2]**Nyaunggyo** (Nyoungyo).—Oates (1883) mentioned collecting a specimen in the 'Arrakan hills near Nyoungyo'; this is possibly his specimen in NHMUK dated January 1872. According to the maps in Oates (1883) and Stanford & Ticehurst (1931: 666), Nyaunggyo is, or was, in the middle of the Rakhine Yoma, seemingly at *c*.18.66°N, 94.80°E (*c*.750 m), but perhaps slightly further west nearer the crestline given the description earlier (Oates 1883: 26) of Nyaunggyo being 'near the summit of the Arrakan hills'. Other taxa collected at or near this locality include hill-forest species such as Blue-naped Pitta *Hydrornis nipalensis* and Rufous-throated Partridge *Arborophila rufogularis* (Oates 1883), such that notwithstanding

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the vagueness of 'near Nyoungyo', there can be little doubt that this specimen was collected in the hills, rather than the adjacent plains.

[3]**Nyaungdon** (Yandoon).—Oates (1882) claimed to possess 'many specimens procured' near Nyaungdon on the Ayeyarwady, although a year later, oddly, he made no mention of this evidence of apparent abundance, merely stating that the species 'appears to be common in some portions of the Irrawaddy Delta, for Capt. Raikes observed it round about Yandoon' (Oates 1883). There is no direct contradiction in Capt. Raikes here being named as recording the species at a lowland site while also being identified in NHMUK as the collector of two specimens from the 'Arakan hills', but the fact that the latter were (or had been) in Oates's possession yet not mentioned in his 1883 volume—where his only source for the Arakan hills is material he himself (or his collectors) procured—suggests some possibility that one or other ascription of provenance is a mistake.

[4]**Yangon** (Rangoon).—NHMUK 87.5.1.666 from Yangon (see above) was Sclater's (1888) source for including Pegu (now Bago) in the range (already then established by Oates 1882). Confusingly, despite the specimen label bearing his name, Armstrong (1876) did not mention collecting *affinis* in his notes on the birds he recorded in the Ayeyarwady Delta region, perhaps because (a) he had not by that time sent the specimen to Hume (who is thanked for identifying the material Armstrong collected), (b) Hume was not sure what the bird was at the time, or most plausibly (c) Armstrong could not remember collecting the bird and therefore had no information to supply about it. Separately, Oates (1882) reported being given a specimen 'labelled as "10 miles east of [Yangon]"', this presumably being the same as the one 'said to have been killed near Rangoon' that he reported the following year (Oates 1883).

[5]**Pathein** (Bassein).—Oates (1882) reported the species 'at many points' between Pathein and Yangon (it is possible this statement includes specimens procured near Nyaungdon; even so, we assume here that Pathein was mentioned because the species had been encountered in its eastern vicinity).

[6]**Maw Tin Soon** (Mawtinzun, Cape Negrais, 'Pagoda Point' [Peters 1951]).—This locality cannot be treated with the same confidence as the preceding five. Oates (1875) indicated Maw Tin Soon as part of the range, but eight years later he qualified this with the word 'probably' (Oates 1883), a significant adjustment missed by Blanford (1895), Baker (1926), Meyer de Schauensee & Ripley (1939) and Peters (1951).

Discussion

Taxonomic status.—We confirm the plumage and mensural distinctiveness of *affinis* enumerated by del Hoyo & Collar (2016), including in four specimens not analysed by them. We also find two further points of divergence not previously identified. First, bill depth is 22% shallower but only 15% shorter than adjacent *malaccensis*. Second, while the greater proportion of white on the rectrices was noted by del Hoyo & Collar (2016), the extension of white onto five, instead of three, outer feathers was missed. Overall, the impression of the sample of *affinis* available to us is of a bird very different to other *Cymbirhynchus* taxa.

The distinctiveness of *affinis* is further emphasised by the virtual invariability of *Cymbirhynchus* across the rest of its range, which spans 2,300 km of latitude, 2,650 km of longitude and includes insular populations on and between Borneo and Sumatra. Across this vast area we find evidence for recognising no more than two subspecies, and these are so weakly diagnosable, possibly reflecting only clinal differences, that, as we suggest above, the species may better be considered monotypic.

There is some uncertainty over the historical distribution of *affinis* (see below) and the northernmost limit in Peninsular Myanmar (Tenasserim) of *siamensis* (if recognised).

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Oates (1883) reported the latter 'as far north in Myanmar as the Dawna range near Kokarit [Kawkareik: 16.54°N, 98.15°E], east of Moulmein [Mawlamyine]', *c*.190 km east of the easternmost locality traced for *affinis* ('10 miles east of [Yangon]': Oates 1882). In neighbouring Thailand, the species once occurred in Umphang District, Tak, at around 16°N (Lowe 1933) and slightly further north in Kamphaengphet at approximately 16.03°N (specimens in FMNH *per* P. Round *in litt*. 2025) and at Hua Thanon at *c*.16.05°N (Deignan 1953), a latitude similar to that of Mawlamyine. If *affinis* does (or did) occur in the Ayeyarwady Delta around and east of Yangon, as reported by Oates (1882) and Sclater (1888), it is plausible that the two taxa were formerly parapatric, given the once uninterrupted habitat (Murray *et al*. 2020) and lack of any obvious geographic barrier between Yangon and the west side of the Dawna range.

We contend that *affinis* differs from other *Cymbirhynchus* taxa to a degree comparable to that used to justify the widely recognised separation of other broadbill species pairs, including Mindanao *Sarcophanops steerii* and Visayan Wattled Broadbills *S. samarensis* (Lambert 1996, Bruce 2003, Collar 2011, del Hoyo & Collar 2016, Allen 2020, Clements *et al*. 2024, Gill *et al*. 2024), and Silver-breasted *Serilophus lunatus* and Grey-lored Broadbills *S. rubropygius* (del Hoyo & Collar 2016, Clements *et al*. 2024, Gill *et al*. 2024). Both these splits were upheld during a recent taxonomic overview of species limits to produce a new global bird checklist (AviList; PFD pers. obs.).

Distribution and conservation status.—All facets of the ecology and distribution of *affinis* are poorly known. Five of the six localities we can trace (sites 1 and 3–6; Fig. 7) are in the lowlands (0–50 m), including one (from Yangon) backed by a museum specimen, and the species was reportedly collected 'at many points' between Pathein and Yangon (an area that is entirely lowland and at the time of collection was probably still largely forested). However, site 2 (Fig. 7) is in the Rakhine Yoma near Nyaunggyo, probably at an elevation of around 750 m, depending on how near Nyaunggyo the site of collection was. Thus it seems most likely that *affinis* once occupied both the Rakhine Yoma and Ayeyarwady Delta, but confidence in this ascription is inhibited by Oates's apparent inconsistency in his accounts of the bird. His evident retraction of Maw Tin Soon and his unmatching testimony over Nyaungdon create a degree of doubt, while his report that the bird 'appears to be abundant on the Arrakan hills' (Oates 1875) finds no repetition in Oates (1883), where, although in a text clearly intended to be a summary of knowledge, his only reference to status is that it 'appears to be common in some portions of the Irrawaddy Delta'. Baker (1926) pooled these various pieces of information to give its distribution as 'Arakan from about lat. 19 southwards to Cape Negrais, also the Irrawaddy Delta as far east as Rangoon' and its elevational distribution as 'principally in the plains but apparently also in the lower hills'. Apart from the inclusion of the unreliable Cape Negrais, we see no option but to endorse this account.

Although Oates has his name on at least one specimen, it is possible that he did not collect it himself: he used the words 'I procured this bird' when recording its occurrence at Nyaunggyo but his 'I' may have been shorthand for his collectors, whom he credited for taking another species at the same site (Oates 1883: 412). This would help explain why his last words on *affinis* were: 'I have had no opportunity of observing its habits'. This leaves a troubling gap in knowledge of its habitat choices, which can only be predicted from those of other taxa in *Cymbirhynchus*, an assumption that may not be wholly safe given the taxon's morphological divergence. This situation is all the more lamentable because, unless a publication or specimen has been overlooked, the evidence points to the species being undocumented since the NHMUK specimen of 1874, more than 150 years ago. This renders Ayeyarwady Broadbill the longest-'lost' bird species in continental Asia and one of only two

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(the other being Himalayan Quail *Ophrysia superciliosa*) continental Asian species to have gone unrecorded since the 19th century (Rutt *et al*. 2024). Hopwood (1912) did not report it. J. K. Stanford found 'no sign of it' at Nyaunggyo in the late 1920s, when he considered broadbills 'remarkably scarce' (Stanford & Ticehurst 1931: 915). A two-month collecting trip in the lowlands and foothills on the mainland opposite Ramri (Toungup south to Ngapali) also failed to yield a specimen (Ticehurst 1933). Meyer de Schauensee & Ripley (1939) ruminated that

> '*Cymbirhynchus* seems to become rarer in the northern part of its range. *Affinis* would appear to be seldom met with, for two recent expeditions, one to southern Arrakan [no such expedition traced; this may refer to Hopwood (1912)] and the other to the Prome district of Pegu failed to secure specimens.'

Moreover, *Cymbirhynchus* does not feature among the nearly 300 species documented from the Rakhine Yoma foothills and their adjacent plains by Christison *et al*. (1946) while stationed in the region during 1943–45. Smythies (1986) was silent on the subject, and while recent search effort has been far from comprehensive, visits to the Rakhine Yoma and nearby lowlands by local birdwatchers have failed to find it (R. J. Tizard *in litt*. 2025, Zayar Soe *in litt*. 2025).

Whether or not *affinis* is threatened is open to question. In South-East Asia, Black-and-red Broadbill occurs in a wide range of forested habitats, with a strong predilection for lowland wooded riparian areas, including heavily degraded forests and plantations along rivers (Lambert 1996, Kirwan *et al*. 2021; AJB pers. obs.). Nevertheless, testimony by Timmins *et al*. (2024) that the species has plausibly become much scarcer in Lao PDR (where it occurs narrowly in the south), and indications that its northern range limit in Thailand has contracted southwards (see above), suggest that, at least in parts of its range, this broadbill is not wholly resistant to habitat degradation and/or fragmentation. Seemingly suitable conditions were likely once extensive in the Ayeyarwady Delta (Murray *et al*. 2020) but natural vegetation was almost entirely cleared in the early 20th century for fuelwood (Stamp 1924) and, more recently, agriculture and aquaculture (Polidoro *et al*. 2010). There remain relatively extensive, if degraded, forests in the lower Rakhine Yoma and more locally in the plains west of it (Murray *et al*. 2020, Global Forest Watch 2025, Google Earth 2025). Naturally, these forests would be the most obvious places to target to confirm the species' survival. However, recent birding visits to *c*.40 localities in the plains and foothills (0–300 m) in the southern half of the Rakhine Yoma (between Odein and Maw Tin Soon), including the Rakhine Yoma Elephant Range and Sitsayan Reserved Forest, in habitat ostensibly suitable for *Cymbirhynchus*, have not found it, but have turned up significant range extensions for Banded Broadbill *Eurylaimus javanicus* and Great Iora *Aegithina lafresnayei* (Zayar Soe *in litt*. 2025). On the evidence assembled here, it is difficult to uphold the current conservation status of the species as Least Concern (BirdLife International 2016). This assessment presumably judged that search effort in the species' range had been negligible (rather than simply poor), and that the species had ecological needs as plastic as that of *C. macrorhynchos*, and a range that spanned the entirety of the Rakhine Yoma and Ayeyarwady Delta. In the light of this review it is clear that none of these assumptions can be confidently endorsed. Until more information can be gleaned, we recommend that Ayeyarwady Broadbill is best considered Data Deficient.

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